

The EDT Method

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The EDT Method

The EDT method was designed to provide a practical, science-based approach for developing and implementing watershed plans. The method provides decision makers with the technical information needed to develop plans that will achieve their goals.

The EDT method consists of three components:

- *Conceptual Framework*—a way of organizing information to describe a watershed ecosystem in order to apply scientific principles to the understanding of that ecosystem
- *Analytical Model*—a tool used to analyze environmental information and draw conclusions about the ecosystem
- *Step-by-Step Procedure*—a procedure that explains how to apply the conceptual framework and analytical model to develop plans that achieve goals.

Conceptual Framework

We begin our discussion of the conceptual framework by introducing the principles that form the foundation for the framework and then describing its function. Then we take a close look at the central components of the framework—environmental attributes and biological performance.

Framework Principles

There is an emerging theme in the literature that calls for fish and wildlife management that is both *rational and consistent with an ecosystem approach* (Nehlsen et al. 1991; Lee 1993; Lichatowich et al. 1995; Williams et al. 1997).

By *rational* management, we mean a science-based approach to management based on a system of logic (rationale) that explains how intended actions will be transferred into desired outcomes.

Ecosystem (or watershed) approach refers to the growing realization that management actions should be made in a holistic context that considers interrelationships within the watershed (Simenstad et al. 1992; Doppelt et al. 1993; Williams et al. 1997). Without a holistic, watershed context, it is difficult to prioritize actions and assess their possible combined or cumulative effect. An ecosystem approach is needed to address resource issues from a broader viewpoint than can occur with a management focus on just one or a few species (Haskell et al. 1992; Lichatowich et al. 1995). An ecosystem approach to management promotes coordinated efforts, taking into consideration biological diversity and integrity leading to a balance of sustainable benefits to society (Angermeier 1997).

The inherent complexity of ecosystems, however, makes it difficult to describe and evaluate them. One way deal with this complexity is to look at the ecosystem through the eyes of one or more diagnostic species (Möbrant et al. 1997). A diagnostic species that is properly chosen helps us make inferences about the ability of a watershed to sustain a broad range of natural and social values. See Appendix B for a discussion on the concept of the diagnostic species.

The conceptual framework for the EDT method was developed with an aim toward utility for salmon management but also with the important goal of maintaining consistency with an ecosystem approach. The framework accomplishes this by viewing salmon as the indicator, or diagnostic, species for the ecosystem. The salmon's perspective—its perception of the environment—becomes a filtered view of the system as a whole. Within the limitations of the salmon's perspective and our ability to interpret it, this approach provides a framework for formulating strategies for salmon in the context of watershed management.

Although the framework was designed to have sufficient dimensional complexity to accommodate temporal, spatial and biological detail, it is simple in concept. Conceptual simplicity is important because unless ideas can be communicated clearly and without ambiguity, nothing is gained.

The usefulness of this type of framework should be measured by how well it generates insights into ecological patterns and relationships that might otherwise be missed or glossed over (Bunnell 1989; Lee 1993). As a theoretical construct, it is a caricature of nature against which to test and expand human experience (Walter 1986).

The foundation for the conceptual framework is well described by the following principles endorsed by the Multi-species Ecological Work Group (1999):

- 1) The abundance and productivity of fish and wildlife reflect the conditions they experience in their ecosystems over the course of their lifecycle.
- 2) Natural ecosystems are dynamic, evolutionary and resilient.
- 3) Ecosystems are structured hierarchically.
- 4) Ecosystems are defined relative to specific communities of plant and animal species.
- 5) Biological diversity accommodates environmental variation.
- 6) Ecosystem conditions develop primarily through natural processes.
- 7) Ecological management is adaptive and experimental.
- 8) Human actions can be key factors structuring ecosystems.

Framework Function

Watersheds and ecosystems are by nature hierarchical (O'Neill et al. 1986). Concepts and terms must be consistent at all levels in the hierarchy. Therefore, the EDT framework was designed so that analyses made at different scales—from tributary watersheds to successively larger watersheds—might be related and linked. Ultimately, conditions within these watersheds can be linked to those within the Ocean.

This function of the conceptual framework enables us to consider conditions for sustainability that link all components of an extensive and complex life history, such as that exhibited by salmon, over successively larger spatial scales. It is the key to our ability to assess the cumulative effects of concurrent actions spread across the geographic range of salmon.

In its simplest form, the conceptual framework is a pathway for linking potential land use actions (or natural events) to outcomes that may be relevant to values such as harvest opportunity (Figure 1). It provides a rationale for how actions and events are transferred into resource outcomes.

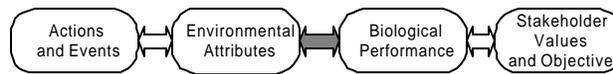


Figure 1. The EDT framework.

The framework consists of a sequence of relationships. The flow of logic proceeds as follows.

- Land use actions (or a natural event) within the ecosystem have some effect on attributes, or conditions, of the environment. These attributes may be abiotic (such as sediment loading or water temperature) or biotic (such as increases in abundance of a particular species by hatchery outplanting).
- These changes in environmental attributes, in turn, affect how populations within the ecosystem perform (i.e., survive and function).
- The resulting performance of populations creates an outcome that has direct relevance to objectives such as those associated with harvest and endangered species recovery.

The flow of information through these relationships is bi-directional—the process of planning, prioritizing, and implementing actions is a cycle that proceeds from goals to actions repeatedly. The implications of events and land use actions flow in the opposite direction as well.

The purpose of this type of logical construct is to promote a better understanding of these relationships. Too often actions are presumed to translate more or less directly to objectives without a clear rationale of how their effects flow through the ecosystem. This framework requires explicit consideration of possible pathways. The framework explains possible consequences in a manner consistent with existing knowledge and information, and it requires that all assumptions necessary to watershed planning are identified—thus it becomes a vehicle for learning and communicating.

