Robert T. Paine

1933–2016

BIOGRAPHICAL *Memoirs*

*A Biographical Memoir by
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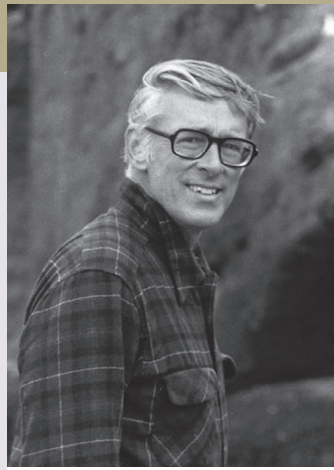
NATIONAL ACADEMY OF SCIENCES

ROBERT TREAT **PAINE**

April 13, 1933–June 13, 2016

Elected to the NAS, 1986



By Mary E. Power, James A. Estes, Peter Kareiva, Simon Levin, Jane Lubchenco, and Stephen Palumbi

Robert Paine changed the science of ecology profoundly. Fascinated with nature and greatly skilled as a naturalist, he took delight in linking results from field experiments to general, often novel concepts. Paine's development of the concepts of keystone species, trophic cascades, and patch dynamics are milestones in community ecology. He will long be revered for his remarkable humanity, including his devotion to and respect for students, both his own and the many others he encouraged and guided. Paine took a bachelor's degree in paleontology from Harvard in 1954. After service in the army he earned a Ph.D. in zoology from the University of Michigan in 1961 followed by a brief but influential postdoc at the Scripps Institution of Oceanography. He then joined the faculty of the University of Washington where he spent the remainder of his career.

Robert Treat Paine was born in Cambridge, Massachusetts, on April 13, 1933, the third of his name in a family line that extends back to the Mayflower and includes a signer of the Declaration of Independence. His father was a curator at the Museum of Fine Arts in Boston, an expert in Japanese art who co-authored *The Art and Architecture of Japan* (1958). After World War II Bob's father played a role in restoration efforts in Japan. Bob's mother, the former Barbara Birkhoff, was a writer and photographer and daughter of the famous mathematician George Birkhoff.

Bob's fascination with natural history was lifelong. Bob's early memories include sitting in the dirt driveway of his home at age 2-3, watching ants. As a boy, he roamed the then "wilderness" 30 miles west of Cambridge (now suburbia), watching birds and hunting earthworms, salamanders, and mushrooms. His expertise with birds was recognized at a young age by the most serious Boston birders of the day.

Bob as an expert teenage bird watcher, Massachusetts, circa 1950.

Bob's horizons expanded beyond the sphere of the Boston Brahmins when, with his mother's support, he struck out on a cross-country trip, arriving in Alaska and working for a summer in the salmon canneries. There he learned practical (and maritime) life skills and relished the society of fisherman and adventurers so very different from the intellectual upper crust of Boston. This experience left Bob feeling adventurous, self-confident, deeply irreverent, and able to enjoy, respect, understand, and communicate with people across the entire social spectrum. The lessons Bob took from his time in Alaska no doubt informed his later scientific protocols. When he became a teacher, he and his students pillaged hardware stores instead of scientific catalogues, and used dog dishes and inverted wire paper trays as field exclosures. They glued apparatus to the rocky, wave-tossed shores with Sea Goin'® Marine Epoxy Putty, and simulated perturbations with scrapers, blow torches, and jack hammers.

After earning an undergraduate degree in paleontology from Harvard University in 1954, Bob served in the army, then entered graduate school at the University of Michigan. Exposure to classes taught by ecologist Frederick E. Smith led to Bob's switching from paleontology to zoology, and with Smith as his graduate advisor, he studied a living fossil: a species of lamp shell, or brachiopod, for his 1961 Ph.D. In a conversation with one of us, Bob recently quipped "Freddie saved me from geology."

Bob with Cathy Pfister, jackhammering for her experimental installations in the rocky intertidal. (Photo by J. Timothy Wootton.)

