Adventures scaling the realized niche, saving the world, and searching for values

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I describe my unlikely path into marine science from a childhood in the Arizona desert and Oregon woods. Without realizing it, I developed a sense of place in nature and the value of open interdisciplinary communication among diverse scientists. My undergraduate education emphasized physiological adaptations to the environment or what might now be considered the “fundamental niche”, and my graduate thinking was inspired by a population/community based evolutionary understanding of how strong interactions define a “realized niche”. I have attempted to define strong interactions in three different ecosystems. This difficult problem is confounded by the loss of natural systems resulting from human impacts. I discuss my frustrations with eroding conservation efforts in a society that is rapidly devaluing nature and consider how we might recover our most fundamental values. I conclude that there is an urgent need to improve field-based teaching of undergraduate non-majors about nature and to be much more effective in our interactions with the general public. If we hope to have our legacy include a liveable world with natural places, we urgently need to act unilaterally to shift some of our values and reward systems towards the challenge of educating the undergraduates and especially the general public.

Keywords: citations, ecological processes, interaction strength, marine biology, natural history, value systems

Foreward

Science is a human endeavour driven by curiosity about our world. We are proud of our accomplishments and are anxious to share our insights. Lost in the normal scientific discourse is the human dimension that drives our individual science. What inspired us to forgo other careers? How did we learn about doing science? What are the natural processes we find most interesting, and how did we define our questions and methodology. To err is...
human; how do we learn from our errors? What are we most proud of, and why? What would we do differently if we could try again? Looking back, what were the highs and lows of our human experience doing science? How did these emotions influence our science? I look to the giants in science and wonder what they were really like as human beings? What were their long-range goals and how did they approach their basic questions? Here, I attempt to integrate my personal development with my ecological research. I discuss the three ecosystems I have studied and review some of the methods that helped understand the strong interactions and how they scale in space and time. In most cases, I have had to rely on natural history to define the appropriate questions.

We will never understand the manifest complexities in community ecology, never disentangle Darwin’s tangled bank, without the benefit of the intuition and biological appreciation garnered by studying nature the way it has evolved, rather than the alternative and dismal shadow associated with accelerating human intervention (Paine, 1994).

Discovering nature while learning to read
My father worked outdoors on Arizona ranches, in mines and, eventually, in logging camps in southern Oregon. I spent my early years mostly alone in nature until I was unsuccessfully thrust into a one room-school in Drew, OR, a tiny logging town. As a hopeless dyslexic, I was dysfunctional and clueless in that rough environment and became the punching bag for the school bully. “Paulie, just try to see the world through his eyes” was the advice my mother offered. However, I was strong for my age, and once I learned how, I derived much more pleasure from beating the shit out of Butch rather than understanding him (forgive me dear reader for the language, but it describes the event); but for a 6-year old coming from the Arizona desert, the Oregon woods were much scarier than the bully and nature was my main adversary. At that time in my life, we and the families around us killed or grew much of the food we ate and nature was something that needed to be exploited, tamed, or modified by clearing gardens, finding food, and eliminating danger. My attitude towards nature was much like it was towards Butch, something to be conquered.

Until I learned to read, much later, I avoided school and spent most of my time in different natural habitats and, without thinking about it, I acquired a rough sense of place at an early age. My mother’s advice finally took hold as I learned to empathize with nature and to understand her. At first, my sense of place lacked the sensitivity, the understanding that my mother advocated for the bully. However, as I learned to consider the plants and animals from their perspective, I developed an awareness of their individual habitats, behaviour, and environmental needs to survive, grow, and reproduce.

The family began making winter trips to San Carlos Bay, near Guaymas, Mexico, where I learned to snorkel and discovered an utterly new world. By age 10, I had a good understanding of terrestrial natural history, but this marine environment was totally different, and more scary, than the bully or the woods; but there was still the challenge to understand it, and when the family returned to our roots in Tucson, AZ, near the Gulf of California, I was able to spend a great deal of time in the water learning a very different natural history integrated with the observations in Steinbeck and Ricketts (1941). At first, my objective was killing things to eat, but with the familiarity came the empathy and understanding of this system.

Cousteau’s Silent World (Cousteau and Dumas, 1953) was an inspiration, and by 1956, I made my own scuba equipment from discarded tanks stolen from a junk yard, a B-29 regulator, and simple pipe from a hardware store. This rig almost killed me, but not before it gave me enough time underwater to begin to understand and empathize with the behaviour of the marine animals from their perspective and to develop a sense of place for this strange new world.

By the 1960s, people were using scuba to over-exploit the large fish and badly damage the gorgonian habitats that so fascinated me and I developed an obsession with becoming a marine biologist. Eugenie Clark and Rachel Carson were marine ecologists I could relate to and, when I read Carson’s Silent Spring (Carson, 1962), I realized how important it was to develop a scientific understanding sufficient to protect the marine systems. The dyslexia prevented me from understanding abstract processes such as learning languages, or worse, mathematics, but I did understand natural history, and I hoped that might be enough for me to become a marine ecologist.

