E. W. FAGER

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BY J. T. ENRIGHT

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The Pre-Scripps Career

Edward William Fager

Edward William Fager—Bill to most of us, but also Ed to some—was an outstanding educator, a skillful and insightful marine ecologist, and a prime mover at Scripps during its Revelle-era expansion and subsequent development as a research-and-teaching institution, but his early career provided no hint whatever that he might become a marine scientist.

Fager earned a Ph.D. in chemistry at Yale University in 1942, following which he taught briefly there. He then worked for a year on the Manhattan Project, and thereafter moved to the University of Chicago as a Frank B. Jewett Fellow. For several years at Chicago, he was deeply involved in the James-Franck/Hans-Gaffron laboratories, investigating the early pathway of carbon in photosynthesis by using green algae and derived cell-free systems (Fager 1952). That research group had objectives similar to those of the Calvin Laboratory at Berkeley, and any interactions between those two groups were by no means collegial. The nature of the relationship had been crystallized by a polemical AAAS-ACS symposium held in Chicago in December 1947 (Franck and Loomis 1949). As an example of the exchanges there: "... the complete and astonishing disagreement between the results of the work done in this laboratory (Chicago) and that done at the University of California..." (Fager 1949). The conclusions of the Calvin lab team were eventually recognized as correct and the group in Chicago must have been quite disappointed about that conclusion.

While at the University of Chicago, Bill also became well acquainted with the group of prominent ecologists in the Biology Department. At that time, ecology was an esoteric

topic, unrecognized in most universities, and was even absent from many dictionaries. But the University of Chicago was home to some of the best and brightest in that budding field, and Fager eventually underwent a conversion, becoming a professional ecologist himself. One of his prime contacts at Chicago, who doubtless contributed to his change of career direction, was Thomas Park who, through his studies of flour beetles, had become one of the world's leading authorities on population dynamics.

Bill was a long-time bird watcher and an enthusiastic gardener; his original major at Yale, before settling on chemistry, had been entomology. Thus we can only speculate about whether it was primarily his associations with those Chicago ecologists that led him to a new career, or whether he made those contacts because of his long-standing interest in ecological phenomena. Perhaps his contacts with some of the world's leading ecologists led him to recognize that his primary scientific interest centered on what animals and plants do in a natural, out-of-doors setting—and that a scientific career could be built out of studying such phenomena. It also seems likely that Bill's decision to change fields of research partly arose from the unpleasant rivalry that permeated the Franck-Calvin photosynthesis-research controversy, and his disappointment with its outcome. Years later, he confided in me that he had never fully accepted the consensus view that the Berkeley research group had been far ahead of the Chicago group.

Whatever the reasons may have been, Fager decided in 1952 to undertake doctoral studies in ecology at the Bureau of Animal Populations in Oxford, England, joining the research group of Charles Elton, a world-renowned pioneer of the subject. That was certainly a courageous, even outrageous move, to abandon a field in which he had been trained and had become a recognized expert—to go back to graduate studies, years after having already been awarded a doctorate degree. It was a decision that had consequences beyond Fager's own career, involving financial security, and of life style of the whole family.

Bill's move to Elton's laboratory was financially facilitated by the award of a Merck Senior Postdoctoral Fellowship, a remarkable program designed to help scholars in one field acquire proficiency in another. When he arrived at Oxford, confronted by experts in the local flora and fauna, Fager had the self-confidence—which could easily have been mistaken for arrogance or effrontery, if he had not otherwise been such a modest person—to announce, "I don't yet know much of anything about ecology, but I **DO** know how to do **RESEARCH**." (Crowcroft 1991) And he did, he did!

Three years later, in 1955, Fager was awarded his second doctorate degree, this one in ecology, from Oxford, which carried with it the British abbreviation of "D.Phil." to supplement his American "Ph.D." This was by no means the more typical "honorary" second doctorate degree. Bill Fager was unusual in having genuinely earned that second degree through the standard process of doing research and submitting a second major thesis.