In 1958 Bob did the field work for his doctorate on a small spit of land called Bay Mouth Bar, near the Florida State University Coastal and Marine Lab (CML) off the western Florida panhandle. When he arrived there with "few funds, no boat, and no place to live," the field station director, Dr. Harold Humm, welcomed him to free lodging and a boat to do what he was clearly prepared to do—study the ecology, range, and habitat of brachiopods and delve into the complex food web and predator-prey interactions of a diverse array of carnivorous snails (1). Several times over the last 10 years of his life, Bob returned to Bay Mouth Bar, bringing FSU graduate students and postdocs to dig for creatures under the sand. During this time Bob chaired the CML Scientific Advisory Board, providing wise counsel as well as forceful arguments to the FSU leadership for its support.

Following a postdoc at the Scripps Institution of Oceanography, Bob joined the faculty of the University of Washington in 1962, where he taught for the next 36 years. From the first time he saw the colorful, charismatic fauna and flora along and off the rocky coast of Washington State, he knew he had found a system that would allow him to test important nascent ideas in ecology, make new discoveries, and feed his love and fascination for nature in all its diverse forms.

Community ecology

Taking his departure point from population biology and natural history, Bob launched a penetrating study of community ecology, a field he described as "deceptively demanding" (3), pursuing the understanding of nature's organizing forces in species-rich communities. A quest for forces organizing complex communities entails, as Bob acknowledged (1994), sacrificing precision for the realism (sensu Levin 1966) needed for ecological prediction in fluctuating, heterogeneous, real-world environments. Communities contain co-occurring populations that "rarely if ever share common boundaries" (3, p. 4). Organisms are buffeted by fluctuating physical factors and disturbances, while interacting—directly and indirectly—with predators, parasites, competitors, and facilitators in food or interaction webs (4). To infer the processes underlying constantly shifting ecological patterns, Bob wrote, "one must intrude experimentally" (3, p. 4).

Bob was an adamant experimentalist. He clarified his view of the near necessity of experimentation in his 1994 book, *Marine Rocky Shores and Community Ecology: An Experimentalist's Perspective*, which was published in the Excellence in Ecology series on his receipt in 1989 of the international Ecology Institute Prize. After acknowledging that description may be an essential first step, Bob goes on to say (3, p. 2):

> *…I place little faith in inferences drawn about underlying processes culled from …observations: nature is too subtle, too many equally appropriate alternative hypotheses can be proffered to explain the observed pattern. Rather, I believe that ecologists must continue the task of disentangling Darwin's bank by experimentally exploring and expanding upon mechanistically understood interactions.*

This view led Bob to groundbreaking achievements, including an experiment that informed his revolutionary insight about ecological communities. Bob and his collaborators contributed three foundational concepts to community ecology. He also made major, early contributions to our understanding of controls over intertidal vertical zonation, and he expanded and clarified the use of "reference states" for evaluating ecological change. Here we interweave some backstories behind his scientific contributions with glimpses of his life chronology. We hope this memoir leaves readers with a sense of the inspirational scientist and mentor we revere, the well-loved and provocative friend we miss, and the delight and sense of adventure that arose unfailingly both from his approach to life and from science and nature.

Keystone Species—the ecological upstart

Bob's last year was also the 50th anniversary of his famous paper on ecological keystone species (1966). It is important to set the stage by describing the field of community ecology at the time of this publication. The then-dominant view in community ecology (and one of the only views based on quantitative theory) was that natural communities were structured by competition (5, 6, 7). Similar species "partitioned their niches"—chose their diets or habitats, arranged their diel (24-hour-cycle) activities, or evolved trait differences—to avoid competition for resources or reduce it to tolerable levels. Observations of slight differences in the life styles or traits of co-existing species were interpreted as confirmation that they were sufficiently divergent to avoid competitive exclusion.

According this view, species richness (the number of species in communities) was to depend on the length of "niche axes" for critical resources and how much overlap could be tolerated before competitive exclusion occurred. That richness, a key component of diversity, should, in turn, stabilize communities through several intuitive mechanisms: redundant control paths, more likely inclusion of at least some successful species, or, by having alternative species that could prosper and replace each other's ecological functions as conditions changed, buffering impacts of environmental fluctuation (7, 8). The last mechanism is now called a "portfolio effect" (8). In short, diversity (or richness) putatively provided ecological stability.

