Robert (Bob) Guillard was a renowned scientist, algal culturist, teacher, environmentalist and friend. He is best known for his extensive algal culture collection and for the founding of the Provasoli-Guillard National Center for Marine Algae and Microbiota (formerly The Provasoli-Guillard Center for the Culture of Marine Algae, CCMA), an important world resource for marine phycological research. He was also an important innovator in the culture of marine algae and shellfish. He was involved in several seminal discoveries and was an author on over 100 scientific papers (see Supplementary Materials for a full listing).

Bob was born Robert Louis Russell in New York City in 1921. His parents, Robert and Susanne Russell, were respectively of Scotch–Irish and Portuguese decent. Bob’s father was a pilot during World War I. His parents divorced when he was young, and his mother remarried François Guillard, a New York City jeweller, when Bob was five years old. After the marriage Bob became Robert Louis Russell Guillard. However, in 1941 while working for the Navy, his two middle names became switched on an official document, and Bob has been Robert R. L. Guillard ever since. Bob grew up in New York City but spent his summers with his grandparents in Stonington, Connecticut, a seaside village on Long Island Sound. It was here that Bob first became familiar with the sea and marine life. Bob completed grammar school in seven years and graduated from prestigious Townsend Harris High School in New York City after only three years. He attended the City College of New York (CCNY) at the age of 16 and received a bachelor’s degree in physics in 1941 at the age of 20 just prior to World War II. After graduation, he was hired by the US Navy to install and maintain antimagnetic mine equipment and continued in this capacity throughout WWII. However, in the evenings he also took physics courses at New York University (NYU). After the war Bob returned to academia as an instructor at NYU and a tutor at CCNY. He also took courses at CCNY, including a botany course taught by J. J. Copeland. It was then that he decided to pursue a graduate education in natural sciences. Bob attended Yale University in 1949 and received a master’s degree in 1951 in microbial ecology. He completed his PhD degree in 1954 with the famous freshwater ecologist G. Evelyn Hutchinson. His dissertation was entitled ‘A mutant of Chlamydomonas moewusii lacking contractile vacuoles’. Bob was awarded a prestigious summer fellowship at the Woods Hole Oceanographic Institution (WHOI) in 1954. The WHOI fellowship strongly influenced his career because it changed his scientific focus from freshwater to marine ecology. Perhaps this was only fitting, since Bob had spent his boyhood summers on the shores of Long Island Sound.

After receiving his PhD, Bob worked as a Research Associate at the University of Hawaii where he studied the primary productivity of phytoplankton in nearby ocean waters with the newly developed 14C radiotracer technique (Fig. 2). Then in late 1955 he was recruited by Victor Loosanoff, the director of the US Fish and Wildlife Service’s Milford Laboratory, to fill a newly formed position to culture algal food for the rearing of clams and oysters. Earlier attempts to raise larval shellfish in nutrient enriched seawater had been unsuccessful, and a new approach was needed, namely, the isolation and culturing of viable algal food species. Dr. Loosanoff had known Bob during his years at Yale and must have seen something to convince him that Bob was the right man for the job. And right he was! This turned out to be a fortuitous hiring for both Bob’s career in marine phycology and for the development of a whole new industry of shellfish mariculture. At Milford, Bob isolated numerous algal species into axenic culture, many of which became fixtures in future algal research, including one, Thalassiosira pseudonana Hasle & Heimdal (originally clone 3H, now CCMP 1335), which was the first algal clone to have its genome sequenced (Armbrust et al. 2004). Bob’s success in isolating and culturing diverse algal species formed the basis of his now famous algal culture collection and allowed for careful testing of the nutritional value of different algal species in the rearing of larval shellfish to adulthood. Indeed two initial papers (Guillard 1957; Davis & Guillard 1958) provided the basic methods used for the establishment of a mariculture based shellfish industry and for countless culture studies on the physiological ecology of shellfish and other planktivorous marine animals and protists. Bob also did yeomen’s work in helping individual shellfish hatcheries with the rearing of algal food. Bob was honoured for these contributions with his induction as an honorary lifetime member of the National Shellfisheries Association (Wikfors 1996) and an honorary life member in the World Aquaculture Society (Anonymous 1998).