Fager's research project at Oxford consisted of field studies of the fauna (predominantly insects) of decomposing leaves and logs on the floor of nearby Wytham Wood. Typical ecological field studies in those days included the collecting, identifying, and counting of the creatures in a habitat, and Bill did his share of that. In addition, however he undertook experimentation in the field, by designing and building "artificial logs," filled with sawdust or with leaf litter, which he placed on the forest floor and later retrieved for analysis. Experimentation arose from his conviction that much firmer scientific conclusions

can be based upon deliberate manipulation of a situation, than simply, as so many ecologist do, by intuitively interpreting correlations observed in an undisturbed system (Fager 1968). That research and his interactions with others at the Bureau of Animal Populations led his sponsor, Elton, to refer to Fager as one of the "topmost brains" ever to be at the Bureau (Crowcroft 1991).

Recruitment to Scripps

This is the background, then, that makes it so remarkable that in 1956 someone like Fager would be recruited as a Visiting Lecturer to an oceanographic institution. Here was a biochemist who had studied photosynthesis, then set aside his expertise in biochemistry, and undertaken experimental studies of the insect fauna on the forest floor—but he could make no claims whatever involving marine experience. The funding that facilitated Fager's recruitment to La Jolla was a million-dollar grant, awarded in 1954 by the Rockefeller Foundation to Scripps, to strengthen the discipline of marine biology, by financing recruitment of postdoctoral scholars to the institution, and by providing the initial salary money for the hiring of new faculty.

Once here at Scripps, Fager immediately began classroom instruction (as was, of course, expected of a "lecturer"); thereafter, teaching became a hallmark of his subsequent activities. During that first year, he developed and taught an introductory ecology course that was very well received by the biology graduate students (relatively few in number at that time), and which was also well attended by the junior faculty and even some of the senior biologists. Much of the substance of that course was drawn from terrestrial and freshwater examples, and that content was in part dictated by the fact that relatively few previous ecological studies had been undertaken in the marine realm. In addition, however, Fager was convinced that most of the processes underlying population dynamics and the interactions within an animal community are sufficiently general that an examination of the best studied populations (which were mainly terrestrial) provided a firm foundation for evaluating and understanding the ecology of other creatures that just happen to live in saltwater. Praise for his initial course included enthusiastic remarks about Fager's organization, his thoroughness and his skills in dealing with vast bodies of original scientific literature, which he not only summarized but also subjected to insightful critiques. (It was during this first year at Scripps, in June of 1957, that his daughter, Ellen, was born.)

In that same year, on the basis of his outstanding teaching contributions and an absolutely sterling set of recommendations about his previously demonstrated skills as a researcher, Fager was appointed to a permanent faculty position as Associate Professor at Scripps. There were some eight other candidates under consideration for that professorship, some of whom were already well-established marine biologists. The recommendations that were mustered in support of Fager's candidacy, however, are remarkably impressive. Brief excerpts, each from a different source, provide the flavor of those letters:

> "... I could hardly be more favorably impressed.... He seems ideal for the position."

> "... a very sound worker with a wide and good background and quite imaginative also."

"... in the top class intellectually ... original ... disciplined ... a clear, fairly ruthless critical mind ... is greatly liked."

"... a scientist with many techniques at his command ... of excellent character ..."

"... the utmost intellectual integrity ... will become an outstanding leader."

"... Dr. Fager has a brilliant future as a research ecologist."

"... Fager is **ABSOLUTELY** first-rate." (Emphasis in the original)

With endorsements like those in hand, the local Rockefeller Faculty Committee unanimously and enthusiastically proposed him to Director Roger Revelle for a tenured faculty appointment, with no evidence of any concern about the absence of prior background in marine studies. That committee doubtless recognized that someone like Fager, who had successfully made the transition from laboratory biochemistry to forest ecology, had demonstrated such remarkable flexibility that becoming a marine scientist should be no big hurdle. Here was someone who had demonstrated that he could teach effectively, and moreover, someone who understood what science is, even if lacking—as he had been when he arrived at Oxford—the background of experience normal to that specialty.