Cooperation and the value of interdisciplinary research
On returning to the family roots in Tucson, we spent much of our time with old family friends from the University. My grandfather arrived in Tucson in the 1920s as a professor at the University of Arizona and then an isolated little school in the desert. In those days, some of the professors met regularly to discuss their research and ideas, and these interactions persisted through my youth. A.E. Douglas and Ed Schulman developed dendro-chronology as a means of dating old trees. They were interested in sunspots and climate, but Emil Haury, an archaeologist, was fast to recognize the value of precise dating, and this precision revolutionized archaeology and is still invaluable for such things as dating the Anasazi migration. Haury and others were also excited about finding Clovis spear points in local mammoth bones demonstrating that early humans were able to kill even the largest mammals. Paul Martin, then a palynologist, inspired by the mammoth sites, used his precise understanding of Holocene climate and astute natural history to develop a theory of overkill to explain the massive Pleistocene/Holocene extinctions in North America. This too revolutionized Pleistocene/Holocene ecology by forcing us to recognize the role of humans in extinctions. Rod Hastings, the mayor of a small mining town (and a meteorologist connected with the University scientists), realized that the old archived photographs of the region showed large-scale changes, and he hooked up with Ray Turner, a brilliant desert ecologist, and together they developed a regional understanding of a changing desert biota by comparing old and recent photographs (Hastings and Turner, 1965). This too resulted in a growth industry of scientists extracting valuable data from archived photographs. This continuum of paleo to historic to recent ecological synthesis was tested and modified by Paul Martin and others at the Desert Research Lab as they developed the science of analysing packrat middens to permit a very precise understanding of the distribution of vegetation through the last 30,000 years. These techniques have been used worldwide to evaluate ecological changes from the Pleistocene through historical time scales.

As I went through high school and college in Tucson in the 1950s, I knew these people as family friends, and I was able to watch this remarkable community of scientists interacting across
that included competition for primary space and sunlight, many place I had for the desert and Oregon woods, but the intertidal the state spending every low tide trying to develop the sense of terrestrial-based type of ecology familiar to me. I drove all over Paine on the intertidal system that seemed appropriate to the University of Washington, where I decided to work with Bob

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Empathizing with nature to understand her Searching for a career

During my undergraduate years at the University of Arizona, I received excellent ecological mentoring from Bob Bezy and other students in Chuck Lowe’s laboratory as well as from Bill Heed, a Drosophila ecologist. At this time, the field of ecology was shifting into the ecosystem emphasis promoted by the Odum’s textbook (Odum, 1953), but in Lowe’s laboratory, there was an emphasis on environmental physiology, especially the role of temperature in defining “niches”. By being exposed to both approaches, I was well grounded in an intuitive understanding of what might be considered the “fundamental niche” of optimizing the physiological needs of the organisms. At the time, I tried unsuccessfully to generalize and apply this perspective to marine systems.

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Intertidal ecology: learning to define questions

On my return in January 1965, I went to graduate school at the University of Washington, where I decided to work with Bob Paine on the intertidal system that seemed appropriate to the terrestrial-based type of ecology familiar to me. I drove all over the state spending every low tide trying to develop the sense of place I had for the desert and Oregon woods, but the intertidal was all new to me, and I was overwhelmed with the complexity that included competition for primary space and sunlight, many types of predation from cryptic flatworms and nemertean, many snails, nudibranchs and crabs, grazing molluscs and crustacea, patchy predation and grazing by asteroids, and urchins, as well as interesting kleptoparasites stealing prey from snails and asteroids. More confusing, each of the many different intertidal habitats in the region was very different from the others.

I was utterly overwhelmed with the seeming chaos of the system and had no idea how to begin a thesis. It was clear that I still did not really understand how science works. The ranchers, prospectors, and loggers of my youth knew a tremendous amount about the natural history of their systems, as did the Native Americans I spent time with, but for the most part they were not interested in generalizing processes. In graduate school, Gordon Orians and Bob Paine introduced me to an evolutionary rather than physiological approach to ecology. Platt’s (1964) paper on strong inference influenced my attempt to disprove hypotheses. I learned that, in ecology, our goal is to make interesting and accurate generalizations about nature based on as few relevant parameters as necessary. The idea of narrowing down the relevant parameters is critical because all nature is somehow related, but the trivial or marginally important relationships need to be weeded out so as to focus on those parameters essential to the generalization. Identifying the appropriate simplifications is critical and cannot be done without a deep sensitivity to the relevant natural history of the systems we study.

Most of the elegant competition-based models of the era seemed interesting but also irrelevant to the reality that I observed as I crawled around the rocky shores. The more I explored, the more I appreciated the complexity of the system that was also difficult to relate to Paine’s (1969) keystone predator perspective that emphasized the importance of a predator reducing the impact of the top competitor in the system. This only applied in relatively rare mussel dominated intertidal habitats exposed to unusually heavy wave exposure where mussel recruitment was much more common. Indeed, few of the various intertidal habitats I visited seemed functionally similar to each other and it was difficult to generalize the processes that I observed from place to place. All of the habitats were strongly influenced by disturbance, but these disturbances ranged from extreme temperatures and desiccation to various predators, to physicalashing by drift logs to grazing and bulldozing by limpets.