In 1958 Bob and his culture collection were recruited by John Ryther to the Woods Hole Oceanographic Institution (WHOI). This turned out to be an ideal marriage, given Bob’s expertise in isolating and culturing diverse algal species and the need at the time at WHOI for a dedicated culture facility for the study of phytoplankton. Bob and his algal collection became a magnet for students and scientists interested in the physiology and ecology of phytoplankton and their interactions with their environment. The ensuing 23 years at WHOI was an extremely productive period, accounting for 60% of Bob’s 114 scientific publications. Some of these were highly influential. An early paper at...
WHOI described a new chemically defined culture medium (f/2), which replaced then widely used soil extract with vitamins and a mixture of the synthetic chelator ethylenediaminetetraacetic acid (EDTA) and various trace metal nutrients. F/2 was to become the most widely used culture medium, and the publication describing it (Guillard & Ryther 1962) has been cited an astounding 5728 times. Another highly cited paper, Blumer, Guillard & Chase (1971; 567 citations), used gas chromatography to identify and quantify the hydrocarbons produced by different species of marine algae. This research allowed for the differentiation between fossil fuel hydrocarbons released into seawater by man from those derived naturally from phytoplankton. Two other papers (Sunda & Guillard 1976, 944 citations, and Anderson, Morel, & Guillard 1978, 246 citations) were to have far reaching implications. They showed that the uptake and biological effects of nutrient and toxic trace metals was heavily influenced by their chemistry. Specifically, they showed that the biological availability of trace metals was related to the free metal ion concentration, and that chelates with EDTA and other organic ligands were not directly available. These results paved the way for the development of chemically defined, chelator-based, trace metal ion buffer systems in metal nutrition and toxicity experiments. The buffer systems allowed the availability of specific bioactive metals (e.g., iron, zinc, copper, cobalt, and manganese) to be regulated at constant values in dilute batch cultures over a wide range of values and to be quantified by equilibrium calculations of the free (or unchelated) metal ion concentrations. Such buffer systems were used to examine growth rate limitation by iron, zinc, and manganese in 21 marine phytoplankton species isolated from oceanic and coastal waters (Brand, Sunda, & Guillard 1983, 433 citations). Systematic differences were observed between species from coastal waters where trace metal concentrations were high and those from oceanic waters where metal levels were much lower. All species from low iron oceanic waters were able to grow well at low iron concentrations, irrespective of algal group, while all coastal species required much higher concentrations. Zinc and manganese showed the same trend but with several exceptions. The oceanic-coastal trends in trace metal requirements suggested that these metals had been important factors in the evolution of marine phytoplankton and that they influenced the growth and species composition of phytoplankton communities in the present day ocean. This prediction for iron was born out years later by the now famous iron addition experiments of the late John Martin and colleagues (Martin et al. 1989, 1994).

Metal chelate buffer systems were also used to examine trends in the toxicity of trace metals (copper and cadmium) in 38 isolates of marine phytoplankton representing three major eukaryotic algal groups (diatoms, coccolithophores, and dinoflagellates) and the cyanobacterium *Synechococcus* (Brand, Sunda, & Guillard 1986; 441 citations). The cyanobacteria were found to be especially sensitive to copper toxicity, suggesting that high copper levels could influence their distribution in the ocean.

The above survey experiments were extremely large and involved the use not only of large numbers of different phytoplankton isolates (21–36) but also six to eight metal treatments per isolate and successive dilution of exponentially growing cells into new culture medium to maintain constant specific culture growth rates. And each culture had to be measured daily for biomass to compute specific algal growth rates. Here, a new technique developed in the Guillard laboratory for the rapid measurement of specific growth rates, in vivo chlorophyll fluorometry (Brand, Guillard, & Murphy 1981; 257 citations), was essential for...
the success of these extremely large experiments. This method is widely used today.

Another important discovery in the late 1970s was the widespread distribution of the cyanobacterium *Synechococcus* in the ocean (Waterbury, Watson, Guillard, & Brand 1979). Several strains of *Synechococcus* had been isolated and identified by Bob Guillard in the previous 20 years and were present in his culture collection. Then in the late 1970s, Bob’s PhD student, Larry Brand, began using newly developed trace metal clean techniques to isolate and culture oceanic species of phytoplankton, techniques that avoided contamination by toxic metals such as copper. As Larry wrote ‘Using the new clean media, I started getting *Synechococcus* contaminants in many of my single cell isolations, which told me that they had to be very abundant in oceanic waters. I told this to John Waterbury a number of times, knowing he was particularly interested in cyanobacteria. One day it clicked in his mind that there may be a connection between all those funny looking fluorescent balls he was seeing in the epifluorescent microscope and all the cyanobacteria I was getting into culture from oceanic waters. He asked me for one of my cultures one day and it was confirmed. The paper was then written within a week’. The resulting Nature paper has been highly influential (775 citations). Subsequent research has verified the widespread distribution of *Synechococcus* in the ocean, where it is estimated to account for ~18% of net primary production (Flombaum et al. 2013).

