

What Are We Missing? Butterflies, Flowers, and Salmon Models

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Abstract.—We understand our environment through our senses and tend to interpret the behavior of other animals in the context of the world we understand. Butterflies and flowers sometimes show distinctive patterns in ultraviolet light that are important to them but invisible to us. Likewise, the senses of fish and their experience of the world are very different from ours. Many aspects of a salmon's environment, such as olfactory stimuli, are completely invisible to us. Other factors, like certain aspects of habitat alteration, are visible but unnoticed because they occurred gradually or long ago. Like Poe's purloined letter they are cryptic—there for us to see if we only knew what to look for. As we build salmon models we base them on what we understand is important to the fish. However, our anthropocentric bias may cause us to overlook or misinterpret factors of importance. In addition, our necessarily simplified models, when applied to management, may result in a pernicious simplification of the salmon populations we wish to preserve. For example, if we model and manage for a dominant (or highly visible or easily monitored) salmon life history we may inadvertently eliminate other life histories of equal importance, or reduce diversity in ways that affect population viability. We should actively seek to identify important factors missing from our models and be aware of critical assumptions. Recognizing that our models are tools used to understand and manage salmon, we should try to understand the broader implications of these models to the future of the salmon we hope to preserve. In this essay, I offer speculation about what we may be missing in freshwater habitat, life history diversity, metapopulation dynamics, ocean survival, and water chemistry. I also consider the question of scale, and the effect our philosophical viewpoint may have on the direction and application of our modeling efforts and the likelihood of successful outcomes.

Introduction

How can it be otherwise? Our understanding of the world is based on our sensory perceptions. The sky is blue and daffodils are yellow. Our human experience of the world is constrained by our senses. To us, reality is what we see, hear, feel, smell, and taste. But our senses are conditioned to be sensitive to things most important to our survival. We theoretically could hear high frequencies

like dogs, or perhaps resolve time in thousandths of seconds, like bees. But there are trade-offs. Our brains can only process so much information, and if we spent our attention listening to whatever it is dogs hear we could be distracted from something more important to our survival. However, this makes it harder for us to understand the worlds—the realities—of other animals because our natural expectation is for them to experience the world as we do.

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But what if our eyes were sensitive to infrared or ultraviolet light (UV)? The world would look different, and we would understand it differently. A well-known example is the ability of many insects to see UV outside the range of human vision. Butterflies may distinguish their world not based on the pattern that we humans see, but on patterns visible only in the ultraviolet. These “invisible” cues affect strategies for finding mates, finding food, and avoiding predators (e.g., Lyytinen et al. 2004). The Cleopatra butterfly, *Gonepteryx cleopatra*, shows different wing patterns in visible and UV light (Figure 1a, b). Likewise, the blackeyed susan flower (*Rudbeckia hirta*, *Compositae*) absorbs UV near its center, thus guiding pollinators (Jones and Buchmann 1974) (Figure 1c, d). Without the ability, through technology, to “see” these patterns we would be unable to correctly understand the mating behavior of the butterfly or the plant-pollinator interactions of the flower. With tools as diverse as polarizing filters, ultraviolet-sensitive film, slow-motion or time-lapse photography, telescopes and microscopes, we extend our senses to see aspects of the world around us that are normally invisible.

Even among those things we can readily perceive, much goes unseen. When you shop for a new car you suddenly notice what others are driving, and especially you notice cars like yours. As a birder I was taught to hear the faint, high-pitched call of Hammond’s Flycatcher *Empidonax hammondi*. At first I heard absolutely nothing—I was completely unaware of the bird call nearby. Only after it was repeatedly pointed out could I hear it, even though it was there all the time. Now the call stands out to me against the background of forest sounds although, as my high-frequency hearing wanes, so will my awareness of this bird call. Part of the world that we perceive to be real is made up of those things we have learned are important. Much that could be seen or heard is not, simply because we

have attached no meaning to it. So, there are two categories of things we are potentially missing—those that are “invisible” to us because of our physiological sensory limitations, and those that are “cryptic;” in plain sight if only we were to look in the right place or in the right way.