Bob's revolutionary rebuttal to this view was based on what he called *keystone species*. A keystone is the small, wedge-shaped stone at the apex of an arch that, once inserted, keeps the arch from collapsing. Bob may have been exposed to this architecture by his father, a curator of Japanese art and architecture at the Boston Museum of Fine Arts. What Bob meant by this phrase was shown in his first demonstration that certain species

Bob pointing to the keystone in a stone arch
(Photo by Robert Steneck.)

were ecological keystones. It occurred when he experimentally manipulated distributions of the carnivorous purple (or ochre) sea stars, *Pisaster ochraceus*, along the rocky coast of Mukkaw Bay at the westernmost tip of Washington State, across the Juan de Fuca Strait from Canada's Vancouver Island. At low tide, these starfish grip the rocky shoreline with thousands of tube feet. Bob pried *Pisaster* off the rocks with a crowbar and pitched them into the sea. Within two years after Bob and his team removed starfish from a stretch of shoreline, California mussels (*Mytilus californianus*) started to monopolize primary space of the rocky substrate that had formerly supported a rich biota of tunicates, anemones, sponges, mussels, barnacles, chitons, limpets, and various seaweeds. *Pisaster* feeds extensively on mussels, along with other prey, including barnacles, limpets, chitons, and snails. But lacking *Pisaster*, mussels are the competitive dominate for primary space. Where starfish were extirpated, mussels established a near monoculture[1] (but see 9), and local species diversity of the primary space occupiers collapsed. Along control shoreline areas where the starfish were not removed, the original diverse community persisted. Five years after the experiment began, when starfish removal was discontinued, the mussel-dominated community persisted, as mussels had escaped in size from starfish predation. Bob had discovered that one keystone species, the purple sea star, kept the diverse structure of its community from collapsing.

1 Species richness and other emergent properties of communities are often in the eye of the beholder. They may change if a community is viewed through different lenses, criteria, or filters (with different extent or resolution). The Paine effect of lowered diversity following predator removal (1966) pertains to the diversity of primary space holders. When Tom Suchanek counted smaller organisms (secondary space holders that attach to or move under or amongst mussels), he found that as mussels dominated, species richness increased "…because… (Mytilus) also happens to be a habitat-forming foundational species (Lafferty and Suchanek, 2016, p. 367)." Bob was well aware of effect of scale in ecological communities, which he viewed as arbitrarily circumscribed and resolved. "How, then," he asked, "does one justify identifying one style of ecological endeavor as 'community ecology' if there remains no agreement on whether or how a community might be identified, the extent to which it may or may not be organized, whether consistent emergent properties exist, or whether its boundaries in space (and time) can be specified? (Paine, 1994, p. 4)." As for many natural entities, operational definitions of communities must include measurement or scale specifications.

"Local species diversity," Bob wrote, "is directly related to the efficiency with which predators prevent the monopolization of the major environmental requisites by one species (10, p. 65)." Bob's first listing of general characteristics to be expected in a keystone predator included voracious feeding and the ability to check an otherwise competitively dominant prey—a species that would monopolize space if left unchecked. This upstart notion was a clear alternative to the prevailing view that system properties (that is, diversity) stabilize ecological systems.

Over the following decades, the charismatic term was widely co-opted and over-extended to describe almost any species considered to have strong impacts on communities (11). To prevent its loss of meaning (and to expand its use beyond predators), Stanford ecologist Hal Mooney convened a meeting with Bob and other researchers who had documented keystone impacts in terrestrial, marine, and freshwater ecosystems in a workshop in Hilo, Hawaii. After considerable discussion and debate, this group redefined keystone species as any species whose impact was both large and disproportionate to its prevalence in a community (12).

This widened the application of the term to non-predators, such as small but essential pollinators, cryptogamic flora on desert crusts, and pathogens. It reiterated Bob's initial distinction between keystones, on the one hand, and, other dominant species, which are also strong interactors, because of their large biomass. The keystone designation has practical implications. Keystone species demand management attention if they affect fundamental community or ecosystem properties, but could be overlooked due to crypticity or diminutive biomass. Bob, as last author on this 1996 paper, was, as co-author David Tilman commented at the time, the Alpha and the Omega of this foundational idea for ecology and conservation biology.