Bob’s culture collection continued to grow during his tenure at Woods Hole (1958–1981) from a number of sources, including his own isolations, cultures obtained from colleagues, and those isolated by his PhD students and postdoctoral students. Ed Carpenter wrote: ‘I still remember the first words that Bob said to me as I nervously entered his lab and started my postdoctoral fellowship with him in September 1969. He said “Do you have any bugs?” I thought he was asking if I had fleas or bedbugs but he was really asking if I had brought any phytoplankton cultures with me’. He was not the only one who received that question.

Although Bob was to isolate numerous clones himself, he was afflicted with acute seasickness, which greatly curtailed his seagoing activities. Ed Carpenter wrote ‘Once Bob and I went to St Croix in the Caribbean to try to get *Trichodesmium* into culture. We were taken offshore in a small (~20 foot) boat and both of us immediately became seasick and started my postdoctoral fellowship with him in September 1969. He said “Do you have any bugs?” I thought he was asking if I had fleas or bedbugs but he was really asking if I had brought any phytoplankton cultures with me’. He was not the only one who received that question.

In 1981, Bob and his culture collection were recruited to the Bigelow Laboratory of Ocean Sciences, Boothbay Harbor, Maine, by director Charles Yentsch, a former WHOI colleague, who had left Woods Hole in 1967 and had founded Bigelow Labs with his wife Clarice in 1974. Bob was brought to Bigelow to initiate a formal national culture collection for marine phytoplankton based largely on his then very large culture collection and that of Luigi Provasoli at Yale University. In 1985 the culture collection became a culturing centre with expanded duties and was renamed the Provasoli–Guillard Center for the Culture of Marine Phytoplankton. The main functions of the Center were to maintain a diverse culture collection for the benefit of the US and global marine science community, to ship cultures to scientists for use in marine algal research, to isolate algal clones from mixed algal communities, and to provide education in the most recent culture methods, all things Bob had been doing his whole career. Bob served as the first director of the culture collection/centre until his retirement in 1989.

During his tenure as director Bob continued to publish significant research findings. One publication (Keller, Selvin, Claus, & Guillard, 1987; 664 citations) described new ‘Media for the culture of oceanic ultraplankton’ while another (Keller, Bellows, & Guillard 1988) described a new microwave method for sterilization of culture media. This method was a great improvement over existing methods of autoclaving (which caused precipitates and contaminated media with trace metals) and sterile filtration (which was very time consuming). The most significant finding during this period came from the use of the CCMA culture collection to conduct a survey of the content of dimethylsulphoniopropionate (DMSP) in 123 axenic clones from diverse groups of marine phytoplankton (Keller, Bellows, & Guillard, 1989; 625 citations). DMSP was of interest not only because it served numerous important cellular functions (osmolyte, antioxidant protection, grazing protection, cell signalling, and cryoprotection) but also because it was the precursor of the volatile compound dimethyl sulphide (DMS), which helps regulate climate through its oxidation in the atmosphere to sulphur aerosols (Charlson et al. 1987). The aerosols seed clouds and thus also influence the hydrological cycle. The survey showed that the DMS concentration in different phytoplankton species was highly variable. Some phytoplankton groups, such as diatoms, chlorophytes, cryptomonads, and cyanobacteria, produced little or no DMSP, while others, such as prymnesiophytes, dinoflagellates, and chrysophytes, contained high concentrations. Thus, the species diversity of a phytoplankton community was of major importance in determining the production of DMS and its influence on climate, and that diversity is exactly what Bob had spent his life studying.