The models that are the topic of this volume treat a range from large-scale climate effects on ocean survival to fine-scale, spatially explicit freshwater habitat. Some incorporate bioenergetics and population or metapopulation dynamics. Others are based on links between physical habitat and salmon life history or survival. All, in one sense or another, attempt to represent our world-view of salmon in the landscape. As such they are selective mirrors, reflecting what we deem to be important but not what we ignore or what is invisible to us. Such models can be useful tools for understanding complex systems and predicting their behavior, but are limited by our prejudices of how a system works. Consequently, they tend to reflect what we already think we know, and often simply reinforce our preconceptions about the systems we are modeling. The risk is that by building our conceptions of salmon in their habitat into these edifices, and by including only what we have measured or quantified, we will focus attention away from factors that are important. Here I will look for potential gaps and blind spots in our understanding and in our models. I will look for invisible and cryptic elements, patterns, and processes that may be important to salmon.

A comprehensive treatment of “what are we missing” is clearly too big for this short essay. Any competent modeler can give you a list of processes left out. The art of building successful ecological models is to simplify down to the important elements or dominant processes. The risk I will address here concerns dominant processes not modeled and questions not asked. Rather than attempting to present a comprehensive list, I will con-

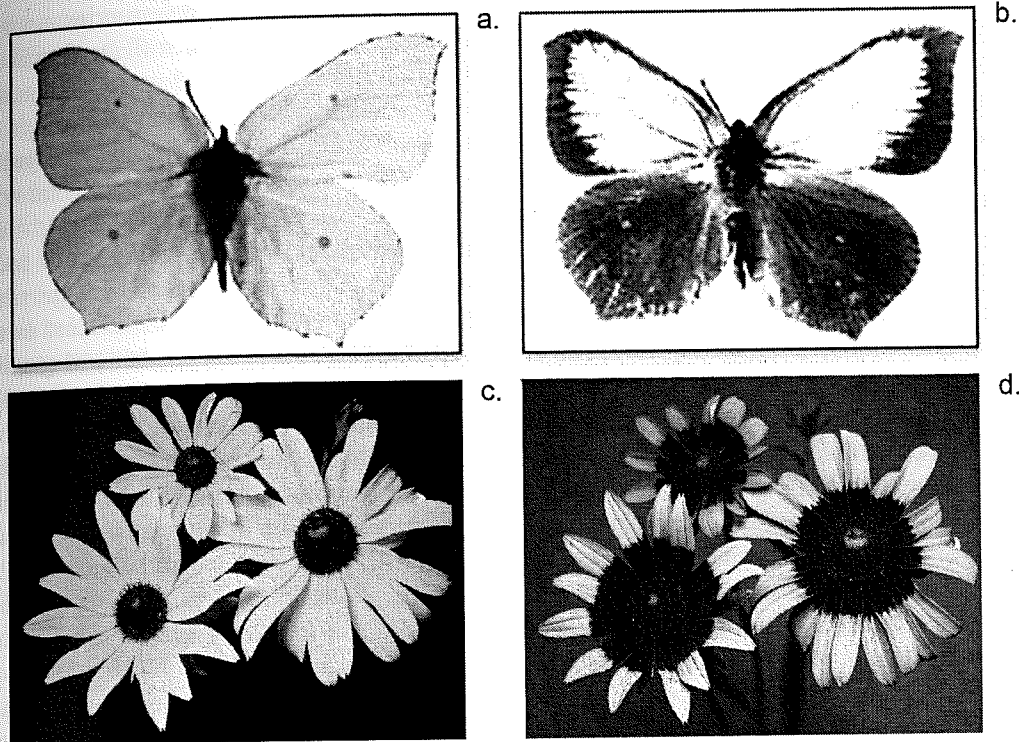


FIGURE 1. Cleopatra butterfly, *Gonepteryx cleopatra*, under visible (a.) and ultraviolet (b.) light. Blackeyed susan *Rudbeckia hirta*, *Compositae* under visible (c.) and ultraviolet (d.) light. Butterfly photographs courtesy of Eddie Aicken. Flower photographs courtesy of Thomas Eisner.

concentrate on my personal prejudices and Oregon coastal biases, with the hope that this consideration will stimulate others to take a fresh look at their models. The topics I have chosen may seem varied and sometimes speculative. Some will seem obvious. Others, I hope, less so. All have received some scientific attention but I do not attempt a literature review. Although I build on specific examples I try to keep my discussion general. I leave the reader to take from this essay what may be useful and appropriate.