Trophic Cascades—why is that tree green?

In January 2016 a crew filming Bob in conversation with one of us—Jim Estes—perfectly captured Bob's look and tone of startled wonder as he recalled first grasping the import of a question posed by his Ph.D. advisor, Fred Smith, to a graduate class at the University of Michigan sometime in the 1950s. Looking out a window, Fred asked: 'Why is that tree green?' A girl answers 'Chlorophyll,' but Fred was asking the larger question of why herbivores had left green leaves on the tree…(13).

When we see lush regions and barren regions, we assume that resources (water, nutrients, light) and conditions (temperature, soil properties, climate) favor plant growth in the former area but not in the latter. These "'bottom-up explanations are sometimes correct, but often not. The importance of herbivores, and predators that can keep these herbivores in check, is usually underestimated because "top-down" interactions are typically invisible unless manipulations (or rigorous comparative studies) are performed (14).

Bob called the sea otter-sea urchin-kelp food chain the poster child for top-down *trophic cascades*—"trophic" being an adjective referring to feeding habits of organisms. Working in subtidal habitats off the Aleutian Islands in the Northeastern Pacific, Jim Estes discovered that where sea otters had been eliminated from their historic range by fur hunters, sea urchins proliferated, and were able to mow down subtidal kelp forests, leaving urchin barrens dominated by low-profile coralline algae and diatoms. Where otters were still present, they preyed on sea urchins, protecting kelp forests. Estes and colleagues documented myriad follow-on effects, as kelp forests provided essential habitat for fin fish and invertebrates and also prevented erosion of shorelines, enabling the development of mud flats that they then subsidized with organic detritus, supporting totally different ancillary food webs (15).

Bob introduced the term *trophic cascade* in his 1979 Tansley Lecture to the British Ecological Society (16), in part to emphasize how non-obvious connections through food webs would ripple and ramify, even across habitats, when certain key species were perturbed. Jim Estes's discovery of otter-mediated trophic cascades was supported by decades of subsequent research that spanned the range of sea otters from the Aleutians down to the central California coast. Archaeological records from Aleut middens in Alaska extended the trophic cascade inference back 5000 years (17).

Contrasts between the co-evolution of grazers and seaweeds in the northern Pacific, where sea otters or similar ancestors have lived for more than 5 million years, and the southern Pacific, where no such sea otter analogues have occurred since the late Miocene/early Pliocene (18), extended the inferred co-evolutionary consequence of trophic cascades back 5 million years. Strong evidence for trophic cascades with myriad important indirect effects has also accumulated in temperate and tropical terrestrial and freshwater ecosystems over the decades following Bob's crucial advice to Jim Estes over a beer in an Alaskan pub: "Ask not what the kelp forests are doing for the otters, but what the otters are doing for the kelp forest?" (19).

Patch Dynamics—the living landscape of the intertidal

In a creative, heuristic collaboration, Bob and theorist Simon Levin conceived, somewhat whimsically, of bare patches in the intertidal landscape as having life histories like individual organisms (20, 21) and, therefore, demography (like populations). The birth of a patch (ironically entailing the death of many organisms) occurs when wave sheer or log bashing creates bare space. As in many species, birth rates are highly seasonal (greater in winter). The patch "ages" through biological infilling, and it dies when infilling is complete. Death (infilling) mechanisms (and rates) depend on initial patch size. Small patches fill when surrounding mussels lean in; intermediate-sized patches close as peripheral mussels move into them; large patches fill their interiors only after larval mussels settle from the plankton and establish themselves. With these rates and initial states quantified, the Paine-Levin models predicted the age distribution and size structure of patches, with rich implications both for the maintenance of ecological diversity and for the evolution of life history phenologies in intertidal organisms. Nine years of field work in the intertidal validated the model's success. Much previous ecological theory was limited by assumptions of equilibria, which appear to be rare in nature. This early non-equilibrium model of a spatially dynamic landscape was a major advance, allowing the prediction of ecological patterns and "intimately associated biological events," an achievement requiring the deep partnership of a keen observer of natural history and ecological dynamics and a mathematically powerful theorist.

