

# 11 *A Sense of Place*

TATOOSH

Robert T. Paine, Timothy Wootton, and Catherine A. Pfister



Figure 11.0. Bob Paine at Tatoosh, with a characteristically massive wave. Photograph by Tim Wootton, 1995.

## **Abstract**

We develop the view that commitment to a single isolated site (Tatoosh Island and its adjacent mainland), experimental manipulation, acquisition of lengthy time-series data on selected species, and what can be called “natural history” have proven to be conceptually rich ecologically. Our loosely bound intellectual consortium of principal investigators and graduate students has focused on central themes of trophic ecology (keystone species, strengths of interaction, indirect effects), disturbance-driven patch dynamics and related successional processes, and the critical connection between individual

variation and population performance. We argue that investigator independence, set within a supportive academic environment, enhances research creativity and the development of novel ideas and techniques, both of which are vital if the fog of biological complexity is to be lifted and natural systems are to be understood.

## Introduction

Some ecologists suggest that we should move away from detailed studies at local sites and instead focus our analyses on data taken across larger geographic scales, because such data promise broad generality (Underwood and Petraitis 1993, Brown 1995, Lawton 1999). Although large-scale studies are undoubtedly worth pursuing, primarily because they establish the general environmental context for more localized studies, we believe it is premature to dispense with intensive site-based studies, for a number of reasons. First, detailed knowledge of natural history and historical dynamics allow one to recognize “surprising” results and identify novel mechanisms that can be generalized to other ecological systems (see also Doak et al. 2008; Grant and Grant, chapter 6; Estes, chapter 8; Ostfeld and Jones, chapter 10). It is hard to know what to be surprised about if the system is studied as a snapshot, which is generally necessary in broad-scale studies for logistical reasons. Second, place-based research provides model systems for ecology. Model systems have proven useful in other areas of biology because they facilitate the identification and understanding of fundamental mechanisms. Studying ecological mechanism is of general value in producing a conceptual toolbox that can be applied elsewhere—for instance, in explicating comparable processes in different ecosystems (Pulliam and Waser, chapter 4). Third, much ecological theory is based on system dynamics. Linking theory to empirical data is therefore done most naturally in systems for which dynamics are documented, and it is best done by detailed long-term studies at defined sites. In this chapter we illustrate some of these points with examples from our studies on the rocky intertidal systems of the northwest corner of the Olympic Peninsula, Washington state, in the United States, and in particular at Tatoosh Island.

## The Major Research Site and Our Collective Approach

Research domains are defined by scale issues: size (in hectares or square kilometers), which is fixed, and duration of study (in years or decades), which brings the added complications of frequency of observation and specific interests of the observer(s). Our focal location is Tatoosh Island (48° 24' N, 124° 44' W), a 17–18-ha cluster of islets, most of which are connected

by land at low tide, about 0.6 km off the northwestern tip of Washington state. A broader definition of “place,” however, is needed to include early studies in the Cape Flattery region, all of which took place within about a 15-km radius of Tatoosh. Latitude, climate, and a physical battering by winter waves of 10-m height and more place the area under the influence of the North Pacific Ocean. The occasional winter freezing events, the general lack of herbivorous fishes, the summer fogs that potentially mitigate heat stress, and an intertidal zone enhanced by wave surge have all produced a pattern- and species-rich intertidal assemblage dominated by mussels, barnacles, and kelp. One of us (Paine) began study in June 1963; Wootton first visited Tatoosh in November 1984, and Pfister in July 1988. Frequency of observation throughout more than 40 years has varied, with trips lasting from 1 to 20 days (usually 3–5 days) and occurring at all seasons. Our research focuses on the intertidal zone studied at low tide. Workable winter (October–March) tides occur at dusk; safety concerns generally limit study to two to three tides. The schedule in summer (April–September), when low tides occur during daylight morning hours, is typically two three- to five-day trips per month.

The importance of this single research site, studied in a collegial and cooperative fashion for a long time, derives from several factors. Discovering the idiosyncratic natural histories of some of the species is a collective endeavor. Species are different in behavior and in ecological impact, and observations on the nature of their intra- and interspecific interactions, enemies, quirky behavior, and reproduction accumulate over time. This shared knowledge helps develop a platform around which testable hypotheses can be formulated and impracticable ones discouraged. Of equal significance is that the solid surface of rocky shores has facilitated studies that manipulate species composition and density. Species removals or additions can be implemented manually or with the aid of stainless steel or antifouling paint enclosures or enclosures, tide pools can be added or their equivalents developed, and the rock readily drilled to secure sophisticated electronics, organism mimics, or a wide variety of structures intended to evaluate or encourage larval settlement. In addition, many of the plant and animal species can be individually marked. Such technical knowledge, like natural history detail, accumulates over time; experimental successes have greatly facilitated our understanding of how the community is organized. Our failures are equally important because they identify challenges that, while not necessarily insignificant, cannot be addressed currently.

Our commitment to experiments has yielded, as a very important by-product, long time-series of observations on both the experimental sites themselves and their controls. Observation in ecology often takes the form of “snapshots”; for instance, a brief, site-specific interlude of intense

quantitative sampling, or even a photograph, both being approaches that are insensitive to temporal variation. Experiments, on the other hand, usually have to be maintained, surfaces cleaned or repainted, invaders removed, and materials replaced or replenished. Thus repeated site visits are a natural by-product of experimental maintenance. A number of Paine's Tatoosh time series began in 1968 or the early 1970s; Wootton has tracked species dynamics within mussel beds since 1993 and bird populations since 1985; Pfister's quantitative censuses of tide pool fishes, brown algal growth, and beach cast drift algae date to 1989. Two factors underlie these lengthy and often continuing data sets. First, many intertidal species, including algae, grow slowly and can attain longevities measured in decades or even centuries. Thus, a month or even a year or more of observation is inadequate in duration. Second, even for species with briefer longevity, our long-term commitment allows us to understand temporal variation and the extent to which there is constancy or variability in population dynamics and species interactions. Thus Paine's 25-year *Pisaster* exclusion failed to reveal any gradually developing novel state, and Wootton's seven-year California mussel removals were basic to a test of the predictive ability of Markov models.

