

## In Memoriam

### Robert Treat Paine III (1933–2016), An Outsized American Naturalist

Brian R. Silliman,<sup>1</sup> Peter Kareiva,<sup>2</sup> and Catherine A. Pfister<sup>3</sup>

1. Division of Marine Science and Conservation, Nicholas School of the Environment, Duke University, Beaufort, North Carolina 28516; 2. Institute for Environmental Change, University of California, Los Angeles, California 90095; 3. Department of Ecology and Evolutionary Biology, University of Chicago, Chicago, Illinois 60637

“This changes everything!” reportedly wrote Robert MacArthur, one of the most influential ecologists of all time, in a handwritten letter to a young Bob Paine sometime in the late 1960s (Roberts 2016). How foretelling those three words would be for the field of ecology. At the time, Bob was an assistant professor of zoology at the University of Washington and had just published his now seminal 1966 paper on keystone predation in *The American Naturalist* (Paine 1966). Community ecology was thriving, with exciting discussions of how many species could coexist in any community and what factors governed the composition of communities. Two theories dominated the conversation. One was that intense competition drove populations to evolve smaller and narrower niches through time, ultimately resulting in more species packing into each habitat (MacArthur 1957). The other idea was physiologically based and posited that species segregated predictably along physical gradients—living where they did best, resulting in diversity patterns generated by physical forcing (Whittaker 1962).

Bob’s work showing that sea stars regulated species coexistence on rocky shores (Paine 1966) transformed the world of ecology for two reasons. First, he convincingly showed that consumers could be the keystones that maintained species richness in a community. Second, it helped to usher in a new era of field experiments and demonstrated the power of manipulations in nature (fig. 1). Although it would take another 20–30 years of dialogue and publications, ecology would shift in large part because of Bob’s findings, from one where physical factors were thought to predominately control species distribution patterns to one in which species interactions, as well as abiotic factors, did so.

Bob Paine’s research extended in influence far beyond rocky shores and inspired ecologists around the world to examine the role of predators in food webs from all kinds of ecosystems. While Bob admired the young Lindeman’s (1942) paper on energy flow in food webs that laid the foundation of ecosystem ecology and the view that communities were regulated overwhelmingly by bottom-up forces, he looked to the top of the food web. Bob Paine’s early and lifelong work, including a paper in *Science* in the early 2000s (Paine 2002), showed unequivocally that powerful trophic feedbacks occurred in ecosystems and could control not only diversity but also key functions, including primary production. His meticulous field investigations, aimed at unraveling the role of individual species, inspired generations of ecologists to look for and ultimately find top-down control in other systems, including kelp (Estes and Palmisano 1974), seagrasses (Moksnes et al. 2008; Hughes et al. 2013), rivers (Power 1990), salt marshes (Silliman and Bertness 2002), forests (Fortin et al. 2005), and grasslands (Holdo et al 2009). From his 50-year study of a single exposed shoreline on an island 4 hours from Seattle, Bob introduced to the world the revolutionary concept of keystone predation (Paine 1969), established firmly the power of experiments in ecology, and, in outsized ways, laid the conceptual and experimental foundations for modern-day food web ecology.

For his extraordinary contributions, Bob received many of the highest honors in science and biology, including election to the National Academy of Sciences (1986) as well as the Robert H. MacArthur Award (1983), the Sewall Wright Award (1996), and the International Cosmos Prize (2013). He also led the Ecological Society of America from 1977 to 1979 as vice president and then president.

But what Bob prized far more than any award, national position, or the recognition gained from his individual papers were the scientific discoveries and personal empowerment he made possible through mentoring. Bob mentored his students and postdocs to become intellectual entre-



**Photo 1:** Bob Paine with sea stars he removed from the predator exclusion area of the rocky shore on Tatoosh Island, Washington. Photo: Anne Paine.

preneurs—scientists who were self-confident and creative, who understood and respected theory, but who could also recognize when nature was showing them where theory was wrong or had stopped short. Mentoring his students rarely took place within the confines of an office. Instead, Bob talked to his students about ecology and science while exploring and conducting investigations in nature.

Braving high waves and unpredictable weather to land on the shorelines of Tatoosh Island using only a Zodiac and Bob's boating judgment, the Paine lab would visit the remote site 8–14 times per year, exploring and experimenting to investigate how species interactions shaped

the rocky shore community (fig. 2). Each evening, the lab would reassemble around a fire perched 100 m above the wave-swept shores on a rocky mount. Each student would pour a glass of their favorite beverage, and Bob would ask them a simple but poignant question: What did you learn today? Bob was not only interested in novel natural history observations but also in how what students were finding could inform ecological theory. His recipe was simple but in today's world of ecological science exceedingly rare: study one system for a long time; know the natural history of the species and the environment they live in so well that they are like family; know the eco-



**Photo 2:** Bob Paine (*left*) and former PhD student and now University of British Columbia professor Chris Harley take tidal height measurements on the shore of Tatoosh Island, Washington, in May 2006. Photo by A. R. Palmer.

logical literature well; use that deep understanding of local natural history and ecological theory to ask important questions; and, of course, employ experiments to test your ideas.

