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# 6

# Experimentation, Observation, and Inference in River and Watershed Investigations

MARY E. POWER, WILLIAM E. DIETRICH, & KATHLEEN O. SULLIVAN

*Ecologists seek to understand the interactions between species and their heterogeneous, changing environments. This work is made more difficult by the fact that the underlying processes are often mediated through complex community- or ecosystem-level interactions. What tools do we have for unraveling this complexity?*

Paine (1994) and Walters (1986, 1992) have reviewed the three fundamental methods available to field scientists: observation, modeling, and experimentation. All new information about nature is initially obtained through the first method: observation, which includes monitoring, mapping, and detecting correlations or other patterns. Observation alone, particularly when done in a hypothesis-free manner, has in the past disappointed ecologists by leaving them with messy data sets open to alternative interpretations. For this reason, ecologists in recent decades considered inferences from observations to be weak relative to inferences drawn from manipulative experiments (e.g., Connell 1974). We believe that field observations have been undervalued in contemporary community ecology, leaving ecologists poorly equipped to contribute to problems at large spatial scales at which manipulative experiments are infeasible. We will elaborate on this point later.

A second fundamental method for studying nature is modeling. We refer here to mechanistic modeling, either mathematical or qualitative, which attempts to portray key process that underlie phenomena of interest. The limitations of modeling are well known (e.g., Starfield and Bleloch 1986, Walters 1992). There is usually an assumption that the system's context is constant, and this is never true of real ecosystems. Also, modelers must assume that many (most) details are unimportant, but inevitably some omitted details will be important, probably more so than others chosen for representation in the model. Nevertheless, as Walters (1992) points out, modeling is unavoidable. If we have an idea about how our system works, we have a model of it. Therefore, he advises that we model openly, making assumptions explicit to ourselves and others.

The third method is experimentation, defined here in the narrow sense that community ecologists typically use. Experiments (sensu strictu, Paine 1994) involve study of replicated sample units which are subject to at least two treatments. One treatment is a control intended to represent the unmanipulated or background condition. In the other treatment(s), one or more factors are altered by the experimentalist, and their influence is evaluated by comparing responses of manipulated to control treatments. Replicated experiments cannot be performed in many situations, either because of logistical constraints (Matson and Carpenter 1990) or because adequate controls do not exist (see discussion of scale issues following).

## Combined or Nested Approaches

While much has been written about the greater power or rigor of experimental over observational approaches (e.g., Paine 1977, Underwood 1990), it is usually more powerful to combine these approaches in a nested fashion (Fig. 6-1; see also Frost et al. 1988:252, Carpenter 1996). How experiments, observations, and modeling are combined depends on the scale of the study and the question addressed. A question that has served as an extremely productive opening gambit for community ecologists as they first explore a system has been: "What would happen if . . . ?" (Fig. 6-1a): "What would happen if I alter the density of species A or change factor B?" motivating what Art Dunham has called "kick it and see" experiments. This is the approach that has revealed important surprises, such as keystone species (Paine 1966, 1969).

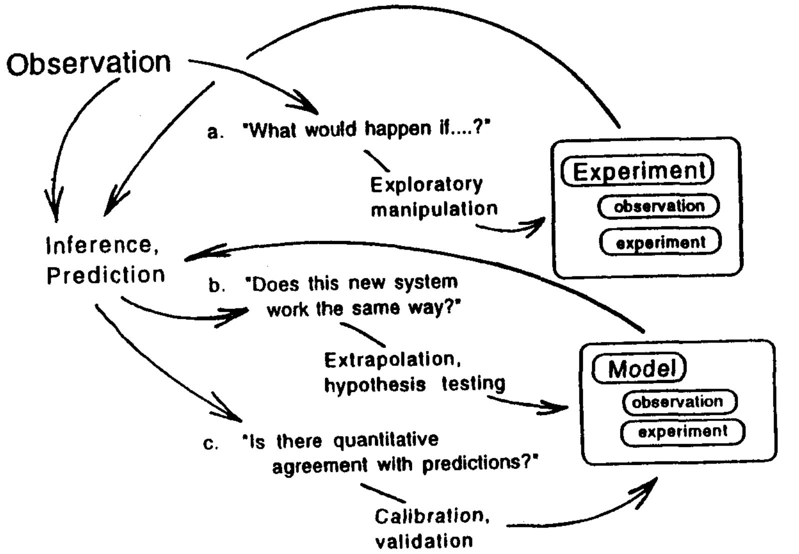

Figure 6-1. Nested experimental, observational, and modeling approaches to ask three types of questions.

When experiments like these are done in intertidal systems on exposed rocky shores, as were the experimental removals of the starfish *Pisaster* that led to the original formulation of the keystone concept (Paine 1966, 1969), direct observations of underlying processes are difficult or impossible. Intertidal "action" (grazing, predation, growth, settlement, export, and reproduction) typically happens under conditions inconvenient for human observers (e.g., crashing surfs on moonless nights). Inferences must be drawn from periodic observations (typically at roughly monthly intervals) of changes in the states of assemblages. These interpretations are bolstered by knowledge of the local biology and the physical environment. When investigators are not able to observe the underlying processes in action, however, uncertainty may arise as to which components of the excluded biota were responsible for treatment effects (e.g., Edwards et al. 1980, Menge 1980, Underwood and Fairweather 1986) or whether alteration of consumer densities or behavior (Menge and Sutherland 1976, Menge 1980) or unintended habitat modifications (Virnstein 1978, Dayton and Oliver 1980, Hulberg and Oliver 1980) have caused or contributed to changes. Consequently, questions and controversies over the interpretations of experimental results persist.