Desperate to start my thesis, I was overwhelmed by this seemingly chaotic world. Happily, I was lucky to be surrounded by a group of fellow graduate students who listened and asked questions and very much helped me focus on a thesis based on the most important species for which primary space would be an easily quantified potentially limiting resource and the environmental factors that controlled their distribution and abundance. There were two zones: a higher barnacle and mussel zone and a lower zone dominated by many species of algae.

My 1950s era ecology education had stressed the importance of understanding successional processes, and this required a focus on recruitment (survivorship to reproduce) processes that represented a slight but important difference from the then-popular focus on competition or predation paradigms of the time. Settlement and survivorship seemed to be generally important processes, and I concentrated on facilitation, long a critical cog in the old succession literature. There was a great deal of evidence for various types of facilitation, including filamentous algae hosting many types of larvae, especially the important mussel larvae, or coralline algae chemically attracting larvae and inducing
metamorphosis, many species offering protection from desiccation, etc. Indeed, facilitation worked both ways as it enhanced the predation on barnacles by whelks in limited areas when the whelks escaped desiccation during spring tides by sheltering in clones of anemones.

In hindsight I realize that I was applying my mother’s advice of seeing the world through the physiological and evolutionary “eyes” of the organisms. It is relatively easy to empathize with animals as they balance their need to procure resources and avoid risks, but this was difficult with the seaweeds that were important players in my intertidal world. Their competition for space and light was obvious, and Vadas (1968) had studied the chemical defences in algae, so I was well aware of defence tactics of algae, but I struggled to see the world view of the small, sometimes filamentous little sea weeds with such bedazzlingly complicated life histories. It was hard to imagine their physiological and ecological needs. Yet, in some cases, they were important players, overgrowing other organisms or serving as nurseries for larvae of important animals such as mussels.

I also realized that the physiologically optimal habitats did not necessarily reflect the actual realized habitat for the species. To be sure, many species have the strongest interactions in habitats to which they are physiologically well adapted. However, in some cases, the physiologically optimal habitat was very different from the habitat where the species was most abundant and dominant (see footnote 1 in the Supplementary data).

This confusing kaleidoscope perspective emphasized the importance of testing hypotheses, not necessarily with the then-popular controlled experiments, but also by comparing observations in the field among habitats and/or across times. I struggled to define hypotheses that were amenable to crude experiments or tests across several intertidal environments. When I succeeded, these experiments demonstrated that some species played stronger roles in the community than other species and they laid the groundwork for studying multiple interactions with varying ecological roles. Most species apparently could be removed without much consequence to the community. More importantly, it was virtually impossible to generalize the strengths of these roles (or dominance as I referred to it then) across spatial and temporal gradients.

Despite the insights drawn from these field experiments, they are but one tool in our tool kit as we strive to understand nature. Careful natural history studies covering large areas and observations over long-time periods offer extremely important insights about prioritizing various mechanistic processes (Able, 2016). Hastings and Turner (1965) successfully synthesized their photographs, natural history observations, and relevant literature to test many existing hypotheses about environmental forcing factors such as fire, grazing, and climate in the American and Mexican Sonora Desert. Unfortunately, even these extremely valuable data are often ignored because many ecologists demand unnecessary tests of and focus on analytical statistics with unnecessarily rigorous restrictions eliminating or devaluing the use of appropriate and important natural history observations (see footnote 2 in the Supplementary data).

Antarctic benthic ecology: lessons from flawed questions
After wintering over in the Antarctic, and as I began my intertidal thesis project at the University of Washington, I wanted to follow up on the example of Verne Peckham who had earlier demonstrated that scuba-based research under the ice at McMurdo Sound was feasible. With the encouragement of George Llano, the best programme manager I ever knew, I persuaded Bob Paine to front an NSF proposal to do a diving project at McMurdo. My proposal was based on remarkable early programmes by Dearborn (1965) who detailed the benthic biota of the area and Littlepage (1965) who described the coastal physical oceanographic processes. Littlepage’s thesis was decades ahead of that field and emphasized the remarkable stability in temperature and oxygen, the processes I considered important at the time. My 1966 proposal was designed to test the relative roles of predation vs. competition in light of the deep-sea ecology controversies of the era, and it was based on the use of cages designed to selectively exclude or include predators to test the roles of predation by fish and seals. I discuss this long-term programme in some detail to demonstrate the importance of learning from and responding to mistakes, to emphasize the importance of being sensitive to spatial and temporal scales and to relate a few lessons of general interest.

The first few 1967 dives in wet suits were memorable. You drop into a dark hole in thick ice, pull yourself down a weighted line, the cold hits your face and stuns you, but this is quickly forgotten in the excitement. As you move below the 2–5-m thick ice your eyes adjust to the darkness you are overwhelmed with the water clarity—the bottom, the distant shore, and a few jelly fish pulsing along in the distance. It is as if you are swimming in air! We immediately discarded the assumption of a totally stable homogeneous habitat as we could see that the bottom was obviously zoned by ice disturbance that extended to depths of 30 m. Thus, we found ourselves working between 30 and 60 m, much deeper than we had anticipated. Our natural history observations persuaded us that my goal of studying fish and seal predation was totally irrelevant to the sponge dominated community below 30 m, and we had to completely drop those questions and refocus on sponges and asteroids, their most conspicuous predators. We installed some 60 cages to a depth of 60 m assuming that sponges would settle and grow and that asteroids would eat enough prey to measure consumption, and we would have clean results when we returned.