Time slowed down when you were with Bob. In long conversations, he freely gave you his curious and wonderful attention. Bob was huge in stature at 199 cm and had a big, caring heart to match. In the field, plopped down on slippery kelps, at his home in a lawn chair under a shady tree, with a bourbon and junk food in front of a fire, in his book-filled office, or in the hallways at annual ecology meetings, Bob always had time to discuss ecology and natural history (and was actually always looking for an excuse to do so). He would sit with you for hours and depart only if you departed from talking about exciting stuff: experiments, natural history, how to navigate the world of science, discoveries in ecology, and the Boston Red Sox. How wonderful it was to experience that generous gift of time that Bob so often gave, especially in today's world when communications are expected to be 140 characters or less.

In these talks, Bob was most keen to hear about, in his own words, what sort of "mischief and fun" you had been up to. What Bob meant was that he wanted to hear about what new thing you had learned about nature or ecology. This may sound daunting, and mostly it was. But knowing that this question was coming at your next meeting often changed the way you led your life. You had to be prepared to answer that question. That meant you had to get out

into the world and poke and prod nature and pay attention to the anomalies. Bob inspired everyone he came in contact with to avoid getting bogged down in administration (even though he himself served as chair as an act of service to his department), to never be self-satisfied with one's own success, and to explore through fieldwork and an eclectic wide-ranging reading of the literature what key ecological phenomenon was being underappreciated or misunderstood. After all, Bob would say, it was mischief and fun while exploring nature that inspired most of us to get into ecology in the first place. Remembering Bob's legacy reminds us to not only give the gift of time to those we are mentoring but to also give that same gift to ourselves, to nurture our own ties with nature and to give it the opportunity to influence us.

Bob's love of nature was heavily influenced by his mother, who wrote her master's thesis on Henry David Thoreau's nature-extolling book *Walden: Or, Life in the Woods*. She took him on many explorations and daylong retreats in the forests of New England. There he spent hour upon hour each summer of his childhood learning how to observe nature. By his teenage years, he had already become an expert natural historian of birds, an art he perfected throughout his life. No matter where he was in the United States, those around him were always astounded by his ability to identify birds by their calls, especially while in the middle of conversations on unrelated topics. One of our favorite stories about Bob is when, at

age 14, he climbed 30 feet up to get a bird's-eye view of an osprey nest; he was attacked by the female soon after he reached the top, but he got what he sought to find out: salmon was on the table for dinner. Bob attended Harvard as an undergraduate, where he was mentored by Ernst Mayr and nurtured his interests in paleontology. After Harvard and a 2-year stint in the army, Bob joined Dr. Frederick Smith's lab at the University of Michigan in 1957 to obtain his PhD. There, he listened to Smith talk about why he thought the world was green. He started to think about food web linkages. His dissertation focused on energy flow on sand flats in northern Florida. Two years of hot summer fieldwork revealed the feeding hierarchy among the large, predatory gastropods that prowled the shallows, as well as how many clams each population might be consuming. It was during those times on the vast sand flats of northern Florida that he began to ponder about the possible linkages among predators, trophic feedbacks, and community diversity.

Bob dove into nature wherever he was in the world. As an assistant professor, he sought out the most wild and energetic coast in Washington. There he found an astounding, species-rich community with conspicuous predators. He got right to work. This time he used experiments, inspired by the work of a physicist in California who espoused the power of manipulating systems to figure out what role its individual parts played in its structure. Almost 50 years later on the coast of Argentina, Bob accompanied a group of 40 Argentine and American scientists as they searched for sea stars (fig. 3). At that time in his life,

Bob's cataracts and worn-down knees made it hard for him to negotiate stairs, much less scramble through a rocky intertidal. Even so, as vans of students and senior ecologists (Ana Parma, Peter Kareiva, Brian Silliman, Jose Orensanz-Lobo, Jim Estes, Claudio Campagna) went from one coastal site to another, Bob was always the first one to be out on the rocky coast. His solution to bad vision and bad knees was to crawl across the rocky shore and use his hands for eyes. So there he was, at 77, down on his knees, searching for new natural history insights up and down the coast of Argentina.

Much of ecology now focuses on advancing theory through macroecological studies that concern global patterns and correlations, often with species lists as the primary data. Bob valued these perspectives but worried they were taking over at the expense of the nature-based, experimental approach. In fact, his address to the American Society of Naturalists in 2010, upon receipt of the Lifetime Honorary Member award, dealt with this very worry; he emphasized that the fastest and most effective way of advancing ecology was by probing via experiments the role of species at a local scale (hence, microecology) and how confirmation bias was likely to occur more often if in situ experimental ecology became a thing of the past and gave way to desktop, synthesis ecology and large-scale correlation studies only (Paine 2010). He emphasized the paramount role of coupling natural history with experimental ecology to identify the specific roles of species within ecosystems and the importance of that understanding for conservation, as well as how this approach, in particular,



**Photo 3:** *From left, Brian Silliman, Bob Paine, and Peter Kareiva chatting about their observations of the rocky shores of the Patagonian coast of Argentina. Photo: Brian Silliman.*

has helped to push the boundaries in ecological theory. Bob was widely read across ecology and evolution and espoused to his students the importance of trying to advance theory by figuring out how nature works. Theory to Bob tied the natural world together, but it needed to be relentlessly questioned and confronted with natural observations and field experiments to move forward. Continuing to follow his scientific recipe for understanding the role of species in communities will undoubtedly be essential for continuing to advance theory in ecology.