Direct observations, when possible, can illuminate experimental black boxes, reducing the danger of misinterpreting experimental results. They are no panacea, given the problem of witnessing, let alone sampling, rare events with high impacts. But even in what would seem unlikely arenas, such as bottle experiments with microorganisms, direct observations have illuminated causality. Gause (1934) directly observed the spatial separation of two competing *Paramecium* species and their food resources (suspended bacteria vs. deposited yeast cells) and deduced his famous principle that this separation contributed to their coexistence. More recently, Balciūnas and Lawler (1995) used direct microscopic observation to detect an escape in size by a prey protozoan, *Colpidium*, from its predator *Euplotes*, which occurred when nutrient levels were increased in bottle experiments. Their observation uncovered the mechanism by which nutrient addition blocked top-down food chain control and shortened the length of the functionally important food chain, in contrast to previous predictions from simple food chain considerations (e.g., Lindeman 1942, Fretwell 1977, Oksanen et al. 1981). Clearly, direct observations can lead ecologists to both propose ecological generalizations and question them.

When we know more about a system, we can work within the framework of models, which are hypotheses about how the system works (Fig. 6-1b,c). For example, we can attempt to extrapolate. We might observe that a different system shares features with one that has been partially understood and ask whether the new system works the same way. We may instead be interested in whether the previously studied system will continue to work the same way under new conditions and whether our understanding is robust beyond the circumstances in which it was first attained. When we have a model of how the system works in mind, we can nest both observations and experiments within this model to test it (Fig. 6-1b). If a model has been developed to the point of making quantitative predictions, we can also use nested experiments and observations to calibrate it (Fig. 6-1c) and eventually to validate it (to test the match between predictions of a fully calibrated model and observations from nature). Nested experimental manipulations may be needed if parameters require calibration under a range of partially controlled conditions.

We will illustrate these three types of nested approaches with case histories drawn from river food web investigations and then discuss constraints on the application of these methods as the spatial extent of the system under study increases.

## Nested Experimental and Observational Studies of River Food Webs

### *"What happens if . . . ?": The Eel River of Northern California*

In the summer of 1989, Power experimentally manipulated fish in the South Fork Eel River to ask: "What happens if . . . the two most common species are excluded?" Enclosures and exclosures were distributed over a 1-km reach within the forested watershed of the Angelo Coast Range Reserve (formerly the Northern California Coast Range Preserve). Only two fishes—juvenile steelhead (*Oncorhynchus mykiss*) and California roach (*Hesperoleucas symmetricus*)—are common after winters with normal scouring floods. Surprisingly dramatic differences arose between fish enclosures and exclosures 5 to 6 weeks after the onset of the experiments. In the presence of fish, the dominant alga, *Cladophora*, which grew as 40 to 60–cm high turfs attached to boulder and bedrock at the start of the experiment, had collapsed down to a prostrate webbed mat no more than 1 to 2 cm high. The algae remained erect in the fish exclosures and became overgrown with nitrogen-fixing bluegreens and diatoms (Power 1990). Densities of benthic insects differed markedly between treatments as well. The fish enclosures were heavily infested with midges, *Pseudochironomus richardsoni*, that lived within the algae and wove it into tufts around its body. Heavy infestations of tuft-weaving midges collapsed the algal mats and produced a webbed and knotted architecture. This occurred several weeks later in the open river. Tuft-weaving midges were rare in the fish exclosures, where large numbers of small predators (lestid nymphs, sialid larvae, and young-of-the-year roach and stickleback) had recruited. These small predators were rare in the open channel and in fish enclosures but recruited in large numbers where larger fish were excluded and apparently suppressed the midge.

Power tested this last inference with a nested experiment and direct observations. She stocked 24 screened (1-mm mesh) buckets with ca. 7 g of cleaned *Cladophora* (picked free under 10× magnification of conspicuous macroinvertebrates). Six buckets received four roach fry, six received four stickleback fry, six received four lestid nymphs, and six were left as predator-free controls. After 20 days, the predator-free controls had been colonized by four times more midges than had any of the predator treatments (Power 1990). This nested experiment supported the interpretation that it was the guild of small predators that had, in fact, suppressed the recruitment of tuft-weaving midges to fish exclosures. Subsequent direct observations of feeding by larger fish and invertebrate predators revealed that the common predatory invertebrates (lestid damselflies, aeshnid dragonflies, and naucorid bugs) all are able to detect midges and extract them from their algal tufts. The odonates, after watching tufts for several minutes, shot their mouthparts in and extracted midges with a "surgical strike." The naucorid bugs probed cocoons with their beaks until they encountered the midge. In contrast, the larger fish in the Eel River did not seem able to detect chironomids within their algal tufts, although when midges were extracted and exposed these fish ate them readily (Power et al. 1992). These behavioral observations documented the predator-specific vulnerability of the prey, which was the mechanism that produced four functionally significant trophic levels in the Eel River. Herbivorous mayflies were the dominant prey in the guts of the larger fishes (Power et al. 1992). Observations of gut contents alone would have suggested that fish should exert control from the third trophic level and enhance, rather than suppress, plant biomass. Clearly, a combination of experimental and observational results produced a better understanding of food web interactions than either approach would alone, but at this early stage of investigating a poorly understood system experiments were particularly critical.