Data obviously accumulate with the passage of time, but so do qualitative impressions. Equally, perhaps, intuition sharpens with experience at a site. These aspects of long-term study bear at least three consequences. First, the natural world is intrinsically variable with population numbers waxing and waning, larval recruitment for all species varying in space and time, and the physical setting changing in subtle yet important ways. That is, the ferocity of a winter cold snap, the magnitude of wave-generated disturbances, the timing of a fog that ameliorates intense intertidal heating, and the resultant organism deaths all matter. These local events are superimposed on more global influences such as Pacific decadal oscillations and El Niño events. The net product is one of biological variation. The transmission of such variance demographically and its consequences is enormously significant; the fundamental, species-specific details can only be revealed by long-term monitoring, and hence time series. Second, there is the occasional extreme event. Some events are obvious, such as desiccating, warm winds coinciding with recruitment of algae or animals. Others can be much more subtle, since the human perception of "benign" may not match that of the resident species. Reduced water-column nutrients or heavy rain during an extreme low tide come to mind. Their usual ecological signature once again is increased variation in population numbers, expressed as a steep decline or even a missing year class. However, there can be positive extreme events as well, in which population numbers exceed all known limits. Familiarity with a site enhances recognition of these events. In all cases, a feeling for baseline conditions is required to recognize a legitimate outlier from "normal"

variation. Third, as one's perspectives mature along with one's biases, one can extend or challenge older interpretations. Such intellectual ontogeny is to be expected. In an ecological world in which context matters, regional and temporal differences in the outcomes of experimental manipulations should be expected. They signal the importance of explicit, relevant details; they also emphasize how variation in demographic properties can influence ecological interactions.

When observations are prolonged rather than being a snapshot, site experience often helps resolve the ultimate source of extreme mortalities. For instance, in late December 1988 the barge *Nestucca* leaked 168,000 to 231,000 gallons of bunker-grade oil south of Tatoosh. The northward oil trajectory killed thousands of common murrelets (*Uria aalge*), swept past Tatoosh, and could have caused substantial mussel mortality. In February 1989 extreme cold froze intertidal organisms from Alaska south to Oregon. We were on Tatoosh from 8 to 12 March 1989 and observed numerous new mussel bed patches, one of which was at least 40m in horizontal extent and 1.5 to 3.2m in width. This relatively huge patch had not been present in November 1988. Familiarity with the site and specific clues such as the presence of byssal fibers, tidal height, and the identity of the impacted species (*Mytilus californianus*, rather than *M. trossulus*) indicated extreme cold, not oil-based trauma or winter waves, as the cause of this mortality. Such discrimination bears obvious ecological and economic implications and is made more certain at frequently visited sites.

Finally, a place develops its own ambience and research traditions. Tatoosh is no exception. The island is difficult to access; travel requires helicopters in winter and a 12 km one-way boat trip in spring and summer, with the actual landing made through the surf by inflatable raft. Most supplies and food must be packed from the beach to where we live on the island's top in two old (probably 1930s vintage) abandoned U.S. Weather Bureau buildings, one of which we have refurbished. There are few if any creature comforts; water and firewood must be hauled, and until recently there was no indoor toilet. A solar panel, installed in 1996, generates enough power for evening lights and battery charging in the 3.5 × 5 m secure building. Maximum human occupancy is 10 adults; 6 is more comfortable.

Research support from the U. S. National Science Foundation has been continuous, though hardly lavish, since 1962—initially to Paine and more recently to Wootton and Pfister. Support from the Andrew W. Mellon Foundation since 1995 has proven invaluable. The NSF grants were given to individuals and funded hypothesis-driven, experimental ecology. The product has been 75 to 100 generally sole-authored papers by us and our students in leading journals, and three Mercer Awards (P. K. Dayton, K. P. Sebens, J. T. Wootton) and one Buell Award (S. R. Palumbi) from the Ecological Society

of America. These are some of the hallmarks of “small” ecology, in this case equally dictated by circumstance (site isolation, limited group size) and a conviction that research independence rather than a primary group-based endeavor is the mother of innovation.

The above circumstances and attitudes also generate constraints. The positive side of relative geographic isolation is lack of interference with or destruction of our sometimes-conspicuous experimental devices. Further, the island, which now belongs to the Makah Indian Nation, is not subject to the biotic plunder increasingly characteristic of mainland sites. On the negative side are two major issues. First, the island’s small size, its isolation, its difficulty of access, and especially its North Pacific maritime environment have limited any attempts at traditional environmental monitoring. Aerosols or salt spray routinely defoliate the island’s dominant plant (salmonberry, *Rubus spectabilis*), consume our lawn mowers, and have destroyed a U.S. Coast Guard power-generating windmill within two years. One of us (Paine) early on dismissed, perhaps wrongly, any attempt to monitor the island’s physical environment, partly because the necessary equipment was expensive and had to be maintained, but primarily because the measurements seemed irrelevant to the microsite variation that dominated individual fitness and survival. Nonetheless, Pfister and Wootton initiated a sampling protocol for water conditions after the 1997 El Niño event. Water temperature, salinity, pH, dissolved oxygen, and water column chlorophyll have been measured essentially continuously from April to September, and these measures were supplemented with monthly water nutrient collections at 10 Tatoosh and 4 offshore sites adjacent to the island (Pfister et al. 2007). As these data have accumulated, they have been a source for unanticipated linkages to global change (Wootton et al. 2008). The second issue on the negative side has been a collective, and traditional, ambivalence about which species to monitor, or even whether to monitor them; the great local species richness (>400 animals, probably >150 benthic macroalgae) only magnifies this dilemma. Clearly, one can at best monitor—let alone identify—a modest fraction of these species in a statistically appropriate fashion. So the task of assembling an island-wide species inventory and a quantitative time series has not been attempted until recently, and even then it is restricted to the well defined but limited conditions of mussel beds on wave-exposed rock benches (Suchanek 1979; Wootton plots, continuously monitored since 1994).

The following paragraphs identify some of our major research themes, and especially their conceptual evolution. One goal is to illustrate the interplay between observation, natural history, hypothesis testing, and experiment. Another theme will be the progressive sophistication of our endeavors; some of our early ideas now seem embarrassingly primitive. We also discuss specific examples of how our site-based research has added to both

conceptual and practical ecological endeavors. Some will see this as shameless advocacy for small science, contra Lawton (1999). A more generous appraisal is that curiosity about the natural world, the esthetic stimulation of working in a truly spectacular setting (Rosenfeld and Paine 2002), and a commitment to manipulation and quantitative assessment have allowed us to challenge and improve our understanding of how nature works.