Antarctic sponges turned out to be more complicated. When we returned in 1968, almost nothing had changed: no growth, no measurable predation, and brooding asteroids still had eggs that seemed to be the same stage of development as they were the year before. Still another critical assumption was spoiled by natural history. I still remember the first few dives the next season that had started with such high expectations of describing competitive relationships and predatory impacts only to realize that nothing had happened, and how acutely disappointed Gordon Robillard and I were as we sat in the ice hut contemplating our failures. We had made over 200 deep dives the year before in marginally functional wet suits with nothing to show for it.

Faced with an almost complete failure of our experiments, with the exception of a single cage that was overloading with a fast growing competitively dominant sponge, we had to retrench once again and apply ecosystem procedures to evaluate energy flow through trophic levels to estimate sponge consumption by the various predators. With this in mind, we used crude measures of potential energy channelled into growth, reproduction, and respiration to estimate the actual consumption of the various asteroids. We had tagged enough asteroids to estimate growth, and we measured gonad indexes and respiration, which gave reasonable estimates of the energy budgets of the predators. We also...
had to collect and process the sponges for bomb calorimetry, done later in Paine’s laboratory by my wife, Linnea. Our paper (Dayton et al., 1974) offered the overwhelming conclusion that the sponge predators were not in any sort of steady-state relationship with their prey, another important preconceived idea of stability disproven by nature (see footnote 3 in the Supplementary data).

When evaluated over decades, my long-term assumption of a stable environment also turned out to be spectacularly wrong (Dayton et al., 2019). At first, the community enjoyed a relative stasis with very little recruitment or growth. Dozens of artificial substrata were deployed in the water column at several different sites for some 30 years with virtually no sponge recruitment, despite the fact that they were removed from the benthic predators. However, in about 2000, following an environmental perturbation involving iceberg-blocking advection of large phytoplankton and sea-ice melting induced by oceanographic changes, there was a massive settlement of a wide range of sponge species on the artificial substrata but almost never on the natural substrata (Dayton, et al., 2016). Most of these were rare species implying that, when conditions were right, there was effective dispersal and recruitment. This suggests that the availability of propagules of these species had been missing for two decades and/or that the propagules were there, but the facilitating environmental factors (probably appropriate food) were limiting. Their absence on natural substrata in the presence of strong recruitment on artificial substrata implies that these propagules were vulnerable to unknown benthic predators, probably including the agglutinated foraminifera, a group ignored by most benthic ecologists. And as with all the other habitats I studied, none of the generalizations travelled well as the benthic associations at McMurdo Station were very different within a few kilometres (2–5) to the north and south. There, the differences were driven by ice conditions, especially the amount of snow that accumulated on the surface of the ice. In this sense, the local wind fields strongly influence the composition of benthic communities by affecting benthic productivity.

All of these programmes were begun in the 1960s, and as my career moved along, I developed my questions by mentally asking the organism how it best maximized fitness. This usually led me to focus on recruitment processes, long the emphasis of the fishery literature, but often forgotten by those working in other systems. In my case, I focused on the species that seemed to be the most important players in the communities. The successful settlement and survival of their propagules was influenced by a myriad of physical–biological interactions that were often not apparent from the experiments (see footnote 4 in the Supplementary data).

**Kelp ecology: the importance of oceanographic processes**

Without mathematical never thought that I was qualified for an academic position, but I applied for, and was surprised to get, a job at the Scripps Institution of Oceanography in 1970. I had long been intrigued with subtidal kelp communities because of the apparent parallels with terrestrial forests, and at Scripps, I was able to build on one of the world’s first kelp ecology programmes led by Wheeler North. As with my thesis research supported by Bob Paine and Joe Connell, I was very fortunate to move into kelp research with a great deal of support and encouragement from North and Mike Neushul, both of whom generously shared advice, equipment, and most importantly, encouragement.

I had been inspired by an early paper (McLean, 1962) demonstrating the important roles of sea otters in kelp ecology by eating the sea urchins that otherwise overgraze kelp forests. I was lucky to be able to pursue this question with research trips to the far ends of the earth in the early 1970s. Amchitka Island in the Aleutian Islands of Alaska had one of the first populations of sea otters to recover from fur harvests and the otters were known to be at their carrying capacity. There, in an area with virtually no grazers, I found a situation with very diverse kelp species and several levels of understory kelps allowing me to evaluate competitive hierarchies at different depths (Dayton, 1975).