Freshwater Habitat

We manage what we measure. Spawning surveys, habitat surveys, even geographical information system (GIS)-based habitat evaluations tend to focus on "wadeable"

streams. These are the streams we see as we drive across mountains and through meadows, forests and clear cuts. These are the easy streams to work in. We can measure channel morphology, count juveniles and spawners, build weirs, electrofish and seine, and sample invertebrates and nutrients. These streams are frequently in areas where the landowners do not object to activities of field crews from natural resource management agencies. Our habitat-based models are usually parameterized from data collected in these streams—spawner abundance, juvenile distributions, pool area, and large woody debris density. They are not the only important macrohabitats, but others receive less attention. Main-stem rivers are too deep, wide, and powerful for the kind of studies we do in the smaller streams, even though fish may spawn or feed

there. Low gradient reaches are frequently silty, warm, and agricultural, thus deemed poor habitat and, therefore, not often surveyed. Adding to the difficulty, small private landowners are often more suspicious of survey crews, denying access even to historical survey sites. Estuaries require different techniques for study. Fish are present at different times of year, the habitat is more dynamic, patchy, and altogether harder to work in. In urban areas we hardly notice the streams. Habitats are so drastically altered, pollution so ubiquitous, and flow regimes so artificial that the problems seem insurmountable. As a result, the majority of our focus is on medium size, medium gradient reaches, primarily on private and public timber and grazing land.

Could this be why logging is the first thing that comes to mind when we think of habitat destruction in salmon streams even though we know there are many human activities that degrade habitat quality for salmon? The cumulative impacts of many small actions may be large, but logging has vastly altered the landscape in a highly visible way. Maybe our personal experience, biased data collection, inability or unwillingness to work in lowlands and estuaries, and difficulty focusing on myriad small impacts is one reason that timber companies take much of the public blame for habitat degradation and timberlands are a major focus for restoration activities.

Another, more subtle root of this habitat myopia may be the cryptic nature of habitat destruction in lowlands and estuaries. A clear-cut, to a fishery biologist, is a violation of the natural order. By contrast, a grassy meadow with a stream running alongside and a barn looks wholesome and productive; a fixture in the rural American landscape. Unless you are actively working in these streams it is easy to forget that they used to meander through the meadow flood plain with banks of willows and cottonwoods, marshy side channels, and beaver dams (Gonor et al. 1988). By the

same token, our nice, wide estuaries, with jetties, harbors, and maybe a fleet of sailboats look wholesome to us. But once they were shallow and braided, tangled with snags and rootwads and bordering marshes and gallery forests. These messy habitats were far more favorable for salmon than the neat, clean, hardened banks, dikes, and riprap of today. For years, scientists and some managers have been calling attention to lowlands and estuaries as important to salmon, but low gradient areas tend to be more heavily populated, so restoration activities create conflicts. These may be among the reasons that riparian buffers, in-stream structures, road closures, and culvert removal are the main restoration tools in use: the focus remains in the woods.

Life History Diversity

Lowland habitats historically have supported a diversity of life history types that is now much reduced. More broadly, habitat change and harvest may have reduced the variety of viable life histories. What once may have been major components of populations are now so rare that we are not even aware of them. The ecological importance of these cryptic alternative life history forms may not be evident under current conditions. Some future turn of events, a climate shift, a new marine predator, or a freshwater pathogen could shift the balance of survival to a life history pattern we currently consider insignificant. Hilborn et al. (2003) documented a major shift in the population structure of Bristol Bay sockeye salmon *Oncorhynchus nerka* over the course of 100 years, with formerly dominant populations now minor, balanced by the resurgence of a few historically small runs. These shifts are attributed to climate changes affecting both marine and freshwater environments. Abundances of Bristol Bay sockeye remain relatively strong, but if some seemingly insignificant segments of the population had been lost 40 years ago what

wide estuaries, with jet-tyes, maybe a fleet of sailboats. But once they were tangled with snags and mangrove marshes and gallery habitats were far more than the neat, clean, riprap of today. And some managers have moved to lowlands and estuaries, but low gradient, heavily populated, so they create conflicts. These are the reasons that riparian buffers, road closures, and other main restoration tools are used in the woods.