### Keystone Species

The starfish *Pisaster ochraceus* is conspicuous and often abundant on rocky intertidal and shallow subtidal shorelines of western North America. Although at times the task can be difficult, and even impossible without damaging the starfish, individuals can be pried off the rock surface and their prey determined. The observation is straightforward, and while revealing by itself neither food preference nor rate of consumption, it does identify a diet dominated by mussels (two species) and barnacles (five species), supplemented by at least 34 other prey items (Paine 1980). One also observes that on exposed and more vertical shores, there is often a conspicuous lower limit to the distribution of the mussel *Mytilus californianus*, and when the barnacle *Balanus glandula* is eaten, a white basal plate persists. These observations encouraged Paine (1966, 1974) to initiate a five-year removal of *Pisaster* (1963–68) specifically testing the hypothesis that “local species diversity is directly related to the efficiency with which predators prevent the monopolizations of the major environmental requisites by one species” (Paine 1966, p. 65). The immediate ecological consequences could have been anticipated: mussels recruited to the removal site, grew, outcompeted other space-requiring species, many of which were not prey species of starfish; and monopolized the spatial resource to the eventual exclusion of all other species capable of attachment to the primary resource, bare rock. Generalization of this result led to the concept of a keystone species (Paine 1969)—basically a statement that certain consumers, by controlling the abundance and distribution of competitively dominant and preferred prey, determine local species composition. The generality of this conclusion seems robust (Power et al. 1996) under certain conditions. Although the concept is clearly not universal, it has furthered an understanding of the significance of ecological “context,” especially the role of consumer density. These studies also motivated the concept of “trophic cascades” (Paine 1980), essentially trophically-linked pairs of strongly-interacting keystone species.

Paine’s results assumed that bird influences were inconsequential—that is, they had little impact on the capacity of California mussels to usurp the spatial resources. On the other hand, there was no doubt that glaucous-winged gulls (*Larus glaucescens*), oystercatchers, and crows exploited

intertidal resources—especially limpets, predatory gastropods, and even sea urchins (Wootton 1992, 1995, 1997). The critical additional observations were that gulls fed heavily on goose barnacles (*Pollicipes polymerus*), and that these animals often recruited densely into patches formed in mussel beds by winter storms (Paine and Levin 1981). Evidence for gull predation is readily observed: large numbers of gulls tugging on goose barnacles in these patches, patches dominated by “headless” barnacles (these barnacles are stalked), and piles of regurgitated plates.

Paine’s view was developed on the assumption that *M. californianus* was ultimately the superior competitor; the goose barnacle observations challenged that assumption. To test this new hypothesis—that on wave-swept shores, goose barnacles are the alpha competitor in the absence of gulls—Wootton had to discover a means of excluding birds. Commercially available vinyl-covered wire letter baskets proved ideal; most survived wave pounding for four years with minimal basket “mortality.” Ultimately, the results supported Paine: interestingly, gull predation does not change the end point of successional replacements, but rather accelerates it (Wootton 1993b). Obviously there is a cost to mussels in terms of achieving spatial supremacy by having to compete with goose barnacles, and gulls mitigate it.

We present the above in some detail as an example of evolved and evolving sophistication in both hypothesis generation and the implementation of experimental tests. First, Wootton’s studies have made our understanding of *M. californianus*’s competitive superiority increasingly robust, and they complement similar discoveries in Oregon (Menge et al. 1994) and British Columbia (Robles et al. 1995). Second, they were a precursor to and an essential ingredient of Wootton’s path-analytic studies of multispecies interactions at Tatoosh (Wootton 1994). Long-term understanding of the resident organisms’ biology at a single site encourages such conceptual advances. At the least, it reduces or eliminates a necessary discovery phase, which by itself is a substantial economy.

### Interaction Strength

Ecologists should need no introduction to the importance of a population’s density. Density can influence behavior, individual growth, survival, and dietary breadth, often in nonlinear ways. Per capita effects of one species on another permeate the dynamic models of Lotka, Volterra, and Gause. MacArthur (1972) captured the sense of these, employing the terms “strong” and “weak”; Paine (1980) extended the interpretation graphically yet qualitatively. Strong interactions could be explored experimentally and recognized by rampant indirect effects. Numerous examples exist. Paine’s illustration of how weak effects might be recognized (Paine 1980, figure 1), while correct,

was experimentally flawed: how does one distinguish a “no effect = weak interaction” result from a failed manipulation?

Paine (1992) attempted to redress this intellectually stagnant situation. Presence and absence data were clearly inadequate. For instance, *Pisaster* is probably ecologically inconsequential and “just another starfish” at Torch Bay, Alaska (Paine 1980, p. 670), whereas it plays a major ecological role along parts of the Oregon coast (Menge et al. 1994), in Washington (Paine 1966), and in British Columbia (Robles et al. 1995). On the other hand, observations had suggested that macroherbivores (urchins, chitons, and limpets) embodied a better system with which to address per capita effects experimentally. We (Paine and Vadas 1969, Paine 1984) and others (Dayton 1975, Duggins and Dethier 1984) had shown that after sites were scraped and grazers removed, they would initially be dominated by brown algae, *Alaria* spp. The next generation of experiments (Paine 1992, 2002) exploited this feature; scrapings of small areas (<600 square cm), site sterilization with oven cleaner, and barriers of epoxy putty painted with copper-based anti-fouling paint permitted the species composition of the grazer community to be controlled within enclosures. An index of “per capita strength of interaction” was developed. Better indices were subsequently identified.

However, concepts and indices evolve. The claim by one of us (Paine) that interaction strengths were best (and probably only) estimated from experiments was challenged by Wootton (1997), who demonstrated that observation of predator and prey density, calculation of consumption rates, and changes in density of the target species could yield a per capita consumption estimate. A log ratio of interaction strength was identified as the metric of choice, and seems generally accepted today, as the review by Laska and Wootton (1998) suggests. Ruesink’s (1998) field microcosm experiments demonstrated that interaction strength could be a strongly nonlinear function of prey abundance. Our conclusions are that (1) empirical estimates of interaction strength remain a critical ingredient of dynamic community models, because they unite consumer density and impact; (2) picking a tractable system is necessary for successful experiments, and depends on familiarity with the manipulated species’ natural history; (3) observationally based estimates require a more intimate understanding of the component species’ activity periods and density; and (4) important ecological concepts evolve because of interplay, debate, and challenge among researchers.