### *"Can we extrapolate?" The Eel River during Drought and Brier Creek, Oklahoma*

Power and colleagues repeated these fish manipulations during the summers of 1990 and 1991, doubling the enclosure numbers from 12 to 24 and expanding the design to study the separate as well as the combined effects of roach and steelhead. In contrast to the 1989 results, however, fish had no functionally significant impacts on algae in either 1990 or 1991. In both the presence and the absence of fish, algae collapsed down to detritus within the first weeks of the experiment. A multiyear drought had begun in 1990, and in the absence of scouring floods large numbers of armored and sessile invertebrate grazers, invulnerable to most predators in the river, survived over the winter. When *Cladophora* began to grow in the late spring, these grazers quickly nibbled it back. These natural history observations finally motivated the definitive experiment, which was a 2 × 2 factorial manipulation of steelhead and the dominant armored caddisfly, *Dicosmoecus gilvipes*. The results showed that *Dicosmoecus*, not fish, controlled algal biomass during drought. Steelhead still had a statistically significant negative effect on algae (suggesting they were still at the fourth trophic level), but their effect was small in comparison to the two-level impact of the predator resistant grazers (Wootton and Power, unpublished data). Cross-watershed surveys of algae and invertebrates in two regulated channels with artificially stabilized flow and four unregulated rivers that all scoured in 1989 were also consistent with the inference that scouring floods reset primary consumers to earlier successional stages that are more vulnerable to predation and set the stage for trophic cascades that affect algal biomass (Power 1992).

The Eel River food web obtained under "normal" Mediterranean winter-flood, summer-drought conditions did not extrapolate to the same system during drought (Power 1995) or to regulated channels in the region that had been subject to anthropogenic "disturbance removal experiments." A food chain that had four functional trophic levels with respect to impacts of predators mediated through consumers on plants collapsed to a drought food chain with two functional trophic levels (Fig. 6-2), despite the fact that all the key species were still represented in the community.

Extrapolation is useful even when it fails, because expectations that one system may resemble another "prepare the mind" to make focused observations that either support

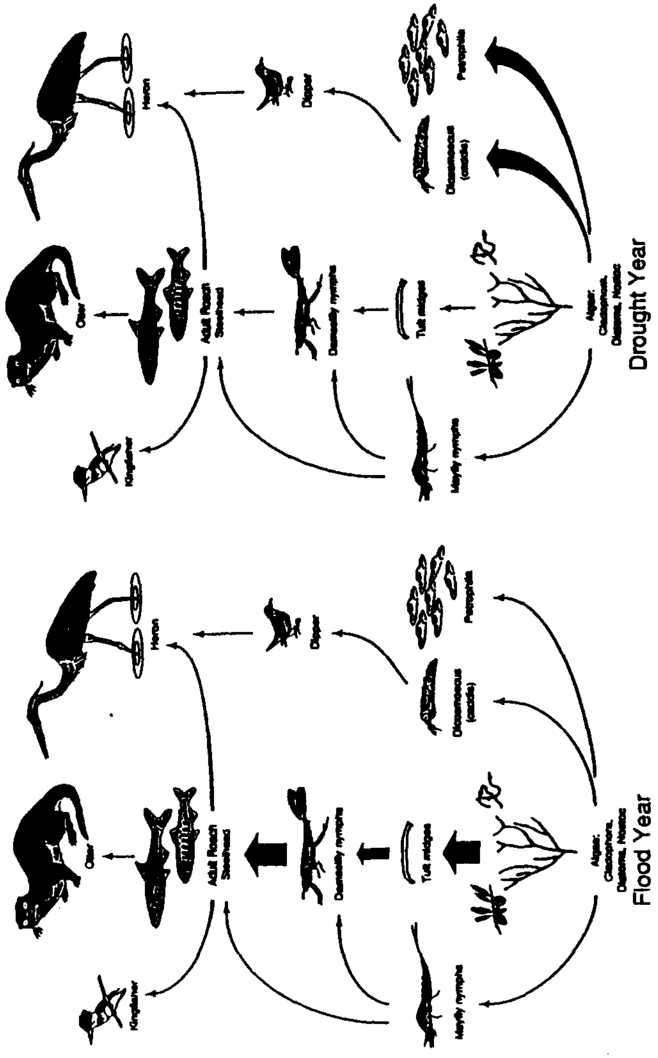

Figure 6-2. Functional food chain length in the Eel River during normal winter-flood, summer-drought regimes (*left*) and during year-round drought (*right*).

or refute the expectations. In contrast to the attempt to extrapolate from flood to drought years for the Eel River web, properties of a food web in an Oklahoma prairie stream were predictable by analogy with subtidal food webs in the northeastern Pacific, where sea otters suppress sea urchins and indirectly maintain kelp forests (e.g., Estes and Palmisano 1974). In Brier Creek, Oklahoma, some pools were filled with filamentous green algae, while adjacent pools were nearly barren. Observations of the distributions of predators and grazers quickly confirmed expectations from the sea otter–urchin–kelp model: piscivorous bass occurred in the green pools and were absent from the barren pools, where schools of grazing minnows (*Campostoma anomalum*) occurred (Power and Matthews 1983). Subsequent experimental transfers of bass and *Campostoma* among stream pools demonstrated that a trophic cascade did underlie the complementarity of bass, *Campostoma*, and algae. We electroshocked bass out of a green pool, split it down the middle, and added *Campostoma* to one side; within 5 weeks, algae on that side were grazed down to a barren state, while the control side without the grazing minnows remained green (Power et al. 1985). Clearly, herbivory accounted for the barren condition of pools with *Campostoma*. It was not obvious, however, whether the mechanism for the complementarity between bass and their minnow prey was predation or predator avoidance because, unlike algae, minnows have potential escape behavior.

We resolved this question about causality with direct observations. We added bass to a pool with a school of *Campostoma* but, before doing so, fenced off the upstream and downstream ends of adjacent pools, which were linked to the *Campostoma* pool by riffles which minnows could cross but which were too shallow for bass passage. These fenced areas served as potential "escape ports" for *Campostoma*. We also gridded the substrate of the *Campostoma* pool and, before bass addition, made behavioral observations of space use by adults and, during a spring repetition of the experiment, by young-of-the-year minnows. The adult fish tended to graze the deepest parts of the pool, with the young in slightly shallower water. After bass addition, both size classes moved into shallower water, which accounted for transient dynamics in the spatial distribution of the algae, which initially declined in these shallow areas (Power et al. 1985, Power 1987). Over the next 5 or 6 weeks, however, the entire pool became overgrown with green algae. Predator avoidance was an important contributing factor: in the spring experiment, we found 40 of the initial 74 adult minnows in the upstream escape port just 1 week after bass had been added. Whether bass convert *Campostoma* to bass meat or simply rearrange them spatially is of long-term significance to ecosystem dynamics. The partitioning of this causality required direct observation, within the context of a manipulative experiment.