I explored kelp habitats at the other end of the earth in South America from Isla de los Estados in Argentina up the coastal fjords of Chile with the idea of studying the large kelp forests that Darwin had discussed. These kelp forests evolved without sea otters and I was interested to learn what controlled the sea urchin populations allowing the kelps forests that Darwin observed. For most of the Chilean southern coast it turned out to be very interesting (Dayton, 2019). At first, the community enjoyed a relative stasis with very little recruitment or growth. Dozens of artificial substrata were deployed in the water column at several different sites for some 30 years with virtually no sponge recruitment, despite the fact that they were removed from the benthic predators. However, in about 2000, following an environmental perturbation involving iceberg-blocking advection of large phytoplankton and sea ice-melting induced by oceanographic changes, there was a massive settlement of a wide range of sponge species on the artificial substrata but almost never on the natural substrata (Dayton et al., 2016). Most of these were rare species implying that, when conditions were right, there was effective dispersal and recruitment. This suggests that the availability of propagules of these species had been missing for two decades and/or that the propagules were there, but the facilitating environmental factors (probably appropriate food) were limiting. Their absence on natural substrata in the presence of strong recruitment on artificial substrata implies that these propagules were vulnerable to unknown benthic predators, probably including the agglutinated foraminifera, a group ignored by most benthic ecologists. And as with all the other habitats I studied, none of the generalizations travelled well as the benthic associations at McMurdo Station were very different within a few kilometres (2–5) to the north and south. There, the differences were driven by ice conditions, especially the amount of snow that accumulated on the surface of the ice. In this sense, the local wind fields strongly influence the composition of benthic communities by affecting benthic productivity.

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In southern California, I set about manipulating canopies with the idea of describing competitive hierarchies while my colleague at the time, Rick Rosenthal, recognized the value of establishing baseline transects that he helped implement, and over time the transects have proven to be gold mines. The competitive relationships I defined turned out to be idiosyncratic because the dominance hierarchies were defined by wave exposure, depth, and surface nutrients and they were extremely variable.

The interaction strengths varied over short distances (hundreds of metres) in both cross-shore and long-shore dimensions. Most of the within kelp community dynamics were driven by substrata and depth, canopy competition for light, the kelps absorption of nutrients, and a strong edge-effect involving nutrient uptake and planktivorous predators. It was frustrating not to be able to generalize between different kelp forests separated even by tens of kilometres. And geographically distinct kelp forests can have utterly different interaction strengths for several oceanographic reasons, usually related to nutrient limitations or wave shock differentially impacting the giant kelp that depends on surface nutrients and is susceptible to wave shock that dislodges the plants. In both cases, but for different reasons, the understory kelps become dominant.

I believe that the evolutionary patterns reflect the kelp demography, especially their recruitment biology. The effective dispersal of their gametes was limited to a metre or so because the male and female gametes had to be almost touching for fertilization to occur. This very much influenced the patch dynamics, as did the grazing by small herbivores whose identities I never learned. The same Allee Effect applied to abalones and other kelp forest invertebrates that Mia Tegner, Ed Parnell, and others in my group worked on.

Because my background had focused on biological interactions rather than physical effects, I was slow to learn the importance of large-scale oceanographic processes. Fortunately, the baseline
responses to heat and nutrient disturbances due to very large-data defined subtle differences in the cross-regime shift kelp term aerial photographs of kelps to produce a very sensitive mea-
Eventually Ed Parnell integrated our time series data with long-
nities are dominated by important species defined by long-lived
Hindsight helps focus research trends over a long and diverse ca-
how to scale the most important community processes in time
Generalizing interaction strengths
Hindsight helps focus research trends over a long and diverse ca-
my early intertidal research focused on the environmental
control of dominance or what we now refer to as interaction
strengths. Paine (1980) introduced the concept of interaction
strength, and he published a figure of the same simplified inter-
tidal system as seen through the perspectives of three approaches
to ecology: descriptive definition of food webs, flow of potential
energy via trophic links, and functional approaches based on
strong interactions. He advocated the latter approach via exper-
imental manipulations. This contrasted with my 1960-era project
in the Antarctic in which my experiments had failed. To salvage
the project, I had to synthesize food web data with the rough
measure of energy flow to define the strong interactions using
the same descriptive and ecosystem approaches that Paine would
later criticize (Paine, 1980). Perhaps the most important immedi-
ate lesson here was the value of using alternative diverse methods
to solve difficult problems. Unfortunately, rather than using these
separate approaches such as ecosystem descriptions, food web
studies, population dynamics, or evolutionary modelling to syn-
thesize a strong holistic understanding of community ecology,
these different disciplines have become more specialized and, in
many cases, more isolated from each other, and importantly, iso-
lated from natural history.
A common problem with the generalizations that ecologists of-
fer is that many are based both on preconceived ideas isolated in
our specialties and inappropriate assumptions rather than on the
reality derived from good natural history. The art of appropriate
simplification and definitions of our hypotheses depends on a ba-

cic understanding of nature and somehow remains an art rather
than a science. Good naturalists have a “feel” for the system and
the ability to weed out the marginally relevant parameters realiz-
ing that all nature is trivially related. However, to be generally in-
teresting and useful, our hypotheses and tests need to address
the most important patterns and processes. Moreover, while rarely
acknowledging the value of anthropomorphic thinking, natural-
ists intuitively employ the suggestion my mother offered so long
ago as they perceive the complex interactions through the evolu-
tionary perspective of the individual organisms. In a sense, we
utilize the ancient art of storytelling as we fantasize different solu-
tions to our questions. Remember that the human brain has ev-
olved around storytelling. For most of human history, storytell-
ing is how people communicated lessons and then remembered
them.
Scaling dispersal, settlement, growth, and survival
The other theme of my career has been the struggle to understand
how to scale the most important community processes in time
and space. In my case, a consistent conclusion of my work was
that the structures of the communities I studied reflected past dis-
turbance and/or recruitment events. That is, the coastal com-