Controls on vertical zonation

Bob's passion for fieldwork and commitment to long-term investigation of the outcomes of ecological perturbations (those caused by experiments and those from natural causes), inevitably led him to a deep sense of place. For almost five decades, Bob and his many students, postdocs, and colleagues worked the rocky shores around the Olympic Peninsula of Washington State. On a salmon fishing trip in 1967 Bob found Tatoosh Island–an uninhabited rocky outcrop off Cape Flattery on the Olympic Peninsula and the most northwestern tip of the lower 48 United States. Tatoosh Island and the peninsula shorelines Bob studied belong to the Mukkaw Nation, and he remained deeply grateful through his life to the tribe for granting him access to study their lands.

Fieldwork on Tatoosh was challenging. During storm surges, boat access was impossible, and ecologists had to be lowered from helicopters. Scientists hefted all their supplies and equipment up 100 homemade steps to derelict Coast Guard structures that housed the scientists during their stay. The field work required "leaps of faith" across surge channels, maintaining footing on slippery algae ("the goddam *Hedophyllum*," as Bob called them), and surviving waves that overturned boats and threatened people clinging to the shore (Bob was once rescued by David Duggins after a rogue wave swept him off). Yet every two weeks during the summer, and at longer intervals in winter, Bob's group visited the island to conduct experiments and track changes. As Bob's eyesight deteriorated over his later years, he continued this work with the stalwart assistance of his daughter, Anne Paine.

Along with the work of Joseph Connell at UC Santa Barbara, Bob's experiments and decades of field surveys showed that opposing gradients of ecological control maintained vertical structure in the rocky intertidal. Physical stresses (desiccation, heat) limit species in the high intertidal zone, but give way to biotic control (by predation or competition) in the lower intertidal.

One frequent visitor to Tatoosh, Egbert Leigh of the Smithsonian Tropical Research Institute, suggested to Bob that he monitor the upper intertidal limit of the red seaweed *Mazzaella*. Thirty years of subsequent monitoring by Bob and his grad student Chris Harley led to a discovery that proved fundamental to our understanding of ecological response to climate change. A sudden, discrete drop in the upper-range limit of this seaweed was not well explained by gradually rising temperatures over these decades, but instead occurred during an episode when warm periods coincided with a period of unusually calm seas (22). A general lesson for ecologists who are focused on system collapse is that such abrupt ecological response to gradual climate change may be contingent on coincident stresses, rather than due to crossing a threshold of a single forcing factor—see also "Compounded perturbations yield ecological surprises" (23, written with subtidal ecologist Mia Tegner and boreal forest and fire ecologist Ed Johnson). Another enduring lesson for science management is written in the acknowledgments of the 2009 Harley and Paine paper, where the authors thank the National Science Foundation for financing decades of "underappreciated monitoring."

Bob's careful thinking about monitoring and reference states or baselines against which to assess the importance of physical or biotic perturbations (3) informed a thoughtful discussion of how ecologists and managers respond to environmental disasters like the Exxon Valdez oil spill of 1989 (24). The paper reviewed our limited ability to understand or even investigate the impacts of such disasters and the well-intentioned but often misguided cleanup and restoration attempts that sometimes follow them. "The few scientific conclusions that can be reached after six years of study and the expenditure of hundreds of millions of dollars," Bob et al. wrote, "suggest the inefficiency of the research effort and the squandering of a rare albeit unfortunate opportunity." Anticipating the inevitable, they went on to describe the "sorts of research and monitoring that we believe might be more useful when future spills occur, as they surely will."

"Thou shalt not commit jargon"

One of Bob's extraordinary gifts and legacies was his mastery of English prose. His writing is so vivid and original that those of us who knew him can still hear, in his written words, his unique inflections of surprise, droll humor, delight, wonder, astonishment. The writing made concepts into living, compelling ideas. Like Winston Churchill, Bob favored old, short words over Latinized terms. We would be surprised to see the verb 'utilize' in his writing. The term "patch dynamics" (21) was like Hutchinson's "contemporaneous disequilibrium," yet with eight fewer syllables, the punchy Paine and Levin phrase, backed up by considerable research, is the one that still lives.