Diversity

Historically have supported life history types that are more broadly, habitat diversity have reduced the variability. What once may be components of populations are not even aware of the importance of these life history forms may not exist in current conditions. Some climate shift, a new freshwater pathogen of survival to a life history type recently considered insignificant (2003) documented a population structure of *Bristol* *Oncorhynchus nerka* years, with formerly low minor, balanced low historically small contributed to climate marine and freshwater abundances of Bristol diversity strong, but if important segments of the 40 years ago what

we see now as a shift in population structure could, instead, have appeared as a major population decline.

Variability confers resilience to environmental fluctuation and change. This is important when we attempt to estimate population viability using population viability analysis (PVA) models. We generally base our analysis on one life history type or a single stock recruit relationship. On one hand, omitting alternate life history strategies may lead to an underestimate of viability. On the other hand, ignoring the effects of reduced life history variability could lead us to underestimate how much more vulnerable populations are now than they were historically. We all recognize that salmon are characterized by the variability in their life cycles. What we may not recognize is how much of this variability has been lost, or what the effects of our assumptions, translated into management actions, may have on diversity. Simple examples of management actions and their effects on diversity are: minimum size limits in fishing leading to smaller average body size, fishing at the peak of a migration altering run timing, and harvest rates based on the most productive populations causing the extirpation of less productive populations. Our simplistic assumptions about variability in salmon life histories may lead to management actions that cause simplification in the real world.

Much of our understanding of estuary use by Chinook salmon *O. tshawytscha* in the Columbia River comes from mark-recapture studies. Usually fish are marked for reasons unrelated to estuary studies. For example, coded-wire tags are used to evaluate hatchery practices and ocean catch distributions. PIT tags are implanted to track movements of individual fish through the hydropower system. They have been used to evaluate smolt migration timing, survival through the hydropower system, population size structure, predation pressure, and life history variability, among other things. Results from these studies and

others like them are the basis of many fishery management decisions. But marked fish are almost always hatchery fish, whose behavior and life histories may differ from wild populations. PIT tags can only be applied to larger juveniles. Beach and purse seines may be size-selective and, more importantly, can only be used in certain habitats, not necessarily representative of the habitats used by some Chinook salmon life histories (Bottom et al. 2005). As a result of these data limitations our management view is blind to some potential life histories, especially those of wild fish that make extensive use of estuaries. Management practices based on tagging data focus on larger hatchery fish to the detriment of the more diverse natural populations. This may be partly responsible for the reduction in life history variability, compression of run timing, and the trend toward more uniform size in Columbia River Chinook (Bottom et al. 2005).

Life history variability is tied to habitat variability. As we delve into the realm of habitat-based models, we need to know how the fish use their habitat in space and time. This means we ideally need to know movement patterns and the associated environmental and developmental events and cues that stimulate these movements. This is clearly beyond our ability to comprehend, but there is some progress in understanding fine-scale movement patterns in freshwater through the use of PIT tags. Ebersole et al. (2006) were able to track movements, survival, and growth rates in coho salmon *O. kisutch* juveniles in the West Fork Smith River, Oregon using PIT tags and a variety of sampling techniques including an array of stationary PIT tag readers. They documented movement of juveniles from the mainstem into tributaries during the winter, and found survival was correlated with temperature, habitat quality, and spawner carcass density. These findings represent important advances in our understanding of local movement

patterns and freshwater habitat utilization. However, they tagged only juveniles greater than 60 mm fork length, and assumed that fish migrating out of the system did not survive. Until the full range of variability is described, our knowledge of the system is incomplete and could potentially lead to management decisions that unknowingly sacrifice important life history strategies.

Metapopulation Dynamics

Classical metapopulation theory is built on habitat that is patchy on a two-dimensional plane, and on organisms that disperse randomly (e.g. Hanski 1997). In contrast, salmon live in a stream network and disperse aggressively, seeming to mix quite widely. Yet they display a considerable amount of fine-scale population structure. The nature of salmon metapopulation dynamics may or may not fit the classical model, but the genetic connections among local breeding aggregates are certainly central to the demographic health and evolutionary persistence of salmon lineages at scales up to Evolutionarily Significant Units (Waples 1991). I would say that we know very little about how this process works, what happens when it breaks down, and how to restore it, assuming restoration is possible. Once a population has experienced the genetic effects of inbreeding or outbreeding depression, the only way to reestablish a healthy genetic diversity may be to restore the natural population processes and allow diversity to increase over generations. We do not know the implications of disruption to genetic structure on short- or long-term viability. Also, once a system has been disrupted we do not know how rapidly it will reach a new equilibrium or what the nature of that equilibrium may be. These questions are central as recovery goals for ESA-listed stocks are developed throughout the Pacific Northwest.