### Indirect Effects

As soon as one acknowledges that natural communities are a highly diverse, multi-trophic-level mix of dynamically interacting species, one must recognize the possible significance of indirect influences. Wootton (1994, p. 151)

has defined these as those “that do not involve physical interaction.” Thus, in systems in which space limitation is commonplace, when species A competes with or preys on species B, indirect influences on the other species that are associated with species B can be anticipated. Rocky shores are replete with examples. Connell (1961) showed experimentally how predation on one barnacle species reduced the impact of interspecific competition on another, and therefore benefited it. Paine (1966) employed the modifier “indirect” in describing how *Pisaster*, by consistently reducing mussel numbers, permitted many non-prey species to coexist on mutually occupiable space. The subject is hardly ecological “news”: it can be traced at least to Darwin (1859). Menge (1995) found that indirect effects accounted for a minimum of 40% of the changes in experimentally manipulated communities. Wootton (1993a) has classified indirect effects into two broad categories: interaction chains and interaction modifications.

What recognition of these often subtle relationships requires is an appreciation for a species’ natural history. We provide a number of Cape Flattery and Tatoosh-based examples in order of increasing complexity to illustrate this assertion. The essence of keystone species and trophic cascades resides in indirect influences transmitted across trophic levels. Dayton (1973b) showed how predatory starfish indirectly feed sessile anemones, *Anthopleura xanthogrammica*, by stampeding sea urchins into the mouths of these sit-and-wait consumers. Wootton (1994) expanded a path-analytic approach to test experimentally eleven predictions of the relative importance of indirect effects in a Tatoosh interaction web; all the predictions were supported. Finally, Parrish et al. (2001) could show that common murre decline at Tatoosh was best understood by considering some combination of direct eagle predation supplemented by the indirect consequences of predation on eggs by gulls and crows. Indirect effects must be rampant in nature, and often they are subtle. Ignoring their presence in interpretations of single or multispecies dynamics surely leads to incompleteness and possibly errors. Commitment to old-fashioned observation and sharing of the resulting information will reduce these problems; familiarity with a site facilitates this vital task.

### **Spatial Ecology**

Spatial patterning permeates the organic world, and rocky shores have provided a fertile venue for exploring the underlying processes. Early focus was on characteristic and conspicuous patterns of zonation (Lewis 1964); initial interest in our own case was stimulated by the obvious role that waves play in generating a mosaic of patches in the intertidal of different sizes, ages, and occupant species. Dayton (1971) described 18 patches observed over a

two-year interval at three Cape Flattery sites. His report that these patches increased in size (area) by 24% to 4,884% implies a system of ever-expanding patches, which seems improbable. By 1971 Paine had begun following the fate of individually marked patches in these same mussel beds, and by 1972 he had carved experimental gaps and begun quantifying their recovery. Levin and Paine (1974) developed a dynamical model in which the rates of patch formation (birth) and closure (death) were considered functions of initial patch size and age. In essence the approach was demographic; it confronted the fact that two patches the same size need not be of similar age and, conversely, that patches of comparable age could range from a few square centimeters to many square meters in area. The conception was of a nonequilibrium spatial “world” of mussel beds and mussel-less patches, with the mix determined by the intensity and frequency of disturbance. Local species richness would be influenced by patch size, invoking species-area relationships, and patch age, permitting successional patterns to be incorporated. Though such a regional integration was never attempted, Paine and Levin (1981), in a six-year study involving thousands of patches, demonstrated the robustness of the model and its independently estimated parameters.

While the above approach hasn't exactly languished (Levin received the 2005 Kyoto Prize based in part on his research at Tatoosh), other methodologies exist for addressing spatially explicit multispecies relationships. The Levin-Paine approach is analytically demanding and it ignores the effects of species interactions within patches. To probe species interactions, Wootton adopted more traditional stationary Markov models to ask whether transition probabilities similarly identified *M. californianus* as the competitive dominant and therefore plausible endpoint of a successional replacement process. Unsurprisingly, the answer is yes (Wootton 2001a). But the approach has proven conceptually richer than this obvious result. Quantitative shifts in species composition were successfully predicted for vertical rock walls lacking obvious bird predation and characterized by little or very reduced recruitment by dislodged adult mussels. The change in system dynamics documented by Wootton's earlier studies (Wootton 1994), in which bird predation on goose barnacles (*Pollicipes polymerus*) was prevented by letter basket cages, was also successfully predicted. Possibly more significant in a broader ecological context, the experimental tractability of rocky shores permitted Wootton to generate and test novel conditions with the Markov models. When the competitively dominant California mussels were routinely hand-plucked from experimental plots, the multispecies Markov models successfully predicted that the community would be dominated by the coralline alga *Corallina vancouveriensis*. When another mussel (the weakly interacting *M. trossulus*) was removed, *M. californianus* continued

to predominate and coralline algae remained a minor community member (Wootton 2004). Such results uniquely show that Markov chain models are robust when challenged to predict the consequences of species removals or absence. Their successful prediction of the equilibrational multispecies mix should complement nicely the Levin-Paine visualization of a simplified and nonequilibrium patchy world in which species presence is determined in part by patch size and age. The direct integration of these very separate approaches has not yet been attempted, but spatially explicit extensions of the Markov chain models to generate cellular automata (Wootton 2001b) provide a compromise approach with encouraging results.

### **Environmental Variation and Its Contribution to Species Dynamics**

An investigator with a long-term presence at a site almost always notices the year-to-year variation in both physical and biotic components. At times the implications of this are obvious, such as the total recruitment failure of sea urchins (*Strongylocentrotus purpuratus*) during the 1982–83 El Niño. At Tatoosh urchins trickle in annually; major recruitment tends to occur during El Niño Southern Oscillation events when near-shore currents move south to north. The 165 mm of rain falling over a 21-hr interval on one of the year's lowest tides in July 1983 substantially reduced both the 1982 and 1983 urchin year classes. But many aspects of environmental variation are more subtle and require established analytical frameworks to understand the implications of a year of poor adult growth, a reduced level of recruitment, or similar events. One of us (Pfister) has focused on the fates of individuals within populations to ask how variation in demographic rates is manifested at the population level. The abundant annual kelp species *Alaria nana* is characterized by highly structured variation among individuals. Individuals have consistencies in growth rates across time intervals such that those that grow well in one interval continue to do so—the phenomenon of growth autocorrelation (Pfister and Stevens 2002, 2003). The implications of this phenomenon are that some individuals get especially large, with increasing reproductive output, and have the potential to contribute disproportionately to future generations. An examination of this pattern over two years shows that growth autocorrelation and size disparities were much less pronounced during an El Niño year (1997), when growth and reproductive output were reduced (Pfister and Wang 2005). Under such conditions, individual fate was much less deterministic, fewer individuals reached a reproductive size, and population growth was much reduced. One can examine the consequences of different individual “pathways” during the El Niño and normal years with matrix projection models (Caswell 2001) and loop analysis, and quantify the much greater contribution to population growth made by good grow-