Formal Teaching at Scripps

Prior to Fager's 1957 appointment to the faculty, the instruction of graduate students at Scripps had taken a backseat to research. A small number of formal courses existed in the various disciplines, but training in doing research usually consisted of little more than providing the graduate student with a lab bench, a plankton net, or a thermometer, and waving the student on in the right direction. This casual attitude toward graduate-student training undoubtedly reflected the fact that all the Scripps faculty (in contrast with those at most other branches of the University of California) had titles of Professor of Organized Research, as opposed to Professor of **INSTRUCTION** and Research.

In part because of Fager's influence, that approach has changed radically. Teaching at Scripps has become an intensive instructional and guidance program and a central element of institutional activities. Before Fager's time, the administrative structure for teaching at Scripps had consisted of four so-called "departments" (Marine Biology, Marine Geochemistry, Marine Geophysics, and Marine Geology); but all advanced degrees for studies undertaken at Scripps were conferred through "real" departments of the University of California at Los Angeles, for which Scripps might be considered an adjunct field station. The San Diego branch of the University of California was formally established in 1960, initially as a School of Science and Engineering (graduate studies only), with Roger Revelle serving as its dean. When the multi-departmental undergraduate program of UCSD was initiated shortly thereafter, Scripps was one of the last administrative remnants from the past

to be incorporated, as a single academic "Department of Oceanography," and Fager, despite a very modest and very recent background in marine sciences, became its first chairman.

Fager certainly had no doubts about the weaknesses inherent in the existing instructional activities at Scripps, but reforming that established system would not be easy, because most of the senior faculty members regarded themselves mainly as researchers, and were entirely satisfied with the **STATUS QUO**. They had offered occasional courses in their specialties, but the instructional program was weakly organized, with very modest attempts at interdisciplinary coordination, despite the 1930s efforts of former Director Sverdrup to foster cross-disciplinary training and studies, a theme epitomized by the standard textbook, "*The Oceans*" (Sverdrup, Johnson, and Fleming 1942).

Fager's own ecology course provided new strength to instruction in biology at Scripps. In addition, as Chair of the department, Fager supported a resurgence of concern for teaching, and the formalization of that function in an ocean-oriented interdisciplinary mode in the very early 1960s. Bill encouraged all disciplines to upgrade their teaching programs. He enlisted the support of some of the junior faculty who cared as much about education as he himself, including Bob Arthur (physical oceanography), Doug Inman (marine geology), Ed Goldberg (marine chemistry), and John McGowan (biological oceanography). Fager allied himself with those people under the self-chosen title of "biological oceanographer," so as to emphasize his ecological and environmental (and interdisciplinary) interests and to distinguish himself from the other more laboratory-oriented marine biologists.

Fager with bongo nets, Piquero Expedition, Leg I, 1965. Photo by E. Venrick.

A few years later, this emphasis on educational activities at Scripps culminated in the formation of disciplinary units called "Curricular Groups." Those groups became sub-departments, while "the Department of Scripps Institution of Oceanography" remained the

official administrative unit formally in charge of instructional resources and activities. The Curricular Group coordinators made quasi-independent decisions about graduate-student admissions, teaching programs, proposals for new faculty appointments, and all the other administrative issues that underlie a structured teaching department that has survived to the present.

During his Scripps years, Fager's formal classroom lecturing consisted of two courses. Every second year he gave a general, introductory ecology course derived from that which he had taught during his initial years as lecturer at Scripps, supplemented by field research projects. (He regularly and conscientiously updated the course's content on the basis of current literature.) In alternate years, he gave a very demanding and successful course in statistical analysis and experimental design "applicable to marine studies." The novelty of that latter course lay in its emphasis on "non-parametric" methods, which avoided some of the assumptions of more standard statistical methodology that are unrealistic for biological field data. His enthusiasm for and expertise in statistical analysis were doubtless another consequence of his association at the University of Chicago with Thomas Park, whose elegant statistical treatments of his own carefully replicated beetle-population experiments brought rigor and an air of quantitative respectability to the burgeoning field of ecology. For Fager, this was not number-work for its own sake, such as can readily be used as window dressing to obfuscate weaknesses in the design of a study or in a data set. Instead, he considered statistics to be a research tool for distinguishing between strong evidence in favor of a given interpretation, and those other possibilities that might well have arisen by chance alone. Fager made it clear that in this role statistics is as important a tool for the careful ecologist as any expensive analytical device is for a chemist.