We do know that healthy salmon populations consist of individuals that return

faithfully to their natal stream, as well as individuals that wander or stray, sometimes locally and sometimes widely. These movement patterns are highly variable and depend on cues not readily apparent to us. Movement patterns are most likely responses to environmental conditions including fish density and distribution, food and habitat availability, water quality, temperature, flow, and predators. These movements affect the likelihood of local extinction and recolonization, and have major implications for the expected population dynamics and genetic structure of metapopulations. In the design of recovery strategies, the spatial distribution of habitats is important because the juxtaposition of suitable spawning and rearing habitat, along with open migration corridors, structures populations and metapopulation dynamics. Our choices will determine the future options available to the fish.

PVA models frequently assume that once a population reaches a critically low level its likelihood of extinction is very high and "unmodelable." We typically, and somewhat arbitrarily, set a numerical value of critical population level as a "quasi-extinction threshold" (QET). Populations below this abundance are treated as functionally extinct. Postulated mechanisms for such a threshold are depensatory dynamics, in which fewer spawners produce disproportionately fewer offspring or are much more variable in their production, and Allee effects related to reduced reproductive output due to inbreeding depression (Dennis 1989). Selection of a QET can be controversial because we have so little basis for the choice, and the estimated extinction probabilities in some PVA models are quite sensitive to QET.

We could improve our estimates of QET or perhaps eliminate this factor altogether if we were to improve our knowledge of the dynamics and genetics of very small salmon populations. It is difficult, and not very rewarding, to study extinction events. However,

we could learn about the mechanisms of local extinction and recolonization by studying the dynamics of sink populations of a metapopulation. New techniques to augment conventional tagging, such as parentage analysis (Jones and Ardren 2003) and otolith microchemistry (Miller and Shanks 2004), would be valuable in tracking individuals and recognizing immigrants. Detailed study of small or low-density populations could yield insight into the dynamics that are likely to lead to local extinction.

Ocean Survival

In contrast to freshwater processes that are modeled on a scale of meters to kilometers, ocean processes are modeled at 100 s of kilometers. These models are universally based on statistical correlations between large-scale ocean environmental indices and survival. The most common indices are sea surface temperature, upwelling, and sea level (e.g., Logerwell et al. 2003). The difficulties are two-fold: large-scale indices can only be applied to large-scale patterns in survival, and the link between the physical environment and the mechanisms driving changes in survival rates are obscure. The differences in scale between marine and freshwater understanding are an obstacle to developing models that include the entire salmon life cycle. A finer-scale understanding of the marine system would include predators, competitors, and food supplies. Ideally we would build these models from the bottom up, starting with an understanding of local processes. In practice we may remain limited to correlations, but at a finer scale and more closely tied to the relevant mechanisms. Survival has been shown to correlate with sea surface temperature at a scale of 200–300 km (Mueter et al. 2005). If we could model marine survival at a scale of 20–30 km we could account for differences in survival between individual river basins.

After several years of purse-seining juve-

nile salmon from the nearshore ocean off of Oregon, Brodeur and Pearcy (1990) found little relationship between survival and stomach contents in most years. This led them to conclude that size-dependent predation is the dominant factor influencing marine survival for coho salmon juveniles entering the ocean. Subsequent studies have produced a variety of results, including relationships between various measures of ocean productivity and survival (Ware and Thomson 2005), and between baitfish abundance and survival (Emmett et al. 2006). With each study, a plausible mechanism explaining the observed correlation is presented. In general, these mechanisms are couched in terms of top-down or bottom-up control. We tend to view the two as mutually exclusive, and this may be limiting our ability to ask the right questions. Vadas (1989) suggests that we consider both top-down and bottom-up processes to be operating at the same time with their relative strengths changing from year to year. This would include the two simplistic boundary conditions of all top-down or all bottom-up while bringing the spectrum of intermediate conditions into consideration. We would then be led to investigate the circumstances that make one or the other dominant or situations where both were strong or weak at the same time. For example, we could postulate that, for juvenile salmon off the Oregon Coast, top-down processes are dominant during warm climatic conditions when predators such as hake or mackerel are present in the nearshore ocean as juveniles are entering the ocean. During cold ocean conditions predators are locally less abundant so feeding conditions dominate the survival pattern. Maybe, maybe not, but thinking this way opens up a range of new possibilities for investigation.