Bob's doctrine stressed usefulness as well as simplicity. He held that the word "community" should be reserved for groups of co-occurring organisms that contained a food web. Lizards, plants, or birds of a locale are often called communities for no obvious reason except to inflate the importance of the sound of the language. These co-occurrences of a taxon in a time and place might better be called lizard, plant, or bird assemblages, or, perhaps even better, simply lizards, plants, or birds (of, for example, the West Indies). Bob's avoidance of puffery in conversation, speech, and writing was part of what made his scientific vision so vivid, clear, and compelling for others.

Bob was never afraid to take on scientific sacred cows. A delightfully unfiltered rant was transcribed by UW undergraduate students when they interviewed him in 2013 about receiving the Cosmos award (26). Bob:

> *It's turned out to be more time consuming than expected, not that I'm complaining. I have to give two lectures in Japan in which I'm going to discuss biodiversity as a false religion. All of the recent winners have talked about biodiversity as enumerating species and divining meaning from this…nature is a better term than biodiversity, and has inspired all sorts of art, culture, etc.*

Bob went on to describe his experiences as a postdoc:

I...did a one year post-doc at Scripps Institution of Oceanography where there was a clash between two really wonderful professors. One man said, 'you have to go out and sample the world and then use all the power of statistics—you sample it, you don't mess with it, then you mine and crunch the numbers and that describes a static structure of nature.' His work is forgotten, because the world changes.

The other man was...a physical chemist...He said 'you design equipment to understand the physical process you are interested in, you use the equipment to test a hypothesis and need to make a measurement only once. If it doesn't work, you lost, because you know the equipment is right. If it works, you learn something.' He said hypothesis testing and experiments are a vastly more satisfying and fun way of doing science. He was absolutely correct. So that's what I did when I came here...to the outer coast of Washington and thought 'my god, this is my playground.' There were lots of things that could be manipulated, there were wonderful patterns, and you could see interactions and you could change the structure of those interactions and in the process learn how nature works.

Robert T. Paine's 1979 portrait as President of the Ecological Society of America.
(Photo provided from ESA archives, courtesy of Katherine McCarter, Sally White, and Alan Covich.)