Bill Fager can legitimately be credited with introducing statistical analysis into the field of biological oceanography. Students who took his course have subsequently taught similar courses at other universities to another generation of students who themselves later also have gone on to teach courses much like Fager's. And the lecture notes from such courses represent an invaluable reference work that former students (myself included, even these 40 years later) consult regularly.

Those two courses originated by Fager represent the very best and most demanding classroom instruction that I have ever experienced. Each of the lectures in the ecology course—for which there was no textbook—began by Bill listing on the blackboard the original journal literature underlying that day's topic, often 6 or 8 citations. Every lecture in the statistics course was accompanied by a carefully chosen set of take-home problems that involved application of the analytical methods discussed that day.

In previous college courses, I had encountered a few teachers who were more entertaining lecturers than Fager, those who could more readily capture and hold the attention of disinterested undergraduates, instructors who made their lectures "fun." Bill was certainly not an entertainer; his courses were designed for a more mature audience and his forte was an intensity and an enthusiasm for the intellectual content of the material and the logic of its interpretation. His breakneck pace meant that it often was difficult to scribble down an adequate set of lecture notes—notes that required intensive study afterwards at leisure, when the real learning process took place. It was simply impossible to sit through one of Fager's lectures and hope to absorb all the important facts and ideas by passive listening.

He was a tense lecturer, and every sentence was important. Each class was a writing marathon, and subsequent, detailed study of the material was essential.

Built into the very fabric of both the ecology and the statistics courses was a well-honed skeptical approach to all scientific problem areas: not the viewpoint of ancient Greek skeptics (disbelief in **EVERYTHING**) but an insistence that any novel and interesting claim about nature should be supported by adequate, rigorous, and persuasive evidence before it is accepted into the framework of our knowledge. Once that approach has been systematically and regularly applied to research results reported by others, the natural consequence is the recognition that a similarly careful skepticism can—and should—be applied to one's own research as well. Hence, the most important question that a scientist should insistently ask himself is: "Where or how could I be mistaken about this interpretation?"—and not the more facile query of the salesman, "How can I convince others that I'm right?" The frequent result of such examination of alternative explanations will be the recognition that additional measurements or control experiments are needed. In this regard, Fager was an enthusiastic advocate of the ideas of Chamberlin (1897) and Popper (1959), later popularized by Platt (1964), three philosophers who insisted that genuine scientific progress only comes from systematic, deliberate efforts to **DISPROVE** a particular hypothesis, by performing truly "critical" experiments: those, the outcome of which can clearly distinguish between a given hypothesis of primary interest and one or more of its alternatives.

Learning such a lesson was often a discomfiting experience. When we were first confronted with hard-nosed skepticism toward our own interpretations, the experience was more than disheartening. In some, it even evoked hasty rejection as "negativism," because it is so entirely natural to **WANT** to believe one's own conclusions! But with Bill Fager's help, we learned to apply healthy skepticism to the research and conclusions of others. It then became evident that when a colleague justifiably voices skeptical concerns about our own conclusions, it is not hostility or negativism. Instead, Fager taught us that that kind of criticism provides a truly invaluable form of friendly collaboration.

In spite of Fager's emphasis on systematically questioning what we think we know for sure, or collecting the data or designing the experiment that would permit a rigorous test, he was an enthusiastic naturalist. Bill was convinced that the intuition of experienced field observers deserves careful consideration by the serious scientist. He did not, of course, advocate facile acceptance of all the intuitive conclusions of the naturalist. Instead, he considered those interpretations to be invaluable sources of testable hypotheses and worthwhile foundations for more rigorous quantitative investigation.

A clear example of Fager's dual approach is provided by his ecology course lectures on the plankton "exclusion principle"—the proposal that grazing invertebrates in the ocean tend to avoid places with heavy phytoplankton populations—an idea that had been proposed by Sir Alister Hardy (1956), one of the world's leading marine biologists. In dealing with that topic, Fager demonstrated to the class that the "principle" in fact had very little support in the original data on which it was said to be based. Nevertheless, Bill did not urge casual dismissal of Hardy's generalization. He proposed instead the Scottish verdict of "not proven." Because of Hardy's intuition and insight, derived from long experience with the plankton, the notion might well be correct, and was certainly worthy of further examination, even though the available published data provided inadequate objective evidence.