Chemical Factors

We humans largely ignore our sense of smell. We smell water to see if it is fit to drink but we do not consciously use smell

to guide our everyday activities. Salmon use olfactory cues to home to their natal stream (Hasler et al. 1978). They also are likely to use smell (I am guessing here) to recognize their location, detect potential predators or competitors, assess food densities, find suitable habitat, collect "way points" on their downstream travels, assess estuary and ocean conditions, select ocean habitat, find their way back upstream, and select mates. These olfactory cues affect their behavior on a daily or hourly basis, determining, in large part, the dynamic movement patterns that generate epi-phenomena such as metapopulation dynamics. These cues are invisible to us—we have no personal experience and no intuitive understanding of how this may work. I know of no models that incorporate olfactory cues in salmon behavior.

Olfactory cues are a key to habitat selection and migratory behavior in salmon. Our models of migration patterns and straying usually assume random straying or use a diffusion model of dispersal, imparting no will to the fish. Yet, these choices are so critical to successful spawning that it is hard to imagine the fish are moving blindly. This may be a key to the difference between wild and hatchery fish spawning in the wild. How can fish reared in a hatchery respond appropriately to an environment they have never experienced? Juvenile salmon moving down through a river system gain knowledge that is useful to them as adults on the upstream migration. Certainly this could explain why hatchery fish tend to stray more than naturally reared fish—they are lost! They may, in fact, be behaving more like our random models than are the wild fish. We are a long way from being able to include olfactory cues in models of the movements of individual fish. On a larger scale, we could recognize the importance of this factor by using correlated random walks or directional diffusion models to simulate directed search behaviors for homing and mates.

There is another aspect to water chemistry that may be even more important to salmon recovery than migration cues. Herbicides, pesticides, and other chemicals in the water alter behavior patterns, sex ratios, maturation schedules, and migration paths (e.g., Scholz et al. 2000; Arsenault et al. 2004). Sub-lethal effects are difficult to quantify. We do not know to what extent these chemicals may be disrupting salmon life cycles and leading to reduced productivity or ability to respond appropriately to their environment, but we do know that such disruptions are likely. Spawner-recruit models based on recent data may implicitly incorporate some of these effects, but this is not satisfactory if we are looking for ways to improve productivity—chemical influences are invisible. If chemical pollution is getting worse, we may observe a declining trend in abundance or survival, or a tendency for models based on historical data to over-predict current run sizes. Without recognizing the effects of chemical pollution we may fail to understand such a trend, or ascribe its cause incorrectly. It will not be easy to develop an understanding of chemical effects that is useful for survival or life cycle modeling, but the first step is to recognize the potential importance of chemical pollution.

We are beginning to understand that stress can make humans more susceptible to disease. The same is true for salmon. Stress can take the form of warm water temperatures, high predator concentrations, passage over, under, around or through dams, and chemical exposure. A model by Loge et al. (2005) suggests that the migratory path of salmon smolts in the Columbia River can affect their exposure to these chemicals. In a worst case scenario, chemical exposure in the lower Columbia River theoretically could impair Chinook salmon immune systems to the point that delayed, disease-induced mortality from chemical exposure is equivalent to delayed mortalities from exposure to other in-river (i.e., predators and dams) stressors. De-

pending on the path the smolts take through the estuary, total stress-related mortality from exposure to two classes of chemical pollutants (polycyclic aromatic hydrocarbons and polychlorinated biphenyls) was modeled in the range of 3–18%; a potentially significant factor in the declines of many Columbia River runs (Ginn et al. 2007). The degree of exposure is dependent on the pattern of estuary use. Fish that move quickly through the main channel of the estuary experience lower exposures than those that use off-channel habitats or reside in the estuary for a longer time (Loge et al. 2005). Naturally produced smolts are likely to make greater use of estuaries than hatchery smolts. They could experience higher mortality as a result, leading to a reduction in life history variability independent of, and in addition to, the variability potentially lost to management actions discussed earlier.

Together, these and other chemical effects may be a much more serious problem for salmon than we realize. Although we measure some aspects of water chemistry routinely in many cases, chemical pollutants are only rarely assessed. Our inability to sense water chemistry directly may have led us to ignore it in our models and in our thinking about salmon restoration. These invisible factors may be one of the most important things we are missing.