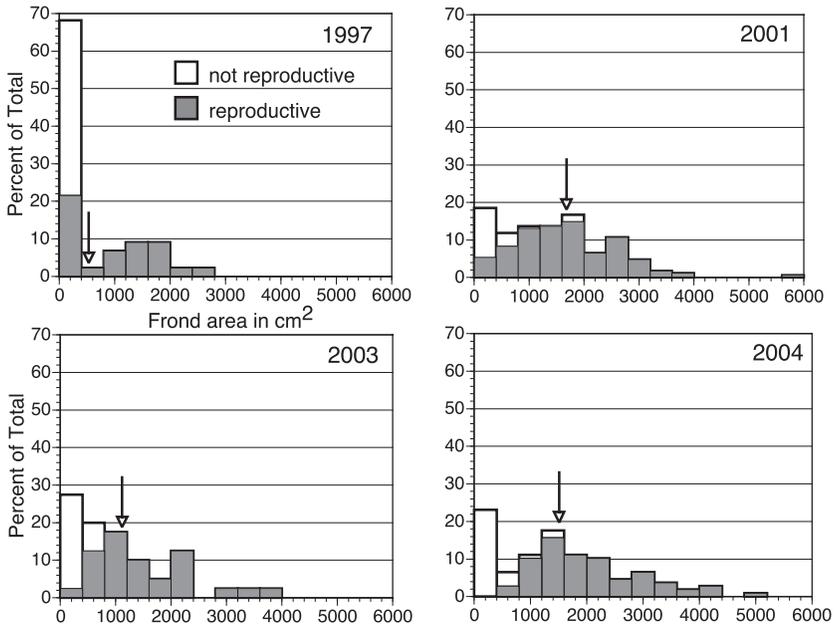


Figure 11.1. The size distribution of the kelp *Alaria nana* in four years of study. The shaded areas denote the presence of individuals within a size grouping that are reproductive; arrows show mean size within a year. Note that mean-sized individuals may not reproduce. The El Niño year (1997) shows a failure of individuals to reach larger size classes. In all years, a relatively small fraction (5%) contributes at least a third of the reproductive output.

ers in good years. These patterns continue to be borne out by the data. 1997 was an aberrant year in kelp demography, not because of mass mortality but because the El Niño conditions allowed relatively few individuals in the population to do persistently well (figure 11.1). As a consequence, only 53% of individuals reproduced in 1997, whereas 81%, 68%, and 77% reproduced in 2001, 2003, and 2004. A look at growth autocorrelation estimates during these four years (estimated from growth rates between May and September), showed that the “good” years of 2001, 2003, and 2004 had estimates of 0.54, 0.68, and 0.57, while the El Niño year was only 0.48. In a related 1997–98 El Niño study, Paine and Trimble (2004) documented that an ENSO-forced brown algal “disaster,” coupled to major *M. californianus* recruitment, might lead to the establishment of an intertidal alternative state. Time series dating to 1978 of percentage of cover by the brown alga *Hedophyllum sessile* were used to identify the prevalence of the original state; ongoing *Pisaster* removals to protect the mussels until they become too large to be eaten are now testing this possibility.

## Linking Populations to Communities

Communities at local spatial scales are composed of interacting populations. Pfister has used the same analytical techniques described for kelp to ask how recruitment variability among years affects the interaction and coexistence of fishes in a multispecies assemblage. Tidepool sculpins are conspicuous and species-rich in our study area. They are characterized by high site fidelity to a single or group of tidepools, and tidepools rarely contain only one species. Young-of-the-year fishes are numerous during the months from April to June (Pfister 1996, 1997), settling into tidepools with resident adults after a period in the water column that may last from 30 to 60 days. Short-term (two-month long) experiments more than a decade ago showed the competitive dominance of *Oligocottus maculosus* over *Clinocottus globiceps* (Pfister 1995), and the superiority of dynamic regression techniques (state-space models) that relied on multiple census points (also known as time series data) to estimate interaction strengths for replicating this empirical result. Quantifying the competitive interaction set up the prediction that *C. globiceps* must recruit consistently into the system to persist, a prediction that has been borne out from 16 years of annual censuses. The long-term data also did not support an earlier favored hypothesis that variability among species in success of recruitment would provide a mechanism for coexistence via the storage effect. Instead, the relative ranking of species abundances as recruits is remarkably constant, and it shows no evidence that environmental variation, including two El Niño events, has altered this ranking (Pfister 2006).

The above gives us the insight that the links between individuals, populations, and communities in aquatic systems often develop via variability in individual growth. For example, individual fish that recruit relatively early in the spring experience high early growth, and reach a larger size by winter. This head start appears to give them an increased probability of reproducing in their first year (Pfister 1997). Traits of individuals, or small microhabitat advantages, can result in variability in growth that has “memory” through time, resulting in some individuals that become large. In the case of the kelp, *Alaria nana* (figure 11.1), an individual of average size for a population might not reproduce, but attention to variance would reveal that few individuals contribute disproportionately to reproduction. For *A. nana*, the largest 5% of the individuals can contribute as much as a third of the reproductive output of the entire population. In addition to the possible beneficial effects this has for ameliorating population viability, it may be an important aspect of size-based species interactions. In other examples, Paine (1976) has shown how the susceptibility of mussels to *Pisaster* predation depended on their respective sizes; mussels can coexist with their major

consumer simply by becoming too large. Wootton (1993b) demonstrated that the original size hierarchies of competitors could influence both the rate of successional change and susceptibility to disturbance. Our experience with this system has shown that variation detected on a scale of weeks has potential implications for generations. In the context of global change, such variation may play a pivotal role. Many of the predictions from global climate models call for changes in mean temperatures, increased variability in environmental variables such as temperature (Intergovernmental Panel on Climate Change 2001), and for an increased frequency of El Niño events (Timmerman 1999).

