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PERSPECTIVE

PHYCOLOGY FOR THE ECOLOGIST[1]

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Fifty years ago, Robert Treat Paine published his seminal paper on food web complexity and biodiversity (Paine 1966). In this work, Paine used sea stars to illustrate how relationships among species were key determinants of emergent ecological patterns, and in doing so, he injected a healthy dose of testable mechanism into a field that was largely phenomenological at the time. The case of the sea star *Pisaster ochraceus* as a keystone predator (Paine 1966, 1969) remains a standard example in Ecology textbooks, and undergraduates who take ecology courses today are likely to associate the name Paine with starfish. But Paine made many more significant contributions over the course of his career, and it was not all about *Pisaster*. For while he remained committed to answering the big questions in ecology as his career progressed, Paine largely shifted his focus from sea stars to seaweeds. What was it about seaweeds that attracted him? What does phycology have to offer ecology, and vice versa?

Bob Paine's phycological interests were clearly on display, both literally and figuratively, the first time I walked into his office as a prospective graduate student some 20 years ago. He did not regale me with tales of voracious *P. ochraceus*, or show me shells of the species that *Pisaster* prefers to eat. Rather, he reverently opened his drawer full of "epoxy patties" upon which he had out-planted crustose coralline algae to explore their ecological relationships (Fig. 1). For Paine, coralline crusts represented an ideal system in which to test the importance of competition in ecological communities, and the degree to which the determinism of competitive outcomes were influenced by other species, particularly grazers (Paine 1984). Paine's phycological work extended to numerous other taxa, including erect corallines (e.g., Johnson and Paine, this issue), fleshy red algae (e.g., Paine 1986), and intertidal kelps (e.g., Paine 1984, 1992, 2000), and his seaweed research has greatly informed our understanding of fundamental ecological issues, some of which are discussed in more general terms below.

Why did Paine direct so much of his energy toward coralline crusts and other algal species,

which on the surface seem less charismatic than large purple sea stars? One reason was surely the ecological significance of macroalgae—the importance of kelps in nearshore systems is beyond dispute (Steneck and Johnson 2013), and even seemingly less grand species like coralline crusts are ecologically key as habitat in rhodolith beds, as recruitment surfaces for invertebrates, and as cement in otherwise unstable reef systems (Nelson 2009). The ecological importance of seaweeds notwithstanding, I believe the predominant explanation for Paine's increased emphasis on seaweeds is that they offer some of the best opportunities to

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answer key ecological questions. Kelps like the sea palm *Postelsia palmaeformis*, with their limited dispersal, make excellent subjects for studies on demographics, extinction risk, and the importance of genetic diversity (e.g., Wootton and Pfister 2013). Kelps and coralline crusts, with their easily observed competitive outcomes, are ideal for studying competitive strategies and the role of herbivores in competitive relationships (Paine 1984, 1990). Variation in the strength of trophic interactions, long a topic of ecological interest, is often best exemplified by algal–herbivore interactions (Paine 1992). Finally, ongoing ecological responses to global change are often well-recorded in seaweed herbarium records (Wernberg et al. 2011), and our understanding of future ecological change can be greatly enriched by experimental manipulations in seaweed-dominated systems—in the Paine tradition—to establish mechanistic relationships between species and their environment (e.g., Connell and Russell 2010). Developing this long-term perspective brings us back to Paine's drawer full of coralline crusts, which had been vigorously competing with one another for space but became frozen in time at the date of their collection. How many other researchers can claim to have intricate preserved records of biological interactions lying around in their offices? This physical record, as it turns out, was just one more benefit of working with crustose coralline algae, as another phycologist was able to use Paine's patties to study the effects of long-term pH change on coralline crusts over a three-decade span (McCoy 2013).

Clearly, seaweeds are a boon for the ecologist. And just as phycology has much to offer ecology, ecological ideas are becoming more prevalent in the field of phycology. This integration was not necessarily rapid or seamless, in part due to the different cultural traditions in the two fields. Through the 1980s, ecology was heavily focused on experimental manipulations in the field with a strong emphasis on interactions among species. Phycology was often more physiological, developmental, functional, or taxonomic. Researchers like Paine that considered algae in the context of the ecological communities in which they were embedded were referred to as "zoological phycologists," a term that was not necessarily a compliment. However, the cultural landscape within academia continued to change, many botany and zoology departments merged into biology departments, and scientists began working across formerly entrenched disciplinary traditions. One excellent example of this cross-fertilization came at about the time Paine retired. He was invited to speak at the American Society of Mammalogists meeting, presumably on the topic of mammals. Although the organizers may have been hoping for a talk on sea otters, an animal that rivals *Pisaster* in ecological lore, what they got was a primer on seaweeds. Paine's presentation and the subsequent publication (Paine 2000) was entitled "Phycology for the Mammalogist" and used seaweed examples to illustrate what terrestrial ecologists may have been missing in terms of the determinants of ecological pattern in mammal-dominated systems. To what extent have grazers been overlooked when considering nutrient cycling or plant succession? Can rabbits or bison have the same effect on vegetation structure and diversity that chitons and urchins do? The fact that mammalogists stood to learn something from phycologists is emblematic of both the increasingly well-established connections across disciplines and also the future progress we have yet to make in environmental science.

Given Paine's contributions to our greater appreciation of the fascinating biology and ecology of seaweeds in general and of coralline algae in particular, it is only fitting that *Crusticorallina painei* —the generitype for a newly defined genus of coralline algae—is being named for him (Hind et al., this issue). The Hind et al. study clearly illustrates the challenges of working with this group from a taxonomic perspective. But their work also provides an excellent example of how modern molecular techniques can enable dramatic advances in our understanding of evolutionary relationships within a taxon, biodiversity within a region, and biogeography of individual species, all of which bring us one step closer to unveiling the ecological roles that distinct species play in marine communities. Taxonomic advances such as those made by Hind et al. are helping to fulfill the decades-old vision of Adey and Macintyre (1973), who opined that once taxonomic challenges were resolved, coralline crusts had strong potential as "popular subjects" in ecological studies. As it turns out, Paine had conducted research on one or perhaps multiple cryptic species in this newly described genus, although they were formerly lumped under the name *Pseudolithophyllum muricatum*. There is much yet to be learned about this ecologically important group—perhaps Paine's patties will be pressed into service yet again.

Bob Paine passed away on June 13, 2016. He learned of Hind and her colleagues' work on *Crusticorallina painei* shortly before he died, and was deeply honored to have a species named after him. But Bob placed far more value on ideas than on his own personal recognition. What will we learn of *Crusticorallina*'s role in the ecology of rocky shores? How will ongoing environmental change impact this genus, and what will be the cascading consequences to the species that compete with it, consume it, and rely on it for settlement? Let us hope that *C. painei* will stand to remind us of the rich interconnections between phycology and ecology, and of all that seaweeds may yet teach us.

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