dividuals that comprise slowly declining populations character-
ized by variable mortality and episodic recruitment. Sometimes
dormancy or storage effects contributed to their apparent resil-

importance of episodic recruitment is well recognized in the
fishery literature, which focuses on scales of 100 to 1000 s of
kilometres, and represents a continuing issue for the coastal spe-
cies I studied. This implies that the scale of recruitment may be the
single most important component of this research because it pre-
determines the questions and hypotheses as well as the proce-
dures of the research.
In 1985, I had an opportunity to spend a sabbatical year at the
Australian Institute of Marine Sciences where there was an active
programme evaluating the coastal oceanographic processes driv-
ing larval distribution over large scales. I wanted to integrate dis-
persal processes with the actual settlement and survival of sessile
species. We studied the patterns and processes of recruitment of
many species of oysters across the Great Barrier Reef and found
the same factors of dispersal, facilitation, and predation (from the
“wall of mouths” to flatworms) influenced settlement and sur-
vival, and thus the scale and temporal patterns of recruitment.
The post settlement growth and survival reflected nutrients but
most importantly emphasized several different types of predation
(Dayton et al., 1989). I am proud of that paper, although it has
received almost no attention.
I never successfully tested the relative strength of the interac-
tions across spatial or temporal gradients. That is, I found it easy
to identify the strong interactions with observations and simple
experiments, but very difficult to articulate, measure, or test pro-
ces defining the interaction strengths that separated funda-
mental from realized niches. The rest of my career focused on
similar efforts to understand the evolutionary processes in time
and space driving the composition of coastal benthic communi-
ties. I have had some success, but a meaningful synthesis has eluded me, implying that I have not asked the correct questions
to understand scaling of the realized niche. However, it is far bet-
ter to be interestingly wrong than trivially correct and my failures
to solve the big questions have contributed to improved under-
standing of benthic community processes. It is important to take
pride in clear failures that redirect and refocus the questions that
lead to a deeper truth. A common but serious intellectual mistake
is to find an exception to a generalization and discard the general-
ization rather than to understand the exception. The old adage of
an “exception that proves the rule” is based on the Latin probare
meaning to probe or test the rule.
While not being particularly proud of my failures, I fell victim
to social pressures in ecology. The powerful influence of

compensation-based models of the era influenced me to accept the
density dependent focus of David Lack (1954) and ignore the
density independent ideas of Andrewartha and Birch (1954) and
miss the obvious truth that it is never an “either/or” situation. I
should have better respected my undergraduate roots and also fo-
cused on environmental factors as well as the biological interac-
tions. I believe that ecological fads put undue emphasis on quantifying obvious relationships, relying on simplified field
experiments, and using very restricting and inappropriate statis-
tics to demonstrate things I already knew. These very restrictive
views of proper ecological research impeded the larger under-
standing I sought. This was not true for my Antarctic programme
because in the beginning I did not know the natural history, but
otherwise my work was low risk because mostly I knew the
answers from the beginning. In hindsight I simply should have trusted my natural history observations of patterns and process and not wasted time quantifying obvious patterns and testing hypotheses when I already knew the answers. It was obvious that the interaction strengths varied over environmental gradients, I recognized the gradients, and I should have searched for environmentally induced thresholds in the interactions that I studied.

But what are natural communities? Or how I fell out of the ivory tower?

I based my questions on the assumption that I was studying fundamental and realized niches that reflected natural communities embedded in their specific and dynamic environments. Eventually I realized that there were virtually no natural communities left in the face of human intervention. Most natural marine wetlands have been “restored” by human development, and most of those few that have been protected are too small and isolated to experience the flushing and coastal dispersal of larvae necessary to sustain natural populations. The cascading impacts include the loss of nursery habitats for many species of fish and invertebrates as well as most coastal birds. Most importantly, ecosystem overfishing by commercial and recreational fishing has had an enormous impact on marine ecosystems leaving most marine communities with important predators functionally missing and natural benthic habitats virtually obliterated in many important regions. This realization has very much coloured my own perception of my career because it took me far too long to understand the problem, and my conservation efforts were too late and ineffective.

I finally realized in the 1980s that the large reduction in some fish species in kelp forests was from fishing rather than pollution as I had supposed from my Rachel Carson era bias. I double-crossed the Smithsonian Institute to whom I had promised a kelp talk at a large event and instead laid out my concerns about fishing impacts. Afterwards, I was threatened by a couple suits I assumed were fishery lobbyists. I did not realize it at the time, but this resulted in a major change in my career.