At the core of the framework are relationships between environmental attributes and biological performance. The term *biological performance* refers to the way in which a population manifests itself in space and time under a given set of *environmental* conditions. There is a wide array of possible performances (Warren et al. 1979) for species like salmon over the range of conditions that have existed in the Pacific Northwest. The EDT model interprets these relationships from

the perspective of the diagnostic species. An understanding of the diagnostic species concept is important to the discussion of the core elements of the conceptual framework—environmental attributes and biological performance. See Appendix B for a detailed discussion of diagnostic species.

Environmental Attributes

In the conceptual framework, environmental attributes are the link between actions and biological performance. The environmental attributes defined and used in the EDT method are those that traditionally appear in the literature to describe the relationship between biological performance and the environment (see Table 1).

Environmental attributes vary over time and space. For the purpose of describing the biological performance of the diagnostic species, we must select appropriate time and space scales. This selection is made difficult by that fact that people typically view the world at different space and time scales (Walters 1997).

Harvest managers are concerned with short-term (e.g. annual) variations in abundance and distribution of fish, often on a relatively coarse spatial scale like a watershed. Habitat managers tend to focus on a smaller spatial scale (e.g. stream reach) and longer time frames such as multiple salmon generations.

If we hope to link these different perspectives, we must develop a “telescoping” approach. We must be able to zoom in on details (in terms of space, time and life history stage) and pan out to a broader perspective in a consistent way. To accomplish this, the conceptual framework incorporates a hierarchic structure where actions, attributes, performance, and goals can be defined on a variable scale.

Biological Performance

Biological performance is a central feature of the framework. It is defined in terms of three elements—life history diversity, productivity, and capacity¹ as shown in Figure 2. These elements of performance are characteristics of the ecosystem that describe persistence, abundance, and distribution potential of a population.

¹ We use the terms productivity and capacity as defined by Hilborn and Walters (1992). Capacity is the maximum population size for one or more life history segments. Capacity and productivity are not independent.

Table 1. Habitat attributes rated for all life stages, reaches and months.

Attribute	Abbreviation in model	Definition
Channel stability	Chan	Stability of the reach with respect to its streambed, banks, and its channel shape and location.
Chemicals	Chem	Concentrations of toxic substances or the presence of toxic conditions. Substances include chemicals and heavy metals. Toxic conditions include low pH.
Competition (with hatchery fish)	Comp	The relative abundance of hatchery produced animals of the same species as the diagnostic species that compete with the diagnostic species for food or space within the stream reach.
Competition (with other species)	Compo	The relative abundance of other species in the stream reach that compete with the diagnostic species for food or space.
Flow	Flow	Amount of stream flow and the pattern and extent of flow fluctuations within the stream reach.
Food	Food	Amount, diversity, and availability of food that can support the diagnostic species.
Habitat diversity	Hab	The extent of habitat complexity within a stream reach.
Harvest	Harv	Harvest of the diagnostic species by humans. Here, this applies only to poaching.
KeyHabitat	KeyHa	The primary habitat type used during a life stage.
Nutrient load	Nutr	The concentration of dissolved nutrients due to natural or man-induced causes.
Obstructions	Obst	Physical structures that impede movement of the diagnostic species within a stream reach, such as dams, waterfalls, or other structures.
Oxygen	Oxy	Mean concentration of dissolved oxygen in the stream reach's key habitat used by the diagnostic species.
Pathogens	Path	The abundance, concentration, or effect of pathogens in the stream reach. For example, the presence of a fish hatchery or large numbers of livestock along the reach could cause unusually high concentrations of pathogens.
Predation	Pred	The relative abundance of predators that feed upon the diagnostic species.
Riparian condition	Rip	The state of the vegetation component of the narrow strip of land bordering the stream where vegetation species occur that are dependent on the stream or its adjacent water table.
Salinity	Salin	Concentration of salts within the reach (if applicable).
Sediment load	Sedi	The amount of sediment present in, or passing through, the stream reach. This only applies to fine sediment.
Temperature	Temp	Water temperature in the stream reach. Density-independent survival is affected by rapid fluctuations, or by prolonged conditions near the extremes of tolerance.
Withdrawals	Wdrwl	Water withdrawals from the stream reach.

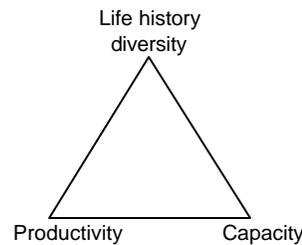


Figure 2. Elements of biological performance.

The performance of indicator species, from a broader ecosystem perspective, may also reflect the potential for species diversity. This conceptualization of performance provides a structure for applying *biological rules* that affect the survival characteristics of populations. We use existing theory to link each of these elements to environmental conditions.

In population dynamics, change is determined by four processes: birth, death, immigration, and emigration. These processes are regulated through *density-independent* and *density-dependent* mechanisms. These mechanisms are affected differently by environmental conditions (Moussalli and Hilborn 1986). As we examine some of these differences, it is important to also remember that population responses are a result of interactions between the two mechanisms.

A density-independent process is one in which the *rate* of response is not affected by population density; although in the case of mortality, the number of deaths goes up as population size increases. In contrast, a density-dependent process is one in which the *rate* of response varies according to population density due to competition for limited food and space resources; the number of deaths also goes up as population size increases.

The combination of these two processes results in the total mortality rate of a population at any given size. The effect of density-dependent mortality is low at low population densities, whereas the density-independent mortality rate is constant across all population densities. It is important to note that the density-independent mortality rate regulates the *rate* of loss that a population can sustain; it is the determinant, for example, of the rate of harvest that a population can sustain.

The identification of these two distinct mechanisms, density-independent and density-dependent, is useful in explaining the way in which various environmental conditions affect population

performance. Habitat or environmental *quality* tends to affect density-independent processes (Moussalli and Hilborn 1986). A deterioration in habitat quality will therefore tend to increase density-independent mortality. For example, sedimentation of a salmon spawning bed will tend to operate in a density-independent manner, causing an increase in mortality rate at all population sizes. In this case, the quality of the spawning bed is determined by the amount of fine sediment passing through, or entrained by, the substrate.

In contrast, habitat *quantity* tends to affect density-dependent processes (Moussalli and Hilborn 1986). The amount of habitat available becomes increasingly important as population densities increase (i.e., as competition for limited resources increases). In a parallel example to the one above, the quantity of spawning beds available to a salmon population could be expected to contribute to the mortality of eggs as spawner densities increase to the point where some spawners dig their nests at the same sites as slightly earlier spawners. In this case, superimposition of nests causes mortality to eggs already deposited. But at very low spawner densities, the chance of superimposition is very small.

These mechanisms of density independence and dependence operate within the three elements that comprise performance. The mechanisms explain how changes in the quality and quantity attributes of the environment affect biological performance. We next take a closer look at each of the three elements of that performance: life history diversity, productivity, and capacity.

Life History Diversity

This element represents the multitude of pathways through space and time available to, and used by, a species in completing its life cycle. A salmon life history consists of a favorable spatial-temporal distribution of a chain of habitats to enable its continuity (Thompson 1959). The life history encompasses many more or less distinct developmental life stages, each having its own set of environmental requirements (Bjornn and Reiser 1991). Species like salmon often exhibit a variety of life history patterns as a result of their adaptability to a heterogeneous and fluctuating environment. These life history patterns can be correlated with environmental variables on a spatial-temporal basis (Wevers 1993; Lichatowich and Moberg 1995).

Populations that can sustain a wide variety of life history patterns are likely to be more resilient to the influences of environmental change. Diverse life history patterns dampen the risk of extinction or reduced production in fluctuating environments (den Boer 1968). Not all life history patterns will be affected uniformly by natural or man-caused perturbations. Thus a loss of life history diversity is an indication of

declining health of a population (Lichatowich and Mobrand 1995) and perhaps its environment.

The life history diversities of existing natural salmon populations can be described by the range of distributions and pathways that are used successfully by these populations. A pathway can be conceptualized as a trace—or trajectory—in space and time available to members of a population (Figure 3).

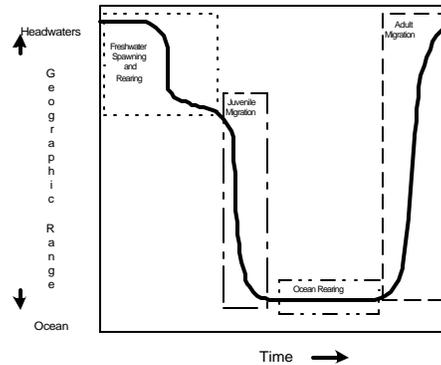


Figure 3. The concept of a life history trajectory across the “space-time landscape.”

We use the term life history pattern to mean a collection of similar pathways. A successful life history pattern is one that is brought to *closure*—some individuals following the pattern survive through all life stages and return to their natal spawning ground (Sinclair 1988). A sustainable life history pattern is one that remains successful over the range of prevailing environmental and man-induced mortality conditions.

Productivity

This element of performance represents the density-independent reproductive rate (or success) of a life history pattern over an entire life cycle. It is probably the most critical measure of the resilience of a life history pattern. It determines the rate of loss that can be sustained. Productivity can be likened to how far a rubber band can be stretched before breaking.

Surprisingly little attention has been given to the subject of salmon productivity within the literature (Hankin and Healey 1986; Moussalli and Hilborn 1986). Hankin and Healey (1986) suggest that biologists

have devoted a disproportionate amount of effort to estimating habitat carrying capacity; greater need exists, they assert, to better understand productivity, especially as stocks decline.

The term is widely used in ecological and fisheries literature where its meaning varies greatly. Classical ecological usage usually relates to trophic productivity. In the fisheries literature, it sometimes refers to total stock size.

The term *productivity* as applied in the EDT framework, follows precisely the recommendations of Moussalli and Hilborn (1986) and Hilborn and Walters (1992). It refers to density-independent survival, as well as to what is often called the basic biological productivity of a population (i.e., the average number of eggs per surviving adult).

Productivity of salmon populations consists of distinct components (Figure 4), each of which can have a significant effect on the overall value. The two major components are reproductive potential and density-independent survival. Reproductive potential is the total number of eggs per adult spawner. This term is further divided into two sub-components: average fecundity of females and average sex ratio of the spawning population. Density-independent survival is also divided into subcomponents: freshwater and marine.

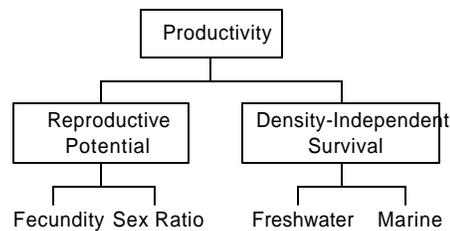


Figure 4. Components of productivity.

An important property of productivity is that its components are multiplicative. From a strictly productivity-based perspective there is no bottleneck—no single limiting factor.

Capacity

There is clearly some upper limit to the number of organisms that an environment can support due to finite amounts of space, food, or other needed resources (Ricklefs 1973). Capacity is the element of performance that determines the effect of this upper limit on survival and distribution. It is the parameter that regulates the density-dependent population responses.

Superficially, the concept of capacity seems simple and easily envisioned. A room can hold only so many people; a tract of land can grow only so much wheat; a fish pond can be stocked with only so many fish. But the concept applied to an ecosystem is more elusive, particularly as it relates to species with complex life histories like salmon (Frissel et al. 1997).

There have been numerous attempts to quantify or characterize the capacity of natural salmon systems (Burns 1971; Marshall 1980; NPPC 1991; Nickelson et al. 1993; Beechie et al. 1994). Most of these efforts are based on a capacity concept that focuses on a single life stage in isolation of others, as set forth by Burns (1971):

“Carrying capacity is defined as the greatest weight of fishes that a stream can naturally support during the period of least available habitat...The stream’s carrying capacity limits the number and weight of salmonid smolts ultimately produced.”

Following the lead of Moussali and Hilborn, we generalize and broaden the notion of capacity. We are most interested in the capacity over the full salmon life cycle. This cumulative population maximum is a function of both the productivities and capacities of all component life history segments (Moussali and Hilborn 1986).

The model uses an expression for cumulative capacity derived from a Beverton-Holt multistage spawner-production relationship (Beverton and Holt 1957). This particular production function has both intuitive and mathematical appeal. It provides a logical and reasonable structure for framing interactions of density-independent and -dependent processes under various environmental conditions. Moussali and Hilborn (1986) postulate that other standard production functions have similar characteristics.

The capacity for a population must be considered over the entire life cycle of the animal. To exclusively consider capacity at the close of an intermediate life stage ignores the effects of subsequent stages on population survival. While cumulative productivity is the same no matter where we define the beginning and end of a complete life cycle, cumulative capacity does depend on this choice.

A logical reference point along the timeline of life history, for defining the unit of capacity for salmon populations, is at reproduction. For salmon, spawning is the point where one generation ends and another begins. It is the point of minimum abundance in the life cycle and, therefore, represents the total amount of genetic material passed from one generation to the next. This point along the life cycle is also most representative of the values ascribed to salmon populations by society over the long term. It is adult salmon, and not juveniles, that relate most directly to societal values such as harvest. An interesting and

important conclusion that emerges from this full life-cycle perspective is that a population may be close to capacity (in the cumulative sense) without a single component life stage being *fully seeded*. Thus diagnoses indicating that habitat is *under-seeded* or fully seeded, unless analyzed from a full life-cycle perspective, can be very misleading. We refer the interested reader to the EDT Primer (Lestelle et al. 1996) for further discussion of the concept of capacity as used in the model.

Analytical Model

The analytical model is the tool used to analyze environmental information and draw conclusions about the ecosystem. The model computes biological performance based on environmental attributes (Figure 5).

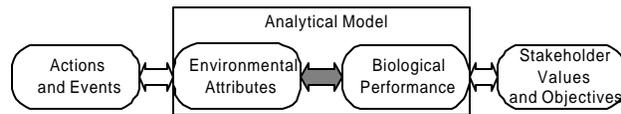


Figure 5. The analytical model in the context of the conceptual framework.

The model incorporates an environmental attributes database and a set of mathematical algorithms that compute productivity and capacity parameters (Figure 6). The analytical model is a scientific rather than a statistical model—an important distinction.

Statistical models are based on correlations between actions and outcomes. They do not attempt to explain why; they simply predict the future based on past observations. Statistical models allow estimation of confidence limits and other statistical properties of the predictions. They are limited, however, to our range of experience.

Scientific models—such as the EDT analytical model—are, on the other hand, based on knowledge and assumptions about how natural systems work. Scientific models *do* attempt to explain relationships and therefore are more appropriate to analyze the consequences of broad combinations of actions that extend beyond our experience.

The Ecosystem Diagnosis and Treatment (EDT) model

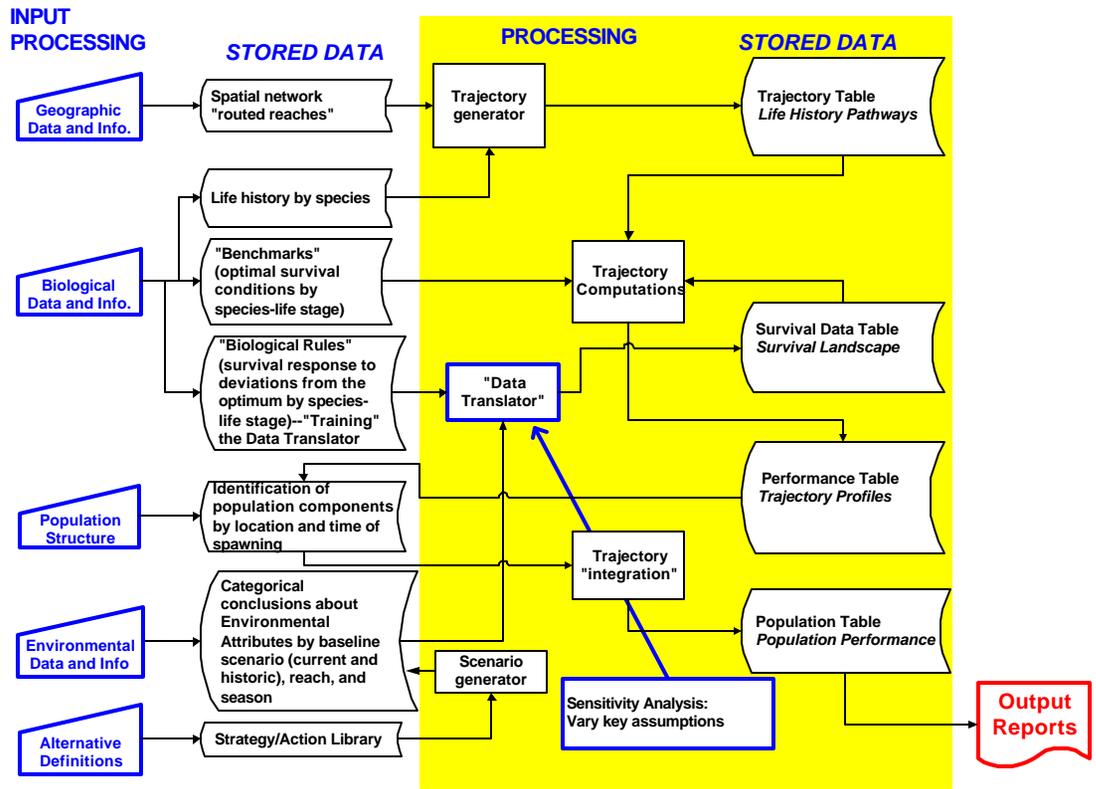


Figure 6. Overview of the EDT analytical approach.

Scientific models are not in themselves hypotheses that can be tested with data. They generate hypotheses that might be tested through observations. Validation of a scientific model means establishing its applicability and utility to the problem at hand. The standard the scientific model should achieve is whether it better meets this purpose than alternative models. Therefore, the way to challenge a scientific model is to propose a better one. Without a scientific model, we have no scientific basis for analyzing a problem. The EDT analytical model provides qualitative insights and understanding about how natural events and human actions affect biological performance. This, according to Hilborn and Mangal (1997), is the ideal use of models. The EDT analysis is based on a habitat, life history approach. The habitat is described in terms of survival conditions along the pathways (waterways) that the fish utilize from birth to death. By habitat, in this context, we mean all conditions within the environment of the fish that affect its behavior and survival (i.e., harvest, dams, ocean conditions). The EDT model computes survivorship of populations along the life history pathways across the habitat. The EDT model input consists of habitat ratings and life history pathways; the output is abundance, productivity, life history diversity, and distribution of fish populations.

The algorithms used to calculate population parameters are based on the Beverton-Holt survival function (after Beverton and Holt 1957). In Appendix B, we derive some of the key relationships used in the model.

Biological Rating of Environmental Attributes

Environmental attribute ratings are derived from observed environmental conditions based on information and knowledge from the scientific literature or from experts in the field of habitat and fish biology. The model captures this knowledge as a set of *biological rules*.

The most efficient way to generate environmental attribute ratings is to apply the rules directly to observed data. This data translation may also be accomplished through a *manual* process, where the ratings are supplied by a panel of experts familiar with the watershed and with the biology of the diagnostic species. Biologists summarize data and reports and then rate habitat, by reach and month, for each of the attributes—relative to benchmark conditions by life stage. The manual data translation process has educational value for the participants.

Trajectory Generation and Sampling

Pacific salmon species are able to survive in a wide range of habitat types—from Alaska to California; and they are able to cope with dynamic variations in environmental conditions over time. An important component of their survival strategy is diversity of life history. However wide this diversity of life history might be, there are limitations imposed by the biology of the species. We refer to these limits as the genetic boundaries of the species. As the environment within a watershed varies, the range of life history diversity available to the species enables it to cope with these variations.

Not all trajectories within the genetic boundaries are used with equal frequency. Within the genetic boundaries, the frequency of use is partly a function of habitat conditions and partly a reflection of the opportunistic nature of the species.

We do not know how quickly—or to what extent—trajectories adapt to the habitat, but we believe that the relationship between life history diversity and habitat is important to the survival of the species. The analytical model includes a mechanism for addressing our limited understanding of these relationships. As a starting point, we suggest a process for generating and subsampling trajectories that produces results that are consistent with what we do know.

The process consists of the following steps:

- 1) Define the starting point of each trajectory as the moment of spawning.
- 2) Start trajectories at uniform time and space intervals within assumed historic ranges for the watershed.
- 3) Identify a set of broad life history patterns (e.g., three patterns for fall chinook).
- 4) Identify, for each life history pattern, windows in time and space through which trajectories must pass (e.g., a time window for entering the river mouth).
- 5) Identify biological limits for travel speed and life stage durations.
- 6) Generate a large number of trajectories at random, subject to above the constraints (this creates a *pool* of trajectories).

- 7) Sub-sample the trajectory pool in proportion to those frequencies, to the extent that we have *a priori* information about the frequency of life history patterns (independent of habitat conditions).
- 8) Include at least one trajectory originating from each reach in the sub-sample.
- 9) Use the same sample of trajectories when comparing different scenarios.
- 10) Test the sensitivity to the sample, as time and resources allow, by re-sampling from the pool.

Benchmarks

The EDT method associates survival with habitat. The productivity and capacity values derived in the EDT process are characteristics of the environment by time and location as interpreted *through the eyes of salmon* by species and life stage (Moberg et al. 1997). It is a shaping of survival conditions over time and space, as salmon might experience them in completing their life cycle. The shaping of survival is done with reference to a defined set of *benchmark* conditions.

From the literature, we can identify habitat requirements by life stage for the species. We can take it a step further and describe optimal conditions and the expected survival and density limits by life stage. When viewed at a fine enough time scale, this information tends to be generic (i.e., not site specific). The EDT process defines the reference benchmarks in terms of these optimal conditions. Thus benchmark descriptions of habitat conditions, associated productivities, and maximum densities by life stage are obtained from the literature describing conditions that are *as good as it gets*.

The systematic shaping of survival conditions is intended to assure that productivity and capacity values for each life history segment along a trajectory are (a) bounded by the biological limits of the species; (b) scaled consistently across time, space, and life stage; and (c) scaled consistently with the benchmark values.

Step-by-Step Procedure

The step-by-step EDT procedure tells you how to apply the conceptual framework and analytical model to develop watershed plans that lead to achievement of goals.

The procedure consists of five steps:

- 1) Identification of goals and values
- 2) Diagnosis
- 3) Identification of treatment alternatives
- 4) Analysis of treatment alternatives
- 5) Adaptive implementation of preferred alternatives

These steps were designed to provide technical support to a structured decision-making process. We will discuss each of these steps below.

Identification of Goals and Values

Watershed goals for fish resources are derived from social, cultural, political and legal considerations in a policy environment. The EDT process does not presume agreement on all values and goals; it only requires that potential goals and values be identified.

These goals and values provide the currency whereby the outcomes of alternatives are described. The EDT analysis clarifies which goals are technically compatible and which are in conflict. The analysis of alternatives will highlight trade-off options associated with each alternative.

The EDT technical analysis enables us to provide policy makers with sets of alternative action plans (treatments) that meet as many of a their stated goals as possible. When not all goals can be met concurrently, we can determine what the trade off options are.

Diagnosis

Through diagnosis we determine why certain watershed goals are not being met. We accomplish this, in part, by comparing the three states of the watershed: the Patient, the Template, and the Benchmark. This type of watershed evaluation was

developed by Lichatowich et al. (1995). It is called a Patient-Template Analysis (PTA).

The Patient refers to the current state of the watershed. The Patient condition is based on the best and most current environmental data and information available.

The Template refers to a hypothetical potential state where conditions are as good as they can be *within* the watershed. The Template is sometimes approximated with a reconstruction of historic conditions. The Template is intended to capture the unique characteristics and limitations of the watershed due to its combination of climate, geography, geomorphology, and history. Sedell and Luchessa (1982), Langston (1995), and Wissmar (1997) argue the importance of historical information to our understanding of the environment today and in the future.

The Benchmark refers to the hypothetical state where conditions are as good as they can be *anywhere* for the diagnostic species. Benchmark values serve as a known reference point drawn from the literature.

The purpose of the PTA is to make statements about the salmon performance potential supported by an explicit set of assumptions and consistent with the available information about the watershed. The PTA describes salmon performance for the Patient and Template in terms of productivity, capacity, and life history diversity.

The PTA highlights the differences between present and potential conditions within the watershed from the salmon's perspective. It explains those differences through a set of environmental attributes that describe the environment as it affects salmon performance. We can then use this comparison to formulate a diagnosis—an assessment of current conditions (for salmon) relative to the potential.

There are four steps in the PTA:

1. System organization, definition, and scale.

The watershed-population system is organized within a spatial-temporal grid consistent with the range of life histories for salmon. Spatially, the watershed is partitioned into stream reaches. Stream reach boundaries and time scales are defined so that within a reach-time stratum we can assume that environmental attributes affecting salmon survival are relatively constant.

2. Information compilation.

Information is assembled and summarized to describe Patient and Template conditions in the watershed. The purpose of this step is to identify the best available information and make it available for the data translation step that follows. This step basically produces a watershed analysis. Information is obtained from many and diverse sources such as published and unpublished studies, habitat surveys, environmental databases, environmental monitoring programs, aerial and ground level photographs, and maps. When a thorough watershed analysis has been completed before, it can be an excellent information source. Both historic and current conditions need to be captured in this compilation.

3. Data translation.

The data and information assembled must now be translated into the input format required by the model. This step converts environmental data into ratings that specify the relative effects of each environmental attribute on life stage survival for the species. This step is done by applying a set of *biological rules* that relates survival to environmental attributes. Once this step is completed, the baseline dataset for the Patient and Template is ready to be analyzed.

4. Life history analysis.

The final step in the PTA is to evaluate the Patient and Template habitat data from a salmon life history perspective. The analysis consists of three parts: 1) Definition of life history patterns and selection of sample trajectories; 2) Assumptions about population genetics, age structure, fecundity, and marine survival; 3) Computation and display of performance measures.

Identification of Alternatives

After the diagnosis, it is time to identify potential actions to achieve watershed goals. Candidate actions are tailored to solve problems that were identified in the diagnosis.

Basin plans are comprehensive, long-term plans for entire watersheds—they consist of suites of actions designed to meet watershed goals. One of the main benefits of the EDT method is that it allows us to build diverse suites of actions and analyze their *cumulative* effects.

The analytical model contains a library of generic strategy and event blocks as starting points for defining watershed-specific actions from which alternative future basin plans can be built.

Analysis of Treatment Alternatives

Following the identification of candidate actions, an analysis of trade-offs is performed to compare benefits and risks of individual or suites of actions. Benefits and risks are expressed relative to goals and values. In the analysis of treatment alternatives, we want to know what the trade-offs among the alternatives are. One alternative may have a high likelihood of achieving some of the goals while other goals are at risk.

The analytical model can be used to compare multiple alternatives with respect to the benefits and risks to productivity, capacity, and life history diversity of the diagnostic species.

All aspects of natural resource management involve uncertainty. Conceptualization of ecological relationships and functions, diagnostic analyses, and selection of treatments incorporate assumptions that create uncertainty—and uncertainty poses risk.

Adaptive Implementation of Preferred Alternatives

Our understanding of ecosystems, and the responses of those systems to intervention, is inevitably incomplete. Our ability to measure progress toward management goals accurately and timely is limited. Adaptive management, supported by the EDT method, provides the means to proceed with implementation while managing and containing risks due to uncertainties.

Because of uncertainty, it is necessary to incorporate in the implementation of watershed plans flexibility so that unsuccessful strategies and unattainable objectives can be replaced with more suitable ones. We also need, however, stability and accountability to ensure that sound strategic decisions are made that lead toward achievement of long-term resource goals.

Literature Cited

- Angermeier, P. 1997. Conceptual roles of biological integrity and diversity. Pages 49-65 in J. E. Williams, C. A. Wood, and M. P. Dombeck, editors. Watershed restoration: principles and practices. American Fisheries Society, Bethesda, Maryland.
- Beechie, T., E. Beamer, and L. Wasserman. 1994. Estimating coho salmon rearing habitat and smolt production losses in a large river basin, and implications for habitat restoration. *North American Journal of Fisheries Management* 14: 797-811.
- Beverton, R. J. H. and S. J. Holt. 1957. *On the Dynamics of Exploited Fish Populations*. Chapman & Hall, London.
- Bjornn, T. C. and D. W. Reiser. 1991. Habitat requirements of salmonids in streams. Pages 83-138 in W. R. Meehan, editor. *Influences of forest and rangeland management on salmonid fishes and their habitats*. American Fisheries Society, Bethesda, Maryland.
- Bunnell, F.L. 1989. *Alchemy and uncertainty: what good are models?* General Technical Report PNW -GTR-232. Report. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon.
- Burns, J. W. 1971. The carrying capacity for juvenile salmonids in some northern California streams. *California Fish and Game* 57(1): 44-57.
- den Boer, P. J. 1968. Spreading of risk and stabilization of animal numbers. *Biotheoretical* 18(19): 165-193.
- Doppelt, B., M. Scurlock, C. Frissell, and J. Karr. 1993. *Entering the watershed: a new approach to save America's river ecosystems*. Island Press, Covelo, California.
- Frissell, C. A., W. J. Liss, R. E. Gresswell, R. K. Nawa, and J. L. Ebersole. 1997. A resource in crisis: changing the measure of salmon management. Pages 411-444 in D. J. Stouder, R. A. Bisson, and Naiman R.J., editors. *Pacific salmon and their ecosystems: status and future options*. Chapman and Hall,
- Hankin, D. and M. Healey. 1986. Dependence of exploitation rates for maximum yield and stock collapse on age and sex structure of chinook salmon (*Oncorhynchus tshawytscha*) stocks. *Canadian Journal of Fisheries and Aquatic Sciences* 43(9): 1746-1759.

- Haskell, B. D., B. G. Norton, and R. Costanza. 1992. Introduction: what is ecosystem health and why should we worry about it? Pages 3-20 in R. Costanza, B. G. Norton, and B. D. Haskell, editors. *Ecosystem Health: new goals for environmental management*. Island Press, Covelo, California.
- Hilborn, R. and C. Walters. 1992. *Quantitative fisheries stock assessment: choice, dynamics & uncertainty*. Routledge, Chapman and Hall, New York.
- Hilborn, R. and M. Mangel. 1997. *The ecological detective: confronting models with data*. Princeton University Press, Princeton, New Jersey.
- Langston, N. 1995. *Forest dreams, forest nightmares*. University of Washington Press, Seattle.
- Lee, K. N. 1993. *Compass and gyroscope: integrating science and politics for the environment*. Island Press, Washington, D.C.
- Lestelle, L.C., L.E. Mobernd, J.A. Lichatowich, and T.S. Vogel. 1996. *Applied ecosystem analysis - a primer, EDT: the ecosystem diagnosis and treatment method*. Project number 9404600. Bonneville Power Administration, Portland, Oregon.
- Lichatowich, J.A. and L.E. Mobernd. 1995. *Analysis of chinook salmon in the Columbia River from an ecosystem perspective*. Project number 92-18; Contract No. DE-AM79-92BP25105. Final Report. Bonneville Power Administration, Portland, Oregon.
- Lichatowich, J., L. E. Mobernd, L. Lestelle, and T. Vogel. 1995. An approach to the diagnosis and treatment of depleted Pacific salmon populations in freshwater ecosystems. *Fisheries* 20(1): 10-18.
- Marshall, D.E. 1980. *Optimum spawning density for coho salmon*. Canada Department of Fisheries and Oceans, Vancouver, British Columbia.
- Mobernd, L. E., J. A. Lichatowich, L. C. Lestelle, and T. S. Vogel. 1997. An approach to describing ecosystem performance "through the eyes of salmon". *Canadian Journal of Fisheries and Aquatic Sciences* 54: 2964-2973.
- Moussalli, E. and R. Hilborn. 1986. Optimal stock size and harvest rate in multistage life history models. *Canadian Journal of Fisheries and Aquatic Sciences* 43(1): 135-141.
- Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries* 16(2): 4-21.

- Nickelson, T. E., M. F. Solazzi, S. L. Johnson, and J. D. Rodgers. 1993. An approach to determining stream carrying capacity and limiting habitat for coho salmon (*Oncorhynchus kisutch*). Pages 251-260 in L. Berg and P. W. Delaney, editors. Proceedings of the coho workshop. British Columbia Department of Fisheries and Oceans, Vancouver, British Columbia.
- Northwest Power Planning Council. 1991. Proposed amendments to the Columbia River Basin fish and wildlife program, Phase II: Mainstem survival, harvest, production and other measures to protect salmon and steelhead. Document 91-25. Northwest Power Planning Council, Portland, Oregon.
- O'Neill, R. V., D. L. DeAngelis, J. B. Waide, and T. F. H. Allen. 1986. A hierarchical concept of ecosystems. Princeton University Press, Princeton, New Jersey.
- Ricklefs, R. E. 1973. Ecology. Chiron Press, Newton, Massachusetts.
- Sedell, J. R. and K. J. Luchessa. 1982. Using the historical record as an aid to salmonid habitat enhancement. in N. B. Armantrout, editor. Proceedings of the Symposium on Acquisition and Utilization of Aquatic habitat inventory information. Western Division of the American Fisheries Society, Bethesda, Maryland.
- Simenstad, C. A., D. A. Jay, and C. R. Sherwood. 1992. Impacts of watershed management on land-margin ecosystems: the Columbia River estuary. Pages 266-306 in R. Naiman, editor. Watershed management: balancing sustainability and environmental change. Springer-Verlag, New York.
- Sinclair, M. 1988. Marine populations: an essay on population regulation and speciation. Washington Sea Grant Program (Distributed by University of Washington Press), Seattle.
- Thompson, W. F. 1959. An approach to population dynamics of the Pacific red salmon. Transactions of the American Fisheries Society 88(3): 206-209.
- Walter, G.F. 1986. Nisqually River drainage basin in-stream habitat assessment and policy recommendations. Technical Report No. 15. Nisqually Indian Tribe, Olympia, Washington.
- Walters, C. 1997. Information requirements for salmon management. Pages 61-68 in D. J. Stouder, P. A. Bisson, and R. J. Naiman, editors. Pacific salmon & their ecosystems: status and future options. Chapman & Hall, San Francisco.
- Warren, C., M. Allen, and J. Haefner. 1979. Conceptual frameworks and the philosophical foundations of general living systems theory. Behavioral Science 24: 296-310.

Wevers, M.J. 1993. Life history and evolutionary adaptation of Pacific salmon and its application in management. Doctoral dissertation. Oregon State University, Corvallis, Oregon.

Williams, J. E., C. A. Wood, and M. P. Dombeck, editors. 1997. Watershed restoration: principles and practices. American Fisheries Society, Bethesda, Maryland.

Wissmar, R. C. 1997. Historical perspectives. Pages 66-79 *in* J. E. Williams, C. A. Wood, and M. P. Dombeck, editors. Watershed restoration: principles and practices. American Fisheries Society, Bethesda, Maryland.

Appendix A

Analytical Approach

We use the conventional method of moment approach to estimate parameters. Statistical properties of these estimators are not discussed here; we refer the interested reader to the general literature on the subject. Based on preliminary simulations, we hypothesize that the model produces reasonable results for populations which follow the Ricker production function as well.

The Basic Survival Model

A fundamental assumption of the model is that the life history of a salmon species can be partitioned into segments within which a) habitat conditions are relatively uniform, and b) the survival response is constant and predictable.

Segments that meet these conditions are defined in terms of space (e.g. stream reach), life stage (e.g. egg incubation), and time (e.g. month). The model further assumes that, within each segment, survival is adequately described by a two-parameter, Beverton-Holt survival function:

$$S = \frac{P}{1 + \frac{PN}{C}}, \quad (\text{Equation 1})$$

where P is productivity (low density reproductive success) and C is carrying capacity for the “uniform” life segment. N is the number of individuals alive at the beginning of the segment.

The Multistage Recursion Formula

Moussali and Hilborn (1986) showed that if survival in a sequence of life stage segments along the life history is either density independent or follows a Beverton-Holt survival function, then so does the full sequence. They showed further that “cumulative” productivity and capacity for a sequence of N segments with productivities p_i and c_i can be computed as:

$$P_N = \prod_{i=1}^N p_i, \quad (\text{Equation 2})$$

and

$$C_N = \frac{P_N}{\sum_{i=1}^N \frac{P_i}{c_i}}, \quad (\text{Equation 3})$$

which leads to the useful recursion:

$$C_N = \frac{P_N}{\frac{1}{C_{N-1}} + \frac{P_N}{c_N}}, \quad (\text{Equation 4})$$

If the N segments comprise the entire life cycle, we can now, for example, predict the equilibrium abundance, Neq , from:

$$Neq = C_N(1 - 1/P_N), \quad (\text{Equation 5})$$

We refer to a sequence of uniform life history segments that begins and ends with the spawning life stage as a life history trajectory. In the next section we talk about how productivity and capacity values for trajectories are used to calculate parameters for a population in a watershed.

Estimating Population Productivity from Life History Trajectories.

Our objective is to find the parameters of the Beverton-Holt production function that best describe survival characteristics of a defined population within a watershed. Suppose that we know the productivity values, P_i 's, for all life history trajectories within the genetic boundaries² of the species. If we also know the relative frequency of use, W_i , of each trajectory, then we suggest that a reasonable estimator of the population productivity P is given by:

$$P = \frac{\sum_i P_i W_i}{\sum_i W_i}. \quad (\text{Equation 6})$$

It seems reasonable that, in the long term, the frequency of use of the different trajectory pathways would be related to both

² By genetic boundaries we mean the range of life history patterns, i.e., spawning time, life stage durations, travels speeds, etc., observed for the species.

quality and quantity of habitat available. The equilibrium population size, which can be calculated for each trajectory, is a function of both. The model in fact assumes that the weights (W_t) are proportional to the equilibrium population size (Equation 5) of each trajectory, in other words:

$$W_t \propto Neq_t = C_t \left(1 - \frac{1}{P_t}\right), \quad (\text{Equation 7})$$

where C_t is the capacity for trajectory t . The population productivity parameter is thus estimated from the trajectory productivities and capacities by:

$$P = \frac{\sum_t C_t (P_t - 1)}{\sum_t C_t \left(1 - \frac{1}{P_t}\right)}. \quad (\text{Equation 8})$$

In practice, the estimate is, of course, based on a sample of trajectories. The question of how this sample is derived is discussed in a later section. The weighting procedure for estimating productivity reduces the sensitivity to the sampling scheme. We next look at the estimator for population capacity.

Estimating Population Capacity from Life History Trajectories

The capacity, C_t , associated with a single life history trajectory assumes that the length of the spawning reach is one meter. For every meter of potential spawning habitat we can estimate the capacity for trajectories associated with that particular stream segment, m , by simply computing their average:

$$C_m = \text{Average}(C_{\epsilon m}), \quad (\text{Equation 9})$$

and the population capacity for a watershed can be estimated as the sum of all C_m for all non-overlapping meter segments. If the distribution of potential trajectories is uniform throughout the watershed, then the population capacity parameter for the watershed can be estimated as the average trajectory capacity, C_{avg} , multiplied by the length of spawning habitat in meters, M .

$$C = C_{avg} M. \quad (\text{Equation 10})$$

Note that the stream width and the quantity and quality of habitat within the meter band are included in the trajectory capacity, C_t . The model estimates capacity from a sampling of

trajectories. The estimate of