### *Model Calibration and Validation—The Rio Frijoles of Central Panama*

In the Rio Frijoles of central Panama, four species of armored catfish are the dominant algal grazers. Their algal foods renew faster in sunny stream pools than in dark pools. Power (1984) used an experimental manipulation to quantify this difference. She placed groups of unglazed clay tiles, with texture similar to that of the natural bedrock substrate, on pegs that elevated them above the streambed—in this position, they were not grazed, and visible standing crops of attached algae accrued over periods of 16 days. Harvesting these standing crops revealed that organic matter (mostly attached algae) accrued about seven times faster in two moderately sunny pools (25 to 50% open canopy) than in two dark pools (<10% open canopy). This difference corresponded quantitatively to the densities of armored catfish, which were about six to seven times denser in moderately sunny than in dark streams. Snorkeling censuses done of 16 stream pools over 12 consecutive months showed a consistent correlation of armored catfish densities (individuals per area grazeable substrate) with canopy and hence with primary productivity in the light-limited stream. These censuses suggested that fish tracked the productivity of their food, but the correspondence could have been misleading, as fish could have grazed outside pools where they were counted when not being observed. To resolve this issue, Power made direct behavioral observations (scan samples for density estimates and focal animal sampling for per capita rates [Altmann 1974]) of armored catfish feeding by day and night in two dark and two moderately sunny pools. These data were combined to compute an estimate of collective grazing pressure: the average return time, by any grazer, to a given small site on the substrate. These estimated return times varied from 9 to 10 hours in the two sunny pools and from 30 to 100 hours in the two dark pools. Multiplying return times by the algal accrual rates measured in each pool gave the standing crop of algae predicted to exist on a site at the time it was about to be regrazed. Estimates for this computed standing crop in the two dark pools bracketed the values estimated for all four pools, suggesting that collective grazing pressure was, as predicted, balanced with local algal growth rate so that standing crops of algae (food availability) were similar in dark, uncrowded pools and sunny, more crowded pools (Power 1984).

The Ideal Free Distribution model (Fretwell and Lucas 1970) predicts that if animals are ideal (able to evaluate the relative quality of habitats in their environment) and free (to settle in the best available habitat at any time), they should distribute themselves so that the fitnesses of individuals in crowded habitats of intrinsic high quality are similar to fitnesses of inhabitants of poorer but less crowded habitats. Data collected by following 1,308 individually marked armored catfish over 3 km of river during a 2.5-year period supported these predictions quantitatively. Growth rates of prereproductive *Ancistrus spinosus* (the most common species in stream pools) were similar among dark, half-shaded, and sunny pools in the dry and in the rainy seasons, and survivorship of all species was indistinguishable among these dark, sunny, and half-shaded pools (Power 1984).

These data on key components of fitness provided extremely strong quantitative support for Fretwell's Ideal Free Distribution model, for which field corroboration is still thought to be largely lacking (Kacelnik et al. 1992). Note that the bulk of this evidence was observational, with experiments nested within comparative observations to calibrate algal productivity in the absence of grazing. Along with other authors in this volume, we have had difficulty publishing observations, even when these provide evidence or contexts crucial to interpretations of results. In our opinion, there has been a bias in the culture of ecological publication that overvalues manipulative experiments and undervalues field observations. We consider this bias unfortunate, as it has left community ecologists relatively unprepared to study longer term, larger scale problems for which experimental approaches are not feasible.

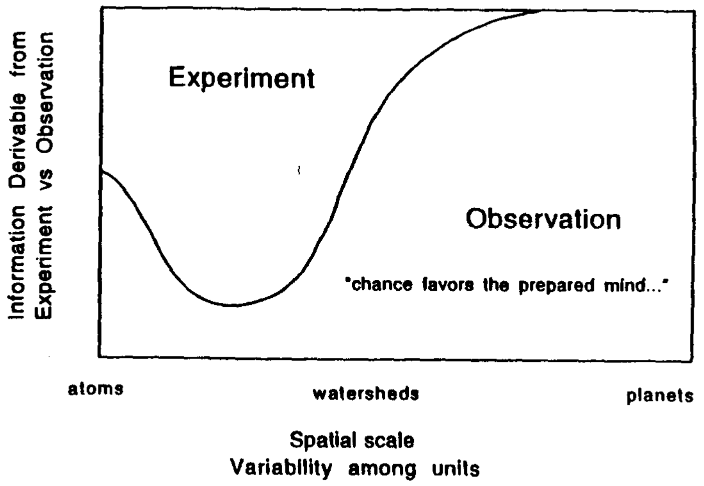

Figure 6-3. Information derivable from experiment versus observation as a function of the spatial scale, or variability among units, of the study system.

## Utility of Experiments versus Observations

The amount of information that can be derived from experiment versus observation clearly depends on the spatial scale, as well as the variability among units of a study system (Fig. 6-3). As objects of study grow from single entities to systems that encompass many interacting components, the importance of experimentation grows. Experiments are the fastest way to learn about the workings of complex dynamic systems like ecological communities and, in some cases, may give us insights we cannot otherwise obtain. We should avoid the temptation, however, to do experiments that are too small or too short-term to manipulate the relevant processes. For example, consider large cattle exclosures in an arid landscape. If one were to observe grassland conversion to shrubland inside as well as outside these exclosures, one might infer that climate, not cattle, caused the conversion. This conclusion could be wrong if, for example, cattle trampling and destruction of vegetation had caused channel incision, which, in turn, lowered the water table and facilitated the invasion of xerophytic shrubs (Odion et al. 1988, Elmore and Kauffman 1994, Dudley et al. unpublished ms). Severe channel incision and water table lowering might not reverse inside cattle exclosures, even if these were several hectares in area and several decades in age. Historical study of geomorphic change is a crucial foundation for landscape-scale hypothesis testing.