When Bob looked back on his career, he was most proud of the students and scientists he had mentored, both those officially in his lab and those he had “adopted”—something he did frequently. He wanted those he mentored to have as much fun as he had doing science and to be fearless in challenging conventional wisdom. When students or colleagues met with resistance and rejection, Bob was always there for support, especially if he thought their ideas were not being given a fair shot.

Bob’s influence through mentoring now stretches the globe. He helped kick off experimental marine ecology in South America and New Zealand, and his mentees discovered top-down control in kelps, coral reefs, rivers, vegetated shorelines, and under the ice in the arctic. His academic tree (<http://academictree.org/mareco/tree.php?pid=26165>) is immense (with >30 PhD students) and always astonishes. When preparing to introduce Bob for a seminar, it took a very short time to realize that most heroes (although Bob would scoff at the use of that word) in marine ecology had come from his lab in one way or another. And his visits to give seminars were always highlights for the year for anyone involved; he would spend days on a university visit, overwhelmingly focused on graduate students, asking about their work and giving feedback. He was very reluctant to talk about his own work. He was not there to tell his story but to help others be inspired by nature and ask them tough but empowering questions that helped them refine their ideas and incorporate and push forward theory.

Bob had endearing rules of engagement, probably heavily influenced by his New England upbringing, involving properly recorded data, specific placement of quadrats and fake mussels, how long to chill cheap white wine, when to have happy hour, how to churn the ice-cream maker, and the exclusion of any spice from meals. Indeed, one graduate student on Tatoosh Island termed it TWID—“The Way It’s Done”—when anyone challenged a convention or tradition. But Bob always had fun exceptions and a playfulness about rituals and tradition. He would push back all meetings to watch the Boston Red Sox; at Zoology faculty meetings, as the chair, he would place a large laboratory timer in the middle of the conference table to make sure the meetings did not drag on and his colleagues did not

“profess” for too long; he would encourage everyone to eat as much ice cream as they could—even as it made them almost immobile; and he would stop anything and everything to watch a bird or to help a friend in need. The one tradition he never violated was supporting the free exchange of ideas.

We and all of Bob’s family are deeply saddened by his passing. But we are also filled with inspiration and immense gratitude. We thank Bob for his guidance, his care, and the gift of great joys that are found in discovery and the small.

### Acknowledgments

We thank Anne Paine for her helpful comments and contribution of wonderful photos.

### Literature Cited

- Estes, J. A., and J. F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. *Science* 185:1058–1060.
- Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86:1320–1330.
- Holdo, R. M., A. R. Sinclair, A. P. Dobson, K. L. Metzger, B. M. Bolker, M. E. Ritchie, and R. D. Holt. 2009. A disease-mediated trophic cascade in the Serengeti and its implications for ecosystem C. *PLoS Biology* 7:e1000210.
- Hughes, B. B., R. Eby, E. Van Dyke, M. T. Tinker, C. I. Marks, K. S. Johnson, and K. Wasson. 2013. Recovery of a top predator mediates negative eutrophic effects on seagrass. *Proceedings of the National Academy of Sciences of the USA* 110:15313–15318.
- Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. *Ecology* 23:399–417.
- MacArthur, R. H. 1957. On the relative abundance of bird species. *Proceedings of the National Academy of Sciences of the USA* 43:293–295.
- Moksnes, P., M. Gullström, K. Tryman, and S. Baden. 2008. Trophic cascades in a temperate seagrass community. *Oikos* 117:763–777.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* 100:65–75.
- . 1969. A note on trophic complexity and community stability. *American Naturalist* 103:91–93.
- . 2002. Trophic control of production in a rocky intertidal community. *Science* 296:736–739.
- . 2010. Macroecology: does it ignore or can it encourage further ecological syntheses based on spatially local experimental manipulations? (American Society of Naturalists Address). *American Naturalist* 176:385–393.
- Power, M. E. 1990. Effects of fish in river food webs. *Science* 250:811–814.
- Roberts, S. 2016. Robert Paine, ecologist who found “keystone species,” dies at 83. *New York Times* (June 17).
- Silliman, B. R., and M. D. Bertness. 2002. A trophic cascade regulates salt marsh primary production. *Proceedings of the National Academy of Sciences of the USA* 99:10500–10505.
- Whittaker, R. H. 1962. Classification of natural communities. *Botanical Review* 28:1–239.