Fager's enthusiasm for natural history and, at the other extreme, his intensely skeptical and quantitative approach to ecology were further transmitted to graduate students through the weekly biological/oceanography seminar that he organized and led. All the ecologically oriented faculty participated, week after week and year after year. The graduate students were individually responsible for the formal, hour/long introductory presentations, but for the students, the most significant aspects of that seminar were the differences of opinion (and sometimes even heated arguments) that arose among the faculty during the discussions that followed. This is a component of the scientific enterprise usually hidden from the neophyte. It further demonstrates that scientific "facts" are usually only provisional interpretations, and that most observations are open to several alternative explanations: an ideal foundation for the healthy skepticism that Bill practiced and advocated.

Research in the Subtidal

During his first year as a lecturer at Scripps, Fager initiated a highly original long/term research program, which became a second hallmark of his Scripps activities. He chose to study the nearshore sand/bottom fauna, but not from the surface of the sea, with dredges or nets dragged on sleds, as others had done so often before, but instead by using scuba (Self/Contained Underwater Breathing Apparatus) diving as a research tool. Those were the days when scuba gear was widely recognized as equipment for a fascinating recreational sport and a tool for the adventurous spear fisherman. A modest training program in scuba was offered at Scripps, and several of the marine geologists used sub/littoral diving for research purposes. Fager, however, recognized the potential of diving for providing direct observational and sampling access to the benthic fauna of the nearshore subtidal. He was one of the very first biologists to enlist the equipment as a major tool for serious scientific studies of marine organisms.

For this subtidal research, Fager's skillful technician and diving co/worker, Art Flechsig, provided essential support over many years. And while Fager's grants paid Art's salary, Flechsig's imaginative suggestions about tools and methods for diving research were also of great assistance to various other biologists at Scripps, including those graduate students who undertook thesis projects that involved scuba.

As an important foundation for his research program, Fager established an array of standard sampling locations in the subtidal region in front of Scripps, in water depths between 6 and 20 meters. He hammered steel rods into the bottom as permanent markers that served as mountings for removable half/meter/diameter rings of stainless steel, rings used for defining replicable sampling locations. He also developed simple sampling tools for complete recovery of the animals in the sand. The main one was a hand corer—a 30/cm/long aluminum cylinder with which about half a cupful of sand could be removed by closing off the bottom with an aluminum plate shoved through the sand. The sample was then decanted underwater into a wide/mouthed pint bottle of the sort used for home canning, labeled, capped, and brought back to the lab for preservation and analysis.

The majority of the creatures in those samples were very small animals, and disconcertingly, most of the tiny creatures that Bill brought back with him turned out to be "undescribed" species (i.e., creatures never formally named nor entered by the experts into the register of "known" and readily identifiable species). Here, within a few hundred meters of a

major marine station, where biologists had worked for more than half a century, many of the smaller animals from the intertidal sand beach, and a majority of those present in the subtidal sand were creatures previously unknown to the experts. That remarkable state of affairs was an unexpected hurdle for Fager, and stood in stark contrast with his forest research in England, where identification of essentially every animal present was a relatively simple matter, based on standard reference works. The explanation, of course, is that most biological researchers at Scripps and at other west coast marine stations had emphasized creatures collected on shipboard in remote locations, frequently at great distances from shore; in those occasional instances in which nearshore creatures had been of interest, they were typically the larger, conspicuous ones that had already been granted official Latin names and that required no great skill or a microscope to identify and recognize.