In general, as systems get larger, the role of manipulative experiments must decrease, for two reasons. One is the well-known limitation by logistical constraints—resources are stretched thinner and thinner to study fewer replicates of larger units until these resources are exhausted. A more fundamental problem, however, is that as systems increase in scale it becomes hard and eventually impossible to find suitable replicates.

Valid controls simply become unavailable. It is clear that this is the case for planets: neither Venus nor Mars is an adequate control for Earth, so scientists who study global change are correct to confine their major efforts to observation and modeling (although experiments nested within observational studies may be useful for calibrating modeled process rates, e.g., effects of temperature or $CO_2$ on rates of photosynthesis or decomposition in particular biomes). As one scales down in size (moving from right to left across Fig. 6-3), where one crosses into the region where experiments are feasible as the primary, overarching approach to a problem (Fig. 6-1a) can be debated. We think this threshold occurs at or near the scale of natural watersheds. This is not to say that excellent, informative watershed-scale experiments do not exist—they clearly do (Likens et al. 1970, 1977). The reason that the Hubbard Brook experiments have been so valuable, however, is that they were preceded and followed by years of detailed observations. Hubbard Brook scientists know a great deal about chemical fluxes in runoff and groundwater following deforestation and during succession. They have studied changes in biological populations, as well as in physical and chemical processes that mediated energy flow and material cycling during the ecosystem's response and recovery period. The follow-up of the basic manipulative experiment with careful, detailed, well-planned, and prolonged observation underlies the great value of this large-scale, long-term project.

Watershed experiments have traditionally been done using a "paired basin" approach in which one or more basins do not receive treatment as others are manipulated. These paired watershed experiments suffer at least three types of problems (Reid et al. 1981). First, independent (treatment) variables are often only loosely characterized with qualitative designations (e.g., "managed vs. unmanaged" or "logged vs. unlogged") that are inadequate for assessing mechanisms. "Control" treatments are usually not "pristine" (areas may have been logged in the past; controls may have active roads). Even if control and treatment watersheds have similar general characteristics (aspect, slope, forest type, drainage density, and geological parent material), they may differ in subtle but important respects (e.g., structural orientation of bedrock, undetected ancient landslides, and disease history of vegetation). A second problem is that rather than making local, process-based observations, investigators have measured highly integrated response variables. Black-boxed signals, such as total sediment yield at the mouths of watersheds or changes in salmon escapement back to watersheds over the experimental period, are noisy and give little insight about causality, particularly when records are short (less than decades in duration).

A third problem in paired watershed studies mentioned by Reid et al. (1981) relates to spatial scale. Watersheds as study units are sufficiently large so that there is a reasonable probability that they will sample rare events with high impacts during an experiment. When, for example, major landslides occur in the "wrong" (control) basin, they can completely override signals from land use that experiments were set up to detect. In addition, lingering but undocumented effects of divergent landslide, fire, or land use histories may influence watershed responses to experimental manipulations in ways that may not be detected (e.g., via the amount of sediment available to be delivered to streams; Judy Meyer, personal communication).

A final problem is that it is now too late for this experimental design. In most parts of the world, comparable "unimpacted" control sites no longer exist for large-scale watershed studies. In the Pacific northwestern United States, for example, there are no large undisturbed forested watersheds left for comparison with harvested areas. One might as well search the solar system for a control for planet Earth.

## *Observations and the Prepared Mind: The Reference State*

Given that there are important ecological problems that cannot be studied with manipulative experiments with controls, can we make observational studies more useful? One potentially useful approach has a long history in geology and is presently being promoted in ecology by Paine (1984, 1994). As background, recall that Connell (1974, 1975) pointed out that field experiments differ from laboratory experiments. In the laboratory, most factors are held constant and one or a few are manipulated in experimental treatments. In the field, a few factors (those being tested) are varied and their effects are then evaluated against a noisy natural background ("controls"). Therefore, only strong signals can generally be detected. Paine (1984, 1994, personal communication) has proposed evaluating noisy nature relative to an experimentally engineered, simplified reference state. This reference state would arise if only well-understood processes are operating. Therefore, it will occur rarely, if ever, in the real world. Once it is defined, however, the more poorly understood processes that complicate natural systems can be studied by evaluating the deviations they produce from the reference state.

This terminology leaves room for confusion, as the term *reference* has also been used by ecosystem scientists to refer to what community ecologists would call controls. For example, unmanipulated "reference lakes" (Schindler 1988, 1990; Carpenter and Kitchell 1993) or "reference streams" (Wallace et al. 1996) are followed to detect regional factors that, independent of the manipulation, may cause changes in response variables. In this sense, references are like Connell's controls in field experiments: their dynamics are not necessarily understood but reflect a noisy background against which we try to detect the impact of one or a few manipulated factors. We would like to distinguish these "background" references from two reference states that are simplified relative to nature: "manipulated" and "analytical" reference states. Manipulated reference states are portions of the real world that have been experimentally engineered so as to remove complicating factors. Analytical reference states are calculated expectations, derived from theoretical or empirical understanding of processes known to affect systems. Both manipulated and analytical reference states reflect conditions we would expect if only well-understood processes are operating. As illustrated in the following discussion, these reference states may be far from any natural (preimpact) background condition.