I set about collecting as much information as I could find with the limited search engines of the era. I gave countless lectures and with colleagues even wrote a review paper (Dayton et al., 1995) about environmental effects of fishing that was difficult to get published. I had the naive idea that talking about this problem would solve it, but I was disabused of this notion by the very hostile responses from some fisheries scientists who I had previously respected. This was to be expected, but I had not expected resistance from academic colleagues. This I came to understand when Mia Tegner and I were sent to a meeting of coastal ecologists, and as we had breakfast before the meeting we found ourselves sitting about a metre from a bearded fellow regaling a table of colleagues about the upcoming meeting. I could not avoid overhearing when suddenly he informed them that they would even see Paul Dayton, a real extremist whose claims were vastly exaggerated. I calmed Mia who was about to launch herself at the fellow and learned that the subtle resentment I was aware of from many academic ichthyologists was based on the fact that I was not an expert on fishes and, therefore, had no business spreading these concerns they thought had a negative impact on their credibility. I had never expected so much opposition to what I thought was a simple but important message, but importantly it also introduced me to the question of whether scientists dealing with objective facts lose their credibility when they advocate some political cause relating to what they have learned. This question continues to be a very important issue for those ecologists who want to share their results and have a voice in social dialogues.

It became clear that my personal efforts had virtually no impact. It was not until Daniel Pauly (Pauly et al., 1998) and RAM Myers (Myers et al., 1997; Myers and Worm, 2003) collected and analysed large amounts of data and, importantly, knew how to get the information into the scientific and public discussions that the tide of public and political awareness began to change.

This experience came full circle when a colleague and I agreed to evaluate a proposed salt-work project in a Mexican lagoon used by grey whales, and we found ourselves pilloried by conservation groups. I was personally opposed to the development but agreed to help research the impact on the whales because I was very interested in the region. The money I earned supported Enric Sala, a postdoc who has gone on to a very successful career in conservation activities. As we learned that the proposed project would have virtually no impact on the whales, our integrity and competence were aggressively attacked by individuals from various environmental organizations. This and equally sleazy activities about alleged Antarctic pollution have persuaded me that many environmental organizations are as deceitful as the other side, and I reluctantly distanced myself from the conservation movement.

However, it remains an inconvenient truth that people have heavily impacted essentially all of the habitats in the biosphere. Consider the massive apparent global loss of insects demonstrating that Rachel Carson’s Silent Spring (1962) has sprung, yet very few people notice or even care as the cascading impacts on pollinating systems and the loss of the myriad insectivore networks slowly changes the world around us. This is a huge crisis that is virtually ignored. It will be virtually impossible to understand the reasons for the loss of insects and their dispersal sources and sinks. That is, how do we separate habitat loss, GMO crops, and insecticides from climate change as our biosphere careens into its unhappy future? Despite this, I suspect most ecologists believe that they are studying natural systems. And worse, unlike the 1960s, the public does not seem to care.

Defining and implementing our values

As I have aged, I have wondered about the real value of all of this work. Is there a need for us to reconsider our values as ecologists struggling for recognition and support? Over the last few decades, the simplistic recognition of our scientific contributions has been formalized such that our academic promotions and success in our field is being evaluated by counting publications and where they are published irrespective of what they actually contribute. When pressed to evaluate the importance of our contributions, the establishment and the new driving forces of science quantify importance by counting citations and producing an “H” index (see Hirsch, 2020). This is a critical change from the time when science drove the science.

Today, sophisticated tools, complicated, often irrelevant meta-analyses, and the conceived standards of prestigious journals seem to define our sense of good science. Many of our awards and formal recognitions seem to relate to “old boy clubs” more than the lasting quality of our science. Scientists are quick to game this system by adding authors to each other’s papers and finding ways to get their papers cited. All citations are not equal, but it is rare to see the lasting importance of a paper recognized...
by our administrators or peers, especially a recent paper that has not been seen long enough to be fully appreciated. And we recognize that the H value heavily depends upon working in a popular discipline (pity those who work in important but obscure disciplines), cultivating influential friends (spending time on the seminar circuit, going to meetings, running for offices in professional societies, etc.), and enjoying a certain amount of longevity. The latter surely has a large role in H values; consider, for example that Robert MacArthur, one of the most influential ecologists of my era, has an H value of only 42 because he died young.

We all well know how hollow these criteria really are, yet even as we complain about it, we meekly continue to work within this flawed value system; but at the end of the day we can ask is this really how we want to define our legacy? Our selves? An H value? I am sure that most would say no, but again, we know what it takes to get a grant or have our papers accepted, get recognition, and be promoted, so we simply play this game we do not like. It is very important to realize that, in the big picture, we define the rules of the game when we review proposals and manuscripts, serve as editors, and write recommendations. In each case, there is the opportunity to serve as mentors rather than gatekeepers. We have the ability to recover our values and redefine our standards with honest reviews that recognize genuinely important ideas and results.

In the long run, most of our work falls by the wayside or in the rare best case contributes to the evolution of our discipline. And as with most foundations, the strictly science-based impact of our papers should, in principle, be subsumed by future research. A much more lasting legacy involves the people we have influenced because they have the potential to continue to be creative scientists and mentors and influential citizens. Many ecologists mentor and take great pride in excellent graduate students in their groups, and personally, I define my career by the success of my students. There is a modest amount of recognition and reward for good graduate mentoring, but our reward systems are heavily focused on the amount of money we bring in plus counting publications, citations, H values, and altmetrics.