The sorry state of the taxonomy of the animals that he encountered led Fager to become his own expert in identifying and distinguishing dozens and dozens of tiny creatures, many species of which, to the unskilled eye, looked identical. The most common of those animals were small worms (of several phyla) and crustaceans, particularly amphipods. Bill sent off dozens of specimens to museum-based experts, to confirm his interpretations of the previously unknown status of the animals, to which he tentatively assigned generic names with numbers, such as "*Pontocrates* species #1," "*Pontocrates* species #2," and so on. Actual formal naming of those animals by the taxonomists typically occurred many years later (*Pontocrates* species, for example, eventually becoming *Synchelidium* new species), but Fager's provisional names, in conjunction with his collections of comparison (voucher) specimens, were an efficient and essential means of overcoming the slow pace of traditional taxonomy. (One can't, of course, fault the busy specialists for the fact that nobody before Fager had presented these particular animals to them.)

Fager and his Ecology Class on a field trip to Dike Rock, north of the SIO pier, 1963. Photo by Elaine Brooks.

Fager's ecology course included extensive coverage of the behavior, physiology, and population dynamics of single species, but his own commitments and research emphasized "community" ecology: the study of the ways in which various species in a habitat interact with each other and with their environment. This approach to ecology differs markedly

from a long tradition of American researchers, who tended to regard the assemblages of creatures in a habitat as constituting a kind of "super organism." Bill's viewpoint was instead derived from that of his Oxford mentor, Elton, who wanted to understand what the various creatures in a habitat **DO**, how they do it, and what the consequences are. A portion of that "doing" involves who eats whom, but the Eltonian viewpoint goes much deeper. As a rough analogy, the ecologist himself becomes the equivalent of a visitor from a foreign land, attempting to understand the organization of a novel human society. Elton urged that one seek in nature the equivalent of information involving the creature's "occupation":

> "When an ecologist says, 'There goes a badger.' he should include in his thoughts some definite idea of the animal's place in the community to which it belongs, just as if he had said 'There goes the vicar.'" (Elton 1951)

Fager emphasized use of quantitative tools as a means of dealing with such issues.

An example of this sort of approach from Fager's subtidal diving studies is summarized in a brief and fascinating research paper (Fager 1964). Field sampling has demonstrated that the tube-building worm, *Owenia fusiformis*, occurred at high density in water depths of six to eighty meters, forming zones several meters wide that stretched for hundreds of meters parallel to the shore. Those polychaetes live inside relatively solid structures, which they assemble by cementing together selected grains of a particular sort of sand (green hornblende) into a coherent tube, that is largely buried into the substrate. Bill found that those dense *Owenia* beds caused major changes in the grain-size of sand surrounding the aggregations, because of the effects of those populations on near-bottom water flow. The consequence was that several species of crustaceans were also unusually abundant there, and other species that would ordinarily be expected in sand at that depth were absent. In terms of Elton's badger-vicar analogy, part of the functional role of *Owenia* might be compared with that of the developer of a new residential subdivision, although Fager quite sensibly left that sort of colorful analogy to the reader's imagination. His overall working assumption was that a more complete understanding of the subtidal sand bottom community would eventually emerge from the integration of dozens of vignettes of this sort.

In addition to this field research, Fager was deeply interested in ecological theory and in developing quantitative tools for the interpretation of ecological observations. The most widely used of those tools is his "recurrent-group" analysis (Fager 1957), which is a means of objectively determining which species in a natural assemblage are often simultaneously found in the same place. The entire recurrent-group analysis, as Fager developed it, takes place within the guts of a large computer, and its logic was summarized in Fager (1957). Bill's development of and early applications of this kind of analysis involved the insect fauna of the forest floor of Wytham Wood, and he later applied the procedure to bacterial assemblages (Fager 1969). In addition, recurrent-group analysis has proved valuable for recognizing communities of interacting creatures in several marine applications. For example, an analysis of extensive data on the various zooplankton of the North Pacific (Fager and McGowan 1963) established a zoogeographic framework for that region that has not required subsequent revision. Applications of recurrent-group analysis to the diatoms of the North Pacific by Venrick (1971), initiated while she was a student under Fager's

guidance, indicated that unicellular-algal communities there have zonal distributions similar to those of the animals. Another study applied the technique to the fish fauna of distant seas (Fager and Longhurst 1968). Fager did not, however, consider the grouping procedure to be an end in itself. Instead, he regarded it as a vehicle that could provide clues about probable interactions among species, which then deserve further study, based on the plausible assumption that co-occurrence indicates the likelihood of significant direct interactions.