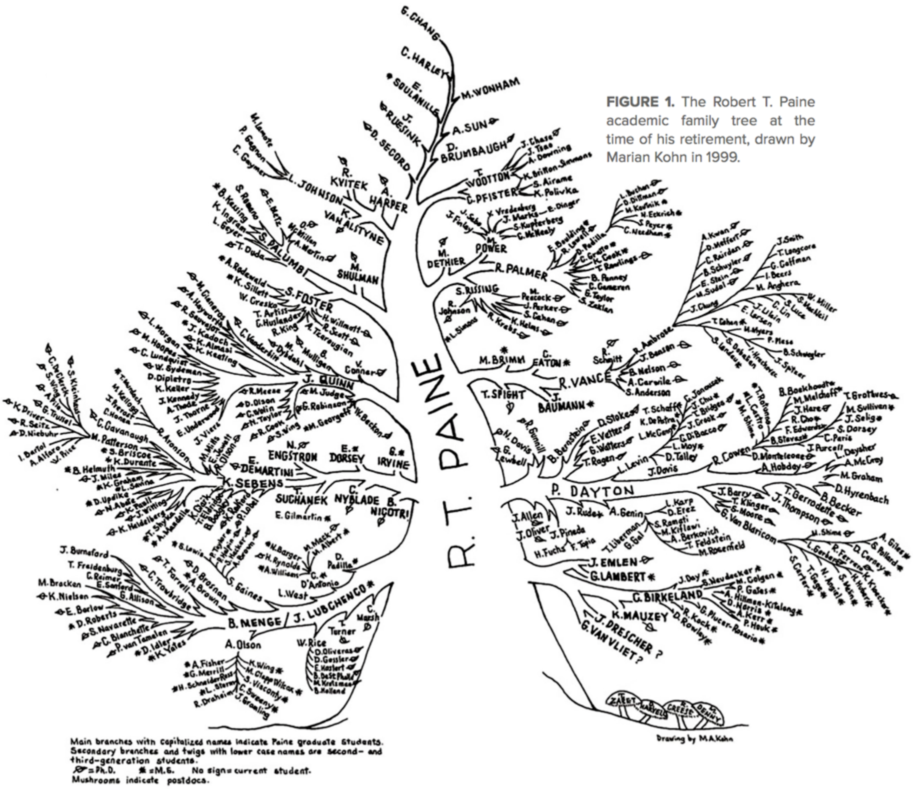


FIGURE 1. The Robert T. Paine academic family tree at the time of his retirement, drawn by Marian Kohn in 1999.

R. T. Paine III Academic Family tree drawn for his retirement celebration in 1999 by Myriam Kohn. (With permission from Alan Kohn.)

Honors and legacy

Bob was deeply ethical. He would not put his name on a scientific paper unless he had collected a significant portion of the primary data. He was grateful for decades of continuous support from the National Science Foundation, and extremely frugal in his use of these taxpayer dollars. The science-per-dollar ratio of his 50 years of intertidal ecological research was extremely high, due not only to the steady stream of insights and deep understanding emanating from his group's experiments and long-term data, but also due to the Spartan conditions they endured while doing fieldwork, often under physically challenging weather and ocean conditions.

A partial list of Bob's fellowships and honors includes: Lerner Marine Fellowship, American Museum of Natural History Fellowship (1959); Sverdrup Postdoctoral Fellowship, Scripps Institution of Oceanography (1961-1962); Third Tansley Lecturer, British Ecological Society (1979); AAAS Fellow (1980); John Simon Guggenheim Memorial Fellowship (1981-1982); Robert H. MacArthur Award, Ecological Society of America (1983); National Academy of Sciences (1986); the Ecology Institute Prize (Germany) (1989); honorary doctorate, Colby College (1996); visiting lectureship, British Ecological Society (1996); Sewall Wright Award, American Society of Naturalists (1997), American Academy of Arts and Sciences (1999); and the International Cosmos Prize (2013).

Far more important to Bob were his three generations of students, as well as the scores other young ecologists and field scientists, he inspired, commemorated in a R. T. Paine III Academic Family Tree drawn for his retirement celebration in 1999 by Myriam Kohn.

"After half a life-time of 'barnacle bites'…" Bob retired in 1998 (an event celebrated in colleague Alan Kohn's poem, "The Fiery Retiree"). He returned to campus regularly and established an endowment to support graduate research in experimental field ecology.

Bob died on June 13, 2016, the 83rd year of his remarkable life, of acute myeloid leukemia. Sean Carroll, the education director for the Howard Hughes Medical Institute, has written a remarkable little book, *Serengeti Rules* (2016), that follows the scientific discoveries of the control paths in molecular genetics that structure cellular metabolism, and those in ecology that structure ecological communities. (Hauntingly, the chapter celebrating Bob's work on food webs is preceded by the story of research by Janet Rowley (University of Chicago) on genetic regulatory mechanisms that determine whether leukemias, including acute myeloid leukemia, manifest, go into remission, or can be managed or even cured.) Carroll, remarkably, comments in this book (2, p. 6):

> *The tribe of molecular biologists, my tribe, is justifiably proud of their collective contributions to the quantity and quality of human life…But…A parallel, but less conspicuous, revolution has been unfolding as a different tribe of biologists has discovered rules that govern nature on much larger scales. And these rules may have as much or more to do with our future welfare than all the molecular rules we may ever discover.*

Through his last days, Bob was surrounded by his tribe—family, friends, and former students—with whom he swapped memories and natural history stories. He also completed an Ecological Monograph manuscript with Peter Kareiva and Simon Levin on the dispersal of spores of the seaweed *Postelsia* that reports three decades of research on this disturbance-dependent, fugitive species. He was interviewed at this time for a Howard Hughes Medical Institute film on trophic cascades, leaving us more eloquent and passionate insight about nature and science. He has left generations of scientists inspired and empowered to continue the vital work of understanding processes structuring our natural world.

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