### **The Intersection of Independent Studies: Improved Understanding**

The study of Dayton (1971) remains an ecological landmark: spatially replicated experiments coupled with superior intuition and observational skills are its hallmarks. Much of the research was conducted in the Cape Flattery region, and only a little at Tatoosh. That paper and its immediate derivatives (Dayton 1973a, 1975) concentrated on spatial patterns and, whenever possible, experimental probes of the underlying causes. One of the conclusions has become ecological dogma. Dayton observed wood splinters embedded in intertidal rock, massive logs commonly deposited in the supratidal, and patches or gaps occurring with regularity in mussel beds. The logical conclusion was that bashing by drift logs had initiated these disturbance events. “Mortality” of two-cm-high nails set in intertidal rock also suggested a role for massive objects like logs. All of Dayton’s natural historical observations can be repeated. Our challenge is to understand the generality, not the condition-specific occurrence, of log bashing.

Some evidence is derived from long-term monitoring of the winter extent of mussel bed patch formation, and especially from tracking the fate of devices used in an unrelated algal fertilization experiment described by Wootton et al. (1996). These devices were 15-cm-diameter, 11.5-cm-high clay flower pots cemented to the rock surface at eight sites around the wave-exposed perimeter of Tatoosh. The four experimental periods ranged from less than two to about four months. Pot “survival” was extraordinary: 23 of 24, 28 of 32, 32 of 32, and 31 of 32. Survival of the third series was followed for one year, with the single pot mortality occurring during winter. Figure 11.2 illustrates the 12-year survival pattern of the fourth series. Pot mortality is about two per year (6.3% per year). Our suspicion is that the primary cause is not log bashing in this case, but rather gradual hydration and thus swelling of the cement base leading to deformation and eventual fracture of the pot.

Huge (>8–10 m high; see figure 11.0) waves and drift logs are a fact of life in the northeast Pacific. Here we argue that the former, acting by themselves,

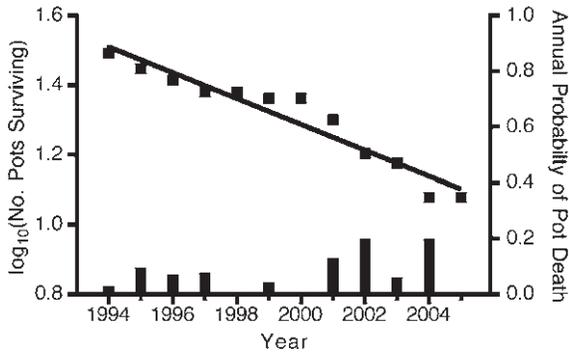


Figure 11.2. Survival of ceramic pots at Tatoosh. The solid line fitted to the actual decline represents a mean mortality of 6.3% per year. Solid bars give the years of pot “death” over 12 years of observation.

are sufficient to disrupt mussel beds. This contention is supported in four ways. First, patches or gaps generally form in the center of mussel beds, or at least rarely include perimeter individuals; Paine and Levin (1981) provide a photograph. Second, Witman and Suchanek (1984) showed that mussel tenacity was higher at the edge than in the middle of mussel beds. Denny (1987), studying mussels at Tatoosh, implicated lift, not shear or drag, as the most important physical force in generating internal patches. Mussel position and tenacity are presumably immaterial factors when and where waterborne logs impact mussels. Third, Dayton’s (1971) nails present a surface area estimated at 40 square mm; our more fragile terra-cotta pots at 17,250 square mm in cross-sectional area are not only 430 times larger, but also project five to six times higher into the water column. On both counts they present a much larger target, and hence are presumably more susceptible to waterborne missiles. And fourth, this evolving perspective, coupled with the development of a data set on community dynamics at the same sites spanning seven years (at the time), prompted Wootton (2001b) to develop a cellular automata model of local interactions among individuals, which included the key process of wave-disturbance transmission via attachment of neighbors to each other in the mussel bed. Wootton’s model, one of the first empirical parameterizations of this important class of models in any field, was able to successfully predict the large-scale spatial structure of a system generated by disturbance events, thus supporting the wave-impact view.

We present these details because Dayton’s observations, measurements, and logic were convincing and remain pertinent to probably all areas in which logs are moved laterally along shorelines. At Tatoosh, longer-term observations on where patches tend to occur, the biomechanical studies of Witman and Suchanek and Denny, and especially the conceptually unrelated pot study, implicate an alternative explanation that a characteristic spatial pattern is generated primarily by hydrodynamic forces.

## Generalizing from Single-Site Studies

The quest for ecological generality must progress beyond the demonstration of macroecological patterns. In other words, species identity does matter (e.g., Paine 1980, 1984; Pfister 1995; Wootton 2005); some interactors are “strong” while others are “weak”; some may be keystones, foundation species, engineers, ruderals, and so forth. Such terms, which are jargon to detractors but have implicit meaning to supporters, seem an unavoidable shorthand in the same league as terms like niche, guild, and food web. All disciplines evolve specialized language, as even a cursory examination of mathematics, physics, chemistry, and molecular biology reveals. Ecology’s semantic curse is that our vocabulary tends towards the qualitative, driven by the complexity of all natural systems and the intrinsic uncertainty so characteristic of the embedded interactions.

How has our Cape Flattery enterprise fared in the marketplace of ecological ideas? “Keystone species” has survived and seems well established, though it is recognized as not being universally applicable (Power et al. 1996). Tatoosh-based research has contributed in a number of ways to the analysis of spatial patterns; the dynamics of food webs; a deeper understanding, analysis, and nomenclature of indirect effects; and an empirical challenge to the storage effect. The concept of trophic cascades, now recognized in many other ecosystems, was born there. Our individual research programs continue to be based on species studied either alone or when interacting in multispecies complexes.

Intertidal, rocky shore communities pose some challenges to generalization that may be either trivial or highly substantive: sessile plants and animals compete for a basic resource, space. Competition between barnacles and kelp or between sponges and coralline algae, for example, is commonplace. If one considers trophic level or status as a crux of ecological interactions, then the fact of competition across trophic levels can be problematic. We have referred to this as an “amusing fact of intertidal ecology”; others studying terrestrial or pelagic systems may interpret it as an intellectual barrier to generalization. Of equivalent importance are the relative openness of marine systems, the astonishing but spatially limited primary production, and the conspicuousness of trophic interactions. Are intertidal systems outliers because of these differences, and are they thus of little significance to broadly acceptable ecological generalizations? We think the answer is no.