We offer three examples: (1) Paine's use of manipulated reference states to study coralline algal interactions on Tatoosh Island of the Washington State coast, (2) the use of an analytical reference state that predicts riverbed sediment size to judge effects of sediment supply changes and channel manipulations, and (3) ongoing efforts to understand the interaction of trophic dynamics and disturbance-succession regimes in rivers by examining, as manipulated reference states, trophic structures that develop in the absence of scouring floods, in channels with artificially regulated flow.

### *Coralline Algal Interactions on Tatoosh Island*

On exposed rocky coasts of the northwestern United States, crustose coralline algae compete for space. Paine (1984, 1994) has experimentally studied this assemblage on Tatoosh Island for over 10 years. On an exposed rock bench from which he has continuously removed most grazers he has transplanted chips of various coralline species into competitive arenas made of nontoxic epoxy putty. Their growth and overgrowth have revealed a very deterministic competitive hierarchy. When the corallines grow into contact with each other, some species are better than others at lifting up their growing edges and overgrowing neighbors. These species tend to win in space competition. Grazing or physical disturbance can undermine the advantage of this trait, however, because herbivory or damage is often disproportionately high on these uplifted edges. In the presence of grazer or physical disturbance (e.g., log bashing), the outcome of competition among the algae is far less predictable. Therefore, the assemblage engineered by the elimination of grazers and disturbance, in which community structure results primarily from competition for space, becomes Paine's manipulated reference state, against which to evaluate the deviations produced by herbivory and other complicating biotic and abiotic factors at work in the natural world (Paine 1984, 1994).

### *The Threshold Channel Concept in a Watershed Context*

In hilly and mountainous areas, riverbeds are typically gravel of mixed sizes, organized into fixed or slowly moving bars which, along with woody debris, create diverse habitat structure. Grain size influences the availability of spawning substrate for adult fish and of habitat and refuges for young fish and aquatic invertebrates (Brusven and Rose 1981, Minshall 1984, Kondolf et al. 1991). Bed movement influences food web structure (Power 1992, 1995) as well as spawning success of fish like salmonids (e.g., Kondolf and Wolman 1993). Habitats are generally degraded by land use that alters the supply to channels of coarse and fine sediment, alters the flow regime, removes the woody debris, or channelizes the river. Considerable effort is now under way to do "snapshot" analyses of river condition to infer effects of land use and possible benefits of land use prescriptions. The analytic reference state may prove useful in this context.

Field, laboratory, and theoretical studies show that for natural size mixtures of sediments found in gravel-bedded rivers significant bed mobility typically begins when stream forces exceed the resistance to motion of the median grain size of the bed (e.g., Leopold et al. 1964, Carling 1988, Parker 1990). When gravels of mixed sizes cooccur, the shear stresses needed to move small and large grains are, respectively, larger and smaller than on homogeneous beds, because the small grains lift large ones out of pockets into the flow, while large grains tend to shield the small grains from flow. Therefore, shear stresses that initiate motion of large grains and those that initiate motions of small grains both approach those needed to move particles of the median size. This suggests that gravel rivers, to a first approximation, are "threshold channels" (Henderson 1966), in which the threshold for initiating bed movement is crossed at some characteristic flow. Many studies have shown that this characteristic flow is typically close to bankfull (e.g., Jackson and Bestcha 1982; Andrews 1983, 1984; Carling 1988). The critical boundary shear stress that will initiate motion of the expected median grain size can be reasonably estimated based on the particle's diameter and specific gravity. Because significant bed motion in gravel-bedded rivers does not begin until flows approach or exceed bankfull, bankfull boundary shear stress can be used to calculate the median grain size of the riverbed. Over a long reach where we can consider the flow on average to be steady and uniform, the boundary shear stress at bankfull stage is just the product of the river slope, bankfull depth, fluid density, and gravity. Because of additional resistance due to drag over bars and woody debris, however, the boundary shear stress actually responsible for grain motion may be much less than the total available at bankfull, but these additional sources of resistance are difficult to estimate (Buffington 1995).

A simple analytical reference state emerges from this description. If we know the bankfull depth and river slope, we can calculate the expected median grain size of the bed. Deviations from this expected grain size arise from effects of woody debris and bar resistance (Buffington 1995) and from effects of sediment supply (Fig. 6-4; Dietrich et al. 1989, Buffington 1995). Form drag resistance from woody debris and bars will reduce the actual grain size from that expected from the depth–slope product alone. High gravel supply will cause the median grain size of the bed to become smaller, reducing the critical boundary shear stress and increasing bed mobility. Large woody debris in channels is common in less disturbed forested basins. This example illustrates the contrast between background and analytical reference states that might be applied, for example, to study effects of timber harvest. The background reference state would be a wood-choked channel before humans removed snags; the analytical reference state would be a bare channel, in which sediment transport and supply could be more easily predicted.

This threshold channel as an analytical reference state can serve as a null hypothesis against which to compare field observations and as a guide to interpretations of channel condition. Deviations from the median sediment size predicted by the analytical reference state would point to hypotheses about the influence of either sediment supply or

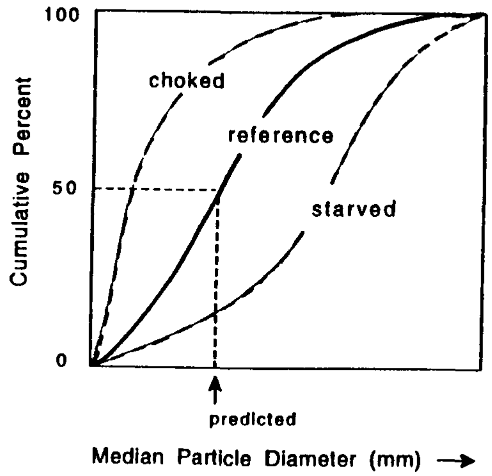

Figure 6-4. Use of an analytical reference state for evaluating sediment supplies to stream channels with mixed-sized gravel beds. Observations of median grain size diameter suggest that sediment supply to streams is higher (choked) or lower (starved) than would be expected for the reference state.