Unfortunately, excellent mentoring of undergraduates is rarely acknowledged and academe punishes those who focus their time on teaching or attempting to educate the public, or doing important public service. Yet it is the non-major undergraduates that are the most important group of citizens that we need to inform and inspire, not necessarily to join our laboratories, but simply to care. My own efforts to reach undergraduates became increasingly disappointing as it was very difficult to extract their minds from their phones. This was especially true in classes with hundreds of students—a norm at almost all of our research institutions. If we hope to have our legacy include a liveable world with natural pla-dards with honest reviews that recognize genuinely important ideas and results.

Looking forward

Most ecologists have probably enjoyed their own efforts to better understand the evolution and maintenance of the various ecosystems that they study, and probably most have shared my frustrations and satisfactions with our results, and hope to continue searching for new insights and questions to better define and generalize the processes they study. I hope that colleagues also consider the more general values we cherish and that they consider how we might protect what is left of our natural world. Circling back to my mother’s concern, consider how your grandchildren will see the world when they are your age. Consider the changes...
in nature over your life, and imagine a planet teeming with people but without nature as we knew it.

Education is our most valuable tool, not only for our ecology students but also for the general public that needs to implement the changes. Sadly, universities themselves are evaluated by high-profile research results and financial success and their faculties are judged by the narrow metrics of career advancement. Most universities have responded by ignoring or discarding the old values of mentoring critical thinking and a broad education in favour of high-profile research activities that often involve pandering to commercial interests rather than general education. Universities define themselves by biomedical and technological advances and the natural sciences are scorned as “old fashioned”. Administrators do not care that many students are anxious to translate their love of nature into science while the universities themselves focus on translating science into revenue producing patents and products. As a result, most university faculties now lack professors able to teach natural history subjects, or worse, any interest in offering them as they continue to focus on money and impact. Yet when natural history courses are offered, the students come!

How many citations equates to the implementation of a programme training over a thousand freshmen a year taking natural history courses in the field? What does it take to recover these values? These changes will not come from above; they must be forced by those of us in the trenches who care. If ecologists hope to fight this trend, the battle begins at home with our colleagues, deans, and university leadership. We need to engage and redirect the risk management offices that so often have responded to litigation by making it so difficult to do and teach field science. Somehow, we need to encourage these people sitting in their comfortable risk averse worlds to facilitate rather than block our efforts to address so many urgent global environmental problems.

More importantly, we need to stop complaining or blaming others for the failures and we need to make an urgent effort to teach natural history at all levels from our laboratories to undergraduate classrooms, to volunteering to talk to grade school classes, and the general public. It is discouraging to watch the public believe the misinformation they get from social media; yet we should recognize the power and influence of social media and try to use it to our advantage by implementing new approaches that go beyond our staid traditional science-speak. We need to find new voices that are passionate and understandable and most of all, convincing.

All of us have a tremendous amount of passion for our work. We have dedicated our careers to interesting research, and we work very hard to do it well. We know much more than we communicate, and we need to share our wisdom, and especially our passion, more broadly. We desperately need to enthuse and educate the general public because ordinary citizens no longer trust science, to some extent because they do not understand it. Rather than shunning our colleagues who attempt to simplify and explain the results of their work and results to the mass media, we all need to become comfortable sharing our emotions and especially our enthusiasm with storytelling techniques that non-scientists can relate to. The public is responsive to honest passion and personal stories about what inspired us to go into science, what keeps us awake at night and what makes us stand in awe, and what we value. Most people hang on to their childhood pleasures of hearing good stories, and all of us are awash in great stories! We just need to share them. We have an obligation “to disseminate what we discover clearly, interestingly, and impartially . . . so as to encourage those writers and elementary teachers whose profession it is to bring the findings to as wide an audience as possible” (Hutchinson, 1983).

This essay has discussed some of my experiences and love of nature, the evolution of some of my questions and my values, and I have talked about problems in science and society that keep me awake at night and make me apprehensive for my grandchildren’s future, but I have failed to address what I consider the single most serious problem: the size of the human population. This is the source of most environmental and social crises. How can we deal with the spectre of a denatured planet without dealing with the growing human population? How might ecologists respond to this crisis? First, while not the focus of this essay, it seems essential to recognize that the crisis exists and realize the terrifying fact that Paul Ehrlich’s Population Bomb (1968) has already exploded and, combined with human greed, is the root cause of most global problems. This is the most serious issue the world faces, and ironically there are various solutions, yet it remains politically incorrect to discuss the crisis of human overpopulation. Instead, we focus on various derivative problems. We certainly cannot solve a problem if we do not talk about it, and every ecologist, yea, every thinking person, should talk about overpopulation as often as possible.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

Acknowledgements

Over many years I have started several drafts of my response to this invitation, but each try was embarrassingly naive, and I let each slide; but Howard Browman gently continued to prod me and since one of the objectives of the food for thought is to explain how we developed our careers, I opted for this path and he has been a wonderful mentor helping me write something very different from what I am used to writing. I also thank the many people who have helped me with my awkward thought process and prose, and I especially thank my family and my own students who have done such a wonderful job mentoring me!

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