Intense study at a single site also allows ancillary monitoring of a number of variables that would be impossible (and unfundable) over a larger spatial scale. Although some of these variables may be found to be trivial, the prospect of a changing climate and species composition makes ecological “surprises” almost a certainty (Doak et al. 2008). This is well-demonstrated

on Tatoosh by the fortuitous placement of a pH probe on an instrument that was intended to measure variables that we hypothesized were of primary importance: chlorophyll *a* and temperature. The notion that ocean pH might be well-buffered to increases in atmospheric CO<sub>2</sub> has recently been challenged, and our monitoring data from Tatoosh over the last nine years shows an alarming decrease in sea water pH at a more rapid rate than that predicted by physical models (Wootton et al. 2008). Because most pH variation we observe can be explained by associated long-term data on drivers with known mechanistic links to pH, the relevance of our results extends beyond this single site. Furthermore, the concomitant long-term record of species dynamics assembled by Wootton over the same time period suggests effects on dominant organisms with calcium carbonate skeletons, and the extensive history of experimentation and modeling to understand biological interactions at this site provides a necessary perspective to untangle the complex responses of this natural ecosystem that arise from indirect effects. Our unique ability to tie the measured pH decline to in-situ biological effects was the result of a commitment to the study of a place; it is research that would have fared poorly in the funding arena a decade ago when this aspect of climate change was underappreciated. Future understanding of the link between ocean chemistry and biology will require intense study at specific locales. It is unlikely that we will gain full insight from snapshot samples scattered throughout the ocean, or from laboratory experiments divorced from the web of interactions and physical processes that characterize real ecosystems.

Finally, because the Cape Flattery ecosystem is essentially intact trophically, with the possible exception of breeding northern fur seals, we have not ignored the roles of higher trophic levels. Our experiments to date have involved roughly 70 species, a small fraction of the total possible. Our challenge—and more broadly, community ecology’s challenge—is how to, or even whether to, confront such species-specific complexity. Resolving this dilemma will involve (1) new analytical techniques; (2) long-term sampling to generate time series data on temporal variation; and, whenever possible, (3) experimental manipulation. Rocky intertidal research has the unique potential to unite these disparate approaches into a cohesive framework. Whether this helps develop common principles through conceptual unification or detracts from this desirable goal remains to be seen.

## Summary

The Cape Flattery region has always been a biologically attractive venue. The Makah Indians, presumably attracted by the marine bounty, were the original inhabitants; Rigg and Miller (1949) undertook intermittent surveys

from 1911 to 1948; at least 10 students from Oberlin College, Ohio, “in the ecology party of Prof. Lynds Jones” (Tatoosh log book) visited Tatoosh on 24 June 1912. Our research began in 1963 and continues today, with Tatoosh being the primary site.

Observations on natural history and species interactions are easily made, at least at low tide. They have proven to be of fundamental importance to hypothesis formation, and they generate an incomplete but expanding collective wisdom. Spatial patterning is obvious. The solid rock platform has permitted sundry experimental and other devices to be secured. One immediate result has been a proliferation of lengthy time series for many plant and animal species, data often coupled to some specific experimental manipulation. The strength of our spatially myopic efforts—rather than the proverbial devil—lies in the details. Our studies focus on food web dynamics, the interplay between disturbance-generated pattern and successional processes, the significance of variation in recruitment, and how and why growth autocorrelations influence population performance. As each of these themes has matured, they have become increasingly quantitative. Further, by providing details of mechanisms and indirect effects, their integration has made rocky intertidal shores into model study systems. Tatoosh Island is miniscule as ecological places go; our site-based research illustrates well how local knowledge advances conceptual understanding and helps realize the “small” ecology goal of relating explicit process to pattern.

### Acknowledgments

Numerous individuals spanning the academic continuum, from undergraduate students to distinguished senior scientists, have contributed both labor and stimulation. Our research has been funded by the National Science and Andrew W. Mellon foundations. We are deeply grateful to the above, but especially to the Makah Nation for permission to conduct research on their spectacular shores.

### References

- Brown, J. H. 1995. *Macroecology*. University of Chicago Press, Chicago.
- Caswell, H. 2001. *Matrix Population Models, Second Edition*. Sinauer Associates, Sunderland, MA.
- Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42:710–23.
- Darwin, C. 1859. *The Origin of Species*, Modern Library edition. Random House, New York.
- Dayton, P. K. 1971. Competition, disturbance and community organization: The provision and subsequent utilization of space in an intertidal community. *Ecological Monographs* 41:351–89.

- . 1973a. Dispersion, dispersal, and persistence of the annual intertidal alga, *Postelsia palmaeformis* Ruprecht. *Ecology* 54:433–38.
- . 1973b. Two cases of resource partitioning in an intertidal community: Making the right prediction for the wrong reason. *American Naturalist* 107:662–70.
- . 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecological Monographs* 45:137–59.
- Denny, M. W. 1987. Lift as a mechanism of patch initiation in mussel beds. *Journal of Experimental Marine Biology and Ecology* 113:231–45.
- Doak, D. F., J. A. Estes, B. S. Halpern, U. Jacob, D. R. Lindberg, J. Lovvorn, D. H. Monson, M. T. Tinker, T. M. Williams, J. T. Wootton, I. Carroll, M. Emmerson, F. Micheli, and M. Novak. 2008. Understanding and predicting ecological dynamics: Are major surprises inevitable? *Ecology* 89:952–61.
- Duggins, D. O., and M. N. Dethier. 1985. Experimental studies of herbivory and algal competition in a low intertidal habitat. *Oecologia* 67:183–91.
- Intergovernmental Panel on Climate Change. 2001. *Climate Change 2001: The Scientific Basis. Contribution of Working Group 1 to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC)*. J. T. Houghton, Y. Ding, D.J. Griggs, M. Noguer, P. J. van der Linden, and D. Xiaosu, eds. Cambridge University Press, Cambridge.
- Laska, M. S., and J. T. Wootton. 1998. Theoretical concepts and empirical approaches to measuring interaction strength. *Ecology* 79:461–76.
- Lawton, J. H. 1999. Are there general laws in ecology? *Oikos* 84:177–92.
- Levin, S. A., and R. T. Paine. 1974. Disturbance, patch formation and community structure. *Proceedings of the National Academy of Sciences (USA)* 71:2744–47.
- Lewis, J. R. 1964. *The Ecology of Rocky Shores*. English Universities Press, London.
- MacArthur, R. H. 1972. Strong, or weak, interactions? *Transactions of the Connecticut Academy of Arts and Sciences* 44:177–88.
- Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs: Patterns and importance. *Ecological Monographs* 65:21–74.
- Menge, B.A., E. L. Berlow, C. Blanchette, S. A. Navarrete, and S. B. Yamada. 1994. The keystone species concept: Variation in interaction strength in a rocky intertidal habitat. *Ecological Monographs* 64:249–86.
- 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.
- . 1974. Intertidal community structure: Experimental studies on the relationships between a dominant competitor and its principle predator. *Oecologia* 15:93–120.
- . 1976. Size-limited predation: An observational approach with the *Mytilus-Pisaster* interaction. *Ecology* 57:858–873.
- . 1980. Food webs: Linkage, interaction strength, and community infrastructure. *Journal of Animal Ecology* 49:667–685.
- . 1984. Ecological determinism in the competition for space. *Ecology* 65:1339–1348.
- . 1992. Food web analysis through field measurements of per capita interaction strength. *Nature* 355:73–75.
- . 2002. Trophic control of production in a rocky intertidal community. *Science* 296:736–739.
- Paine, R. T., and S. A. Levin. 1981. Intertidal landscapes: Disturbance and the dynamics of the pattern. *Ecological Monographs* 51:145–78.