obstructions. Either hypothesis could be tested with additional field observations and nested experiments (e.g., small-scale removal or addition of wood and improvement of roads). For example, a reach of channel which is free of woody debris and which has a median grain size much less than that predicted should have high bed mobility. In order to maintain this high mobility, sediment supply to the channel from the watershed must be high; hence, deviation from the reference state may point upstream to land use effects (roads and forest harvest). Where supply has been cut off (e.g., below a dam), the bed grain size will coarsen until there is no movement at bankfull or higher stages. This may lead to elimination of spawning gravels and greatly reduce flood scour, which serves the role of resetting the stream to earlier successional biological stages in which prey are more vulnerable to predators (e.g., Power 1992, 1995). The addition of large woody debris on an otherwise naturally low-supply coarse gravel bed may cause bed material to reduce to a size more favorable for spawning (Buffington 1995), enhancing salmonid habitat in steep, bouldery channels, which generally lack both spawning gravel and well-formed pools (i.e., Montgomery and Buffington 1993).

### *Separating Disturbance and Succession from Trophic Dynamics in California Rivers*

Our last example is a work in progress. We are attempting to apply the manipulated reference state approach to understanding the interactions of disturbance and succession with trophic dynamics in California rivers. As described in a previous section (on Eel River during drought), the length of functional food chains in the Eel River depends on whether or not scouring winter floods occurred during the previous high-flow season (Fig. 6-2). We are exploring the possibility of using artificially stabilized river channels as reference states against which to evaluate the effects of floods on river food webs.

In the winter of 1993, the South Fork Eel River finally experienced bed-scouring floods once again. In addition to the winter floods, however, the river received an anomalously late spring flood in June, which exported most of the algae, which was blooming at the time. Field experiments during the following summer revealed that effects of juvenile steelhead on algae were not negative but positive, as if steelhead were at the third rather than the fourth trophic level. With the removal of *Cladophora* by the June flood, the tuft-weaving midge did not recruit in large numbers during the experiments. Juvenile steelhead in enclosures consumed small predators, as in 1989, but also consumed all the remaining herbivores capable of suppressing algae. Therefore, in the presence of steelhead during 1993 blooms of diatoms overgrew enclosures, and algal standing crops were higher with these fish than without them. These results suggest that the interplay of disturbance, succession, and trophic dynamics in the Eel River is influenced by the timing as well as the annual occurrence of scouring floods.

Channels in which flow is artificially regulated may be useful for unraveling these interactions. In both channels downstream from dams and a regulated diversion that is not fed by upstream impounded water, preliminary observations suggest that biomass tends to be dominated by predator-resistant sessile or armored grazers. A fairly constant low-standing crop of attached algae is maintained, and biomass of vulnerable (mobile naked) grazers and predators is typically low (Power 1992, Parker and Power, unpublished data). We postulate that this state represents the late successional biomass distribution pattern of disturbance-free systems. This may prove useful as a manipulated reference state against which to evaluate the more indeterminate structures that arise when natural disturbance resets river communities.

This proposed application of a manipulated reference state is quite preliminary compared to the first two examples described here. Paine and Dietrich et al. both have solid empirical and experimental underpinnings for their reference states, based, respectively, on 10 years of field experimentation (Paine 1984, 1994) and on many decades of flume and field studies (Leopold et al. 1964, Henderson 1966, Parker 1978, Carling 1988). In addition, the first two reference states are simpler than the third proposed here. The threshold channel is the product of physical processes that are far simpler than ecological processes. Paine's reference state is ecological, but interactions are restricted to competition for an easily measured resource (space) among organisms that are sessile for most of their life histories (coralline algae). Our proposed third reference state (trophic-level biomass distributions in channels that do not experience scour) includes interactions of mobile higher trophic levels and, in fact, partially corresponds to Paine's less deterministic "natural state" in that consumers, but not disturbance, have been factored back into the system. Clearly, real food webs in streams, even in the absence of flood scour, do not maintain static distributions of trophic-level biomass as portrayed in Figure 6-5. These patterns can be disrupted by a variety of factors. Synchronized pupation or emergence of grazing insects may temporarily release algae. Formerly invulnerable primary consumers may come under attack if new types of predators invade or if epidemics break out (Kohler and Wiley 1992). Changes in physical and chemical factors other than scour will have effects. Would we be quicker to recognize the influence of these other factors if we searched for deviations from an expected state? The value of a reference state does not lie in how likely it is to occur in nature but in whether it prepares the mind to be surprised, triggering the pursuit of profitable new leads. There does remain an issue of how much uncertainty must be removed by a model like a reference state before it proves useful. The decision about how "well understood" processes need to be before they are used to formulate a reference state expectation is the investigator's choice, based on knowledge of the system, practical considerations, and the degree of uncertainty that can be tolerated when addressing particular issues or questions. We argue that manipulated or analytical reference states can be useful even at the onset of investigations of poorly understood systems, as they force fieldworkers to make, as Darwin recommended, observations that are "for or against some view" (Darwin [1861] in a letter to Henry Fawcett, cited in Gould 1995: 148). When systems are poorly understood and preliminary reference states are far from the mark, mental suppleness (rapid feedback between observations, model testing and revision, and new observations) is particularly important.