Fager's Graduate Students

Bill Fager's most significant and enduring contribution to Scripps and to marine science lies in the guidance he provided over the years to an extensive group of graduate students, particularly (but not exclusively) those for whom he was principal advisor and doctoral-thesis committee chair. He was a mentor of outstanding skills. Through his research grants, he provided financial support to "his own" students (who sometimes numbered as many as a dozen simultaneously), but more important, he invested large fractions of his time in advising, directing, and supervising their thesis research. His thoughtful comments were written in red ink with tiny script on essentially every page of text that crossed his desk: report, manuscript, or thesis draft.

Rarely if ever was he included as a co-author on the publications eventually resulting from those theses. Had he encouraged that, as is common practice of many other faculty members, his lifetime publication list would have been several-fold longer. All he expected of those whom he had helped was a brief mention in the acknowledgments sections of the published papers.

Fager's original intent, when he chose to do research on the animals of the sandy benthic nearshore environment, was to create a marine equivalent of Elton's Wytham Wood: a single habitat within which not only would he pursue his own research, but where his advisees would choose some component of the fauna or the environment for their thesis projects, the entire enterprise leading to a more complete understanding of the inter-related ecological system. Fager ultimately planned to write up such a synthesis, as Elton had done for Wytham Wood. However, this ideal broke down at the very outset. The first graduate student to complete a thesis under Fager's chairmanship was Ray Ghelardi (a successful San Francisco wholesale-produce dealer who had, at 40 years of age, decided to do something more interesting with his life). Ray's thesis was based on study of the fauna in kelp holdfasts (the mechanical structures, looking much like a root system, by which giant kelp plants secure themselves in place against waves and tides). Most kelp forests, including those that Ghelardi sampled, are in fact quite remote from the sandy shoreline that Fager envisioned as his marine analog of Wytham Wood. The sandy benthic habitat was indeed utilized by some of those who came later, such as Bob Clutter (who studied crustaceans known as mysids that school just above the bottom), Dick Ford (who studied small flatfish in the nearshore subtidal) and Ann Hurley (who studied a species of barnacles that settle onto subtidal sand dollars), but that habitat was not a serious constraint on the research of students who gravitated toward Fager's group and cherished his advice. Some of Fager's advisees undertook thesis projects on marine fish species predominantly found in other habitats (Garth Murphy and Tom Clarke) and still others on planktonic unicellular algae (Elizabeth Venrick, John Caperon, and Dan Kamykowski). Bill never attempted to dictate what his advisees should undertake as thesis

research, though he was not adverse to offering critical guidance by pointedly noting, for example, that a particular proposed project was perhaps beyond the constraints of time, equipment, or funding available. One of his primary concerns was the feasibility of thesis research (cf. "tractability" in Medewar's (1981) usage), but Bill was also well aware that a self-chosen, self-designed project is much more likely than a dictated one to generate the single-minded concentration of effort necessary for completion of a significant project.

Fager himself was a very private person, intensely dedicated to his wife, Naomi, and his daughter Ellen. He was unemotional and businesslike in his approach to students and colleagues; matter-of-fact, eminently fair and forthright in his critiques and evaluations. Colleagues and students were occasionally invited to the family home, but those were rare situations to chat informally with a visiting scientist and were therefore more professional gatherings than parties. Thus, consideration of Fager's role as a graduate-student mentor would be incomplete without prominent mention of his superb technical assistant, Thea Schultze. Thea not only helped with Fager's research in the laboratory, but also acted as a kind of "den-mother" for his graduate students. A warm-hearted soul, she baked birthday cakes and offered advice and emotional support on everything from pre-exam jitters to broken hearts. Thea was Fager's technician throughout his entire career at Scripps and it is difficult to imagine someone better suited to complement his reserved personality.

If this essay were to be exhaustively complete, this would be the place to list the names and current status of the many other graduate students whose doctoral theses Fager supervised. That sort of listing, however, would neglect the important contributions that Fager made to the research of those grad students who had other thesis sponsors, even including some nonbiologists who undertook thesis research at Scripps during Fager's tenure. No other senior scientist at the institution was more generous with his time, more available for consultation—both by graduate students and by colleagues. Fager was, in fact, so generous with his time for such conferences and activities that it is remarkable that he was able to accomplish anything else.