- Paine, R. T., and A. C. Trimble. 2004. Abrupt community change on a rocky shore: Biological mechanisms contributing to the potential formation of an alternative state. *Ecology Letters* 7:441–45.
- Paine, R. T., and R. L. Vadas. 1969. The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. *Limnology and Oceanography* 14:710–19.
- Parrish, J. K., M. Marvier, and R. T. Paine. 2001. Direct and indirect interactions between bald eagles and common murre. *Ecological Applications* 11:1858–69.
- Pfister, C. A. 1995. Estimating competition coefficients from census data: A test with field manipulations of tidepool fishes. *American Naturalist* 146:271–91.
- . 1996. Consequences of recruitment variation in an assemblage of tidepool fishes. *Ecology* 77:1928–41.
- . 1997. Demographic consequences of within-year variation in recruitment. *Marine Ecology Progress Series* 153:229–38.
- . 2006. Concordance between short-term experiments and long-term censuses in tidepool fishes. *Ecology* 87:2905–14.
- Pfister, C. A., and F. R. Stevens. 2002. The genesis of size variability in plants and animals. *Ecology* 83:59–72.
- . 2003. Individual variation and environmental stochasticity: Implications for matrix model predictions. *Ecology* 84:496–510.
- Pfister, C. A., and M. Wang. 2005. Beyond size: Matrix projection models for populations where size is an incomplete descriptor. *Ecology* 86:2673–83.
- Pfister, C. A., J. T. Wootton, and C. J. Neufeld. 2007. Relative roles of coastal and oceanic processes in determining physical and chemical characteristics of an intensively sampled nearshore system. *Limnology and Oceanography* 52:1767–75.
- Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the quest for keystones. *BioScience* 46:609–20.
- Rigg, G. B., and R. C. Miller. 1949. Intertidal plant and animal zonation in the vicinity of Neah Bay, Washington. *Proceedings of the California Academy of Sciences* 26:323–51.
- Robles, C., R. Sherwood-Stephens, and M. Alvarado. 1995. Responses of a key intertidal predator to varying recruitment of its prey. *Ecology* 76:565–79.
- Rosenfeld, A. W., and R. T. Paine. 2002. *The Intertidal Wilderness*. University of California Press, Berkeley.
- Ruesink, J. R. 1998. Variation in per capita interaction strength: Thresholds due to nonlinear dynamics and nonequilibrium conditions. *Proceedings of the National Academy of Sciences (USA)* 95:6843–47.
- Suchanek, T. H. 1979. *The Mytilus Californianus Community: Studies on the Composition, Structure, Organization, and Dynamics of a Mussel Bed*. PhD dissertation, Department of Zoology, University of Washington, Seattle.
- Timmerman, A., J. Overhuber, J. Bacher, M. Esch, M. Latif, and E. Roeckner. 1999. Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature* 398:694–97.
- Underwood, A. J., and P. S. Petraitis. 1993. Structure of intertidal assemblages in different locations: How can local processes be compared? Pages 39–51 in R. E. Ricklefs and D. Schluter, eds., *Species Diversity in Ecological Communities*. The University of Chicago Press, Chicago.
- Witman, J. D., and T. H. Suchanek. 1984. Mussels in flow: Drag and dislodgment by epizoans. *Marine Ecology Progress Series* 16:259–68.

- Wootton, J. T. 1992. Indirect effects, prey susceptibility, and habitat selection: Impacts of birds on limpets and algae. *Ecology* 73:981–91.
- . 1993a. Indirect effects and habitat use in an intertidal community: Interaction chains and interaction modifications. *American Naturalist* 141:71–89.
- . 1993b. Size-dependent competition: Effects on the dynamics versus the endpoint of mussel bed succession. *Ecology* 74:195–206.
- . 1994. Predicting direct and indirect effects: An integrated approach using experiments and path analysis. *Ecology* 75:151–65.
- . 1995. Effects of birds on sea urchins and algae: A lower-intertidal trophic cascade. *Écoscience* 2:321–28.
- . 1997. Estimates and tests of per-capita interaction strength: Diet, abundance, and impact of intertidally foraging birds. *Ecological Monographs* 67:45–64.
- . 2001a. Prediction in complex communities: Analysis of empirically-derived Markov models. *Ecology* 82:580–98.
- . 2001b. Local interactions predict large-scale pattern in an empirically-derived cellular automata. *Nature* 413:841–43.
- . 2004. Markov chain models predict the consequences of experimental extinctions. *Ecology Letters* 7:653–60.
- . 2005. Field parameterization and experimental test of the neutral theory of biodiversity. *Nature* 433:309–12.
- Wootton, J. T., C. A. Pfister, and J. D. Forester. 2008. Dynamical patterns and ecological impacts of declining ocean pH in a high-resolution multi-year dataset. *Proceedings of the National Academy of Sciences (USA)* 105:18848–18853.
- Wootton, J. T., M. E. Power, R. T. Paine, and C. A. Pfister. 1996. Effects of productivity, consumers, competitors, and El Niño events on food chain patterns in a rocky intertidal community. *Proceedings of the National Academy of Sciences (USA)* 93:13855–58.