Questions of Scale

Modeling, by its nature, is an exercise in oversimplification. The hope is that we have identified the most important factors affecting the process of interest. In many cases this is undoubtedly true, but there are also opportunities to miss by a mile. One of the easiest mistakes to make is to use observations of short-term processes to model behavior of systems in the long-term. One example that comes to my mind is the delivery of large woody debris (LWD) to streams. LWD is an important structural component in Pacific

Northwest streams and rivers. It is generally assumed to come from riparian trees that fall into the stream—a process that is easy to observe and intuitively obvious. Another important source, however, is wood transported from upslope habitat by landslides (Reeves et al. 2003). These landslides are episodic and relatively rare, so we tend to discount their importance when, in fact, more than 60% of the wood in mountainous streams may come from up-slope sources. Up-slope reservoirs of LWD are becoming depleted as trees are repeatedly removed at smaller and smaller sizes. If we attempt to model only the LWD delivery from riparian areas we will miss the longer-term process that once delivered the majority of in-channel wood. This could lead to an imbalance between riparian and upslope management strategies.

Another area where scale problems are frequent is in the use of spawner-recruit curves. Usually, we fit spawner-recruit curves to time series from stocks composed of many populations. We observe that these curves have poor fit, and attribute the residuals to measurement error and environmental factors (which we may then try to identify). The mechanisms underlying the assumptions of spawner-recruit curves work at relatively small scales. It is unreasonable to expect them to work uniformly over entire river basins or ESUs; it is likely they are operating more locally. There will be coherence among neighboring populations such that an overall spawner-recruit relationship can often be identified, but the actual dynamics are occurring at a much smaller scale. In addition, coherent patterns may be driven by climate patterns (e.g., Pyper et al. 2001) rather than population dynamics. The obvious difficulty here is that we rarely have spawner and recruit data at the appropriate scale. At the very least, we should attempt to understand how modeling many spawner-recruit relationships as one may affect our conclusions. Many management decisions are based on such re-

relationships, and unrecognized biases could have long-term implications to harvest management.

Philosophical Viewpoints

The final, perhaps ultimate, factor that we rarely reflect on is our underlying philosophy about resource management (and we are all managers in some way). Lichatowich (1999) has drawn a distinction between the industrial paradigm, a technological/agricultural production viewpoint and the natural paradigm, an ecological/natural history viewpoint. We are using the industrial paradigm whenever we talk about production, hatcheries, harvest, or spawner-recruit curves. Life history variability, diversity, and resiliency are elements of the natural paradigm. In Lichatowich's view the industrial paradigm has failed, and the key to restoring healthy salmon populations depends on basing our management philosophy on the natural paradigm. This view presents difficult challenges, because the political and legal structure surrounding salmon is dominated by the industrial paradigm. The concept of maximum sustained yield is firmly rooted in fishery management structure, and stocks are managed to "produce" a certain number of fish for harvest. Recovery and restoration goals often specify a certain level of production with the purpose of providing a stable and consistent harvestable surplus to serve societal needs. A natural view would manage for variability in abundance and life histories, consider the role of spawners in shaping and nourishing the landscape, and, in the extreme sense, would reject the idea that there are ever harvestable fish. Clearly a balance is needed, but I suggest that restoration activities (and models, goals, and analyses) that ultimately benefit industrial, social, and cultural needs should be informed by the natural paradigm. Success should be measured

in terms of resiliency and variability based on natural processes. Indeed, those factors are more likely to assure long-term production than simply releasing large numbers of hatchery smolts or fixing short-term production bottlenecks. The industrial view based on products will not go away, but it can be linked to the natural processes if restoration activities are appropriately structured. The most important thing is to recognize which paradigm we are working in at the moment, and to be aware of the associated constraints in the context of the contrasting paradigm and the context of management and recovery. Then, at least we will be aware of this particular blind spot.

This brings us back to the butterfly and flower example (Figure 1). We need to be aware of how our understanding of salmon in the landscape relates to the realities experienced by the salmon themselves. Which light we use—industrial or natural—profoundly affects the way we view salmon recovery and thus the models we use to understand biotic and abiotic phenomena related to salmon abundance and persistence. Whether our understanding of salmon biology and our interpretation of salmon behavior will serve the fish well depends on viewing them in the proper light.

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