A Tragic Early Death

During a family vacation in Mexico in 1973, Fager was stricken with pneumonia and was unable to assimilate the oral antibiotic that was prescribed there. By the time he returned to La Jolla, the persistent infection had led to an acute case of meningitis with a variety of subsequent ramifications, including major brain damage. During an extended hospital stay, he had stomach surgery and suffered kidney failure. Thereafter, Bill was bed-ridden at home for more that three years, a ghost of his former self. For those of us who visited him during those years, the sight of this intellectual giant reduced to a helpless shrunken figure who could not even recognize us, much less converse, was one of the saddest situations imaginable. The university generously continued him on extended sick leave until his death at the age of 59 in November of 1976.

Fager's active career of 17 years at Scripps left an enduring legacy and a lasting imprint on the institution and on the entire field of marine ecology, through his teaching, his mentorship, and his own research. Prior to this last illness, he was as active and stimulating a colleague and scientist as when he first arrived. His loss to the institution so many years before a normal retirement was a major tragedy (Haxo, Mullin, and Phleger, 1978). I have

missed him sorely, as have many of his other colleagues. One can't help wondering what more Bill Fager might have accomplished, how many more students he might have inspired and trained, had he lived another decade or two.

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Selected Publications of E. W. Fager

(This listing, with brief annotations, was selected from among those papers that were published during Fager's tenure at Scripps and thereby ignores the body of significant scientific contributions from his earlier research on biochemistry, on photosynthesis, and on forest ecology.)

Fager, E. W., 1957. Determination and analysis of recurrent groups. *Ecology*, v.38. pp.586-595. (Provides details about the methods developed for recognizing natural "groups" of animals, which, on the basis of frequent co-occurrence, are candidates for closely interacting species.)

Fager, E. W., 1963. Communities of organisms. In *The Sea: Ideas and Observations*, E. D. Goldberg, W. H. Munk, M. N. Hill, and C. O'D. Iselin, eds. v.2. pp.415-435. (Broad, general treatment of the definition and identification of "communities" of animals and plants, and their structure and function, with special reference to interacting assemblages of creatures in the sea.)

Fager, E. W., and J. A. McGowan, 1963. Zooplankton species groups in the North Pacific. *Science*, v.140. pp.453-460. (Important application of his method of data analysis [cf. Fager 1957, above] to mid-ocean zooplankton species assemblages.)

Fager, E. W., 1964. Marine sediment: Effects of a tube-building polychaete. *Science*, v.143. pp.356-359. (A report on how populations of a species of a marine worm change the sandy substrate habitat and thereby affect populations of other species.)

Fager, E. W., and A. R. Longhurst, 1968. Recurrent group analysis of species assemblages of demersal fish in the Gulf of Guinea. *Journal of the Fisheries Research Board of Canada*, v.25. pp.1405-1421. (Applications of his method of data analysis [cf. Fager, 1957, above] to fish populations.)

Fager, E. W., 1968. A sand-bottom epifaunal community of invertebrates in shallow water. *Limnology and Oceanography*, v.13. pp.448-464. (An interim report on and capsule summary of six years of quantitative research on the sandy bottom subtidal fauna near Scripps.)

Fager, E. W., 1969. Recurrent group analysis in the classification of flexibacteria. *Journal of General Microbiology*, v.58. pp.179-187. (An application of his method of data analysis [cf Fager 1957 above] to bacterial populations.)

Fager, E. W., 1971. Pattern in the development of a marine community. *Limnology and Oceanography*, v.16. pp.241-253. (A report on secular changes in the fauna and flora of the subtidal community near Scripps, studies on artificial substrates.)

Fager, E. W., 1972. Diversity: a sampling study. *The American Naturalist*, v.106. pp.293-310. (A theoretical treatment demonstrating the extent to which abundance data from limited sampling can be used to draw inferences about an entire assemblage of naturally occurring animals.)