Bob formally retired in 1989 and was honoured by former students, post doctoral students, and colleagues by a Bobfest celebration, part of which included nine papers dedicated to Bob in the journal Biological Oceanography (vol. 5/6, 1988–1989). But the retirement was mainly from his CCMA Director duties, and Bob remained quite active in science. Indeed after ‘retirement’ Bob maintained an office and laboratory at Bigelow Laboratory and continued to publish scientific papers well into his eighties.
After two brief marriages, Bob married Ruth Stimson (née Fredericks) in 1963, a partnership that was to last until his death 53 years later. Ruth had three young boys, whom Bob raised as his own. Ruth was an accomplished musician, with a love for Renaissance and Baroque music, a passion also shared by Bob. Other common interests were transcendental meditation, which they both practiced and Ruth instructed, and folk dancing, which we all enjoyed with a Woods Hole folk dancing group that met every Wednesday evening. In addition, Bob was an accomplished Morris Dancer, a type of English folk dance that dates from at least the mid 15th century. He also was an accomplished fencer and was co-captain in college of the CCNY varsity fencing team. He taught fencing in both Woods Hole and Maine, and one of his students won an Olympic silver medal.

Bob not only collected algae but was also an avid gun collector, and he was happy to show off his extensive gun collection to anyone who visited his house for dinner. He was an excellent marksman and loved target shooting but surprisingly never hunted, likely due to his great love of nature and wildlife. Diane Stoecker noted ‘He was careful never to cut wood or disturb the forest and trees on his farm in Bourne when birds or mammals were nesting. I remember driving with him to a meeting, and along Rte 95 we saw a cormorant entangled in a fence. We stopped and managed to untangle the angry, scared bird and release it unharmed. Bob was a very kind and aware person’.

Bob was an avid environmentalist and had no use for the throwaway society. He was a notorious recycler and hated throwing anything away that might one day prove useful. Bob never used disposable pipettes, and after leaving his lab in 1975, I was surprised to find that this was not the norm in most laboratories. Ed Carpenter wrote ‘Bob ran a very “Green” lab, and was way ahead of his time. We were taught to hang up paper towels to dry for later reuse. Coverslips and microscope slides were also washed and dried after their use. Any other lab would have tossed these items’.

Bob was also an excellent teacher and mentor, based on my own experience and comments from numerous students and colleagues. He mentored six PhD students, including Ken Haines, Dottie Swift, Alan White, myself, Larry Brand, and Mark Wells in rough chronological order. He also had numerous post doctoral students, including Ed Carpenter and Diane Stoecker, who provided comments for this piece. He wrote beautifully, and I once said to him that it must be nice to have such a natural ability with writing, something that I, like most students, was struggling with. He answered that any ability he had came not from any innate gift but from years of hard work and practice. He also noted that writing was no more than organized thinking, and that if you thought clearly, you also could write clearly. Mark Wells noted ‘My other strongest recollections will be the way that he helped me learn how to write. I would spend hours struggling to find the structure, words, and phrases for drafts of my thesis chapters, before getting into my car and driving to Bigelow to see Bob. He would sit down with me at a table, side by side, pull out his pencil and work, sentence by sentence, through the entire draft. In his kindness, he would say after (almost) each sentence “this is good but...what if we were to say it this way...”’. With what seemed like no effort he would transform my text from blatherings to focused insight. Now trying to carry on this support for my students, I know the patience and endurance it required of him’.

Bob was extremely generous with about everything: his time, knowledge, ideas, lab space, equipment, and cultures. In his years at WHOI Bob mailed out hundreds if not thousands of cultures to scientists all over the world for free. His only request was that the mailers be returned to his lab so they could be used again. I visited his new lab in Bigelow in the early 1980s and was admiring a large lighted culture table with a thermostated circulating water bath that Bob and his student Larry Brand had constructed. Bob said ‘Take it, I don’t need it now that Larry has left for Miami’. So I hauled the culture table back to my lab in Beaufort, North Carolina, and used it in virtually all my algal-trace metal culture studies for the next 20 years. Diane Stoecker wrote ‘Sometimes I think he really made administration mad; he’d give things away to scientists that needed them to do research. He didn’t care which institution “owned” it, he focused on what would advance science, not just his lab or career. He freely shared his knowledge, ideas, cultures and equipment with students and colleagues. I am lucky I had him for an example. I think his openness and sharing was unusual among competitive oceanographic scientists’.

So that was Bob. His insight, kindness, and generosity will be sorely missed. But he has left us with a tremendous legacy in his culture collection, his culture methods, and his teaching, mentoring, and scientific discoveries.

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SUPPLEMENTARY DATA

Supplementary data associated with this article can be found online at http://dx.doi.org/10.2216/16-125.1.s1.

REFERENCES


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