Ecologists have come to emphasize a posteriori interpretations of manipulative experiments because these have been more successful than a priori predictions in dealing with our dauntingly complex subject. We may never be able to predict ecological phenomena, but our postdictions will certainly be more timely for the effort we invest in trying to do so. We need to build up our a priori skills, like developing reference state expectations for field observations, if we are to contribute to the urgent problems

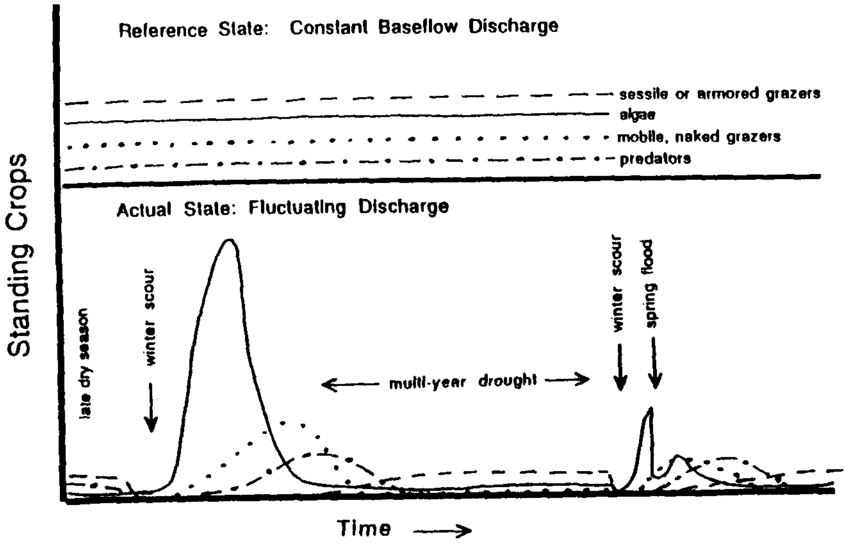

Figure 6-5. Manipulated reference state proposed for evaluating the effects of floods and flood timing on trophic structure and dynamics in western U.S. rivers. Patterns shown here are qualitative simplifications, partially derived from field observations, partially hypothesized. In the upper panel, the reference state expectation in channels that are not subject to periodic bed scour is shown. Trophic-level biomass is largely made up of predator-resistant sessile or armored grazers, which by persistent grazing maintain a constant low-standing crop of algae. Biomasses of vulnerable grazers and predators are relatively low in such channels (Power 1992, Parker and Power, unpublished data). The lower panel suggests trophic biomass changes following floods in a natural channel, represented by the South Fork Eel River. Late in the dry season, a biomass pattern similar to the reference state develops. After scouring winter floods (November 1988) remove most benthic biomass (and dilute water column biomass), algae recovers first during the following spring. Over the following low-flow season and during drought years that follow, a biomass distribution approaching the reference state develops. Floods in January 1993 reset the community, releasing algae initially. This algae was exported during a June 1993 flood, and the consequent recruitment failure of tuft-weaving midges set the stage for a three-trophic-level system, in which recovered algal biomass was protected by steelhead predation on the remaining functionally significant algivores.

of environmental management and biodiversity conservation that arise over spatial scales too large and temporal scales too short to permit experimental study as the primary approach.

## Summary

Experimental approaches have enjoyed justified popularity in community ecology, so much so that they have overshadowed direct observations. Well-designed field experiments will continue to humble ecologists by revealing surprises about how nature works. We argue here, however, that more direct observations should be planned, made, and reported in the literature. Direct observations nested within manipulative experiments illuminate black boxes and can resolve causality. In addition, ecologists should improve their skills at making hypothesis-based field observations that allow them to contribute to problems which cannot be addressed experimentally. These observations should be designed as carefully as field experiments. As the spatial scale of investigation increases (e.g., from pools to reaches to watersheds of rivers), the value of planned observation relative to manipulative experimentation increases, because of logistic constraints on large-scale experimentation and, more fundamentally, because of the lack of comparable control sites. Watersheds for which adequate controls are lacking must be studied by observing and characterizing causal mechanisms and linkages within the watershed. Small-scale manipulative experiments nested within these observational studies can contribute to these efforts by clarifying functional relationships of key variables. Field observations that are motivated by testable hypotheses such as expectations from analytical reference states can, like manipulative experiments, surprise investigators, leading to new insights.

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# 7

# From Cattle Tanks to Carolina Bays

## *The Utility of Model Systems for Understanding Natural Communities*

WILLIAM J. RESETARITS JR. AND JOHN E. FAUTH

> Experimental observations are only experience carefully planned in advance.
>
> —Sir Ronald A. Fisher, 1935

> You cannot step twice into the same river.
>
> —Heraclitus, fl. 513 B.C.

A primary goal of ecological research is to identify generalities that can simpl
natural world from a jumbled collection of special cases to an ordered array o
sifiable sets. This goal is shared by all ecologists and stems from the belief that c
ecological systems operate on a finite set of principles. Once these are unde
ecologists expect some level of predictive ability with regard to ecological phen
It has long been recognized that perhaps the most serious constraint in ecologi
search is the sheer number of factors affecting natural systems, coupled with th
number of unique natural communities we hope to understand. A parallel consid
is that sufficient resources will never be available to study every system on the
Thus, the search for generality and predictive power is not simply an abstract the
pursuit but an absolutely essential component of the ecological research par
Ecologists use observation, experimentation, and deduction to generate predictiv
els that simplify the natural world and permit general statements about how it
Only by obtaining a fundamental and general comprehension of the processes tha
natural systems can we hope to understand not only those systems that are inte
studied but also those innumerable systems that will never be studied. And onl
can our basic understanding give rise to the informed and broadly applicable
vation decisions necessary to keep the world working.

As ecologists develop theories and models about how the world works, th
look for ways to rigorously test them. Experimentation is often referred to as a
of testing observed phenomena; often the "observed phenomena" are generate
theory rather than from observation or they are derived directly from previous
ments (Peckarsky, this volume). Fair tests of observed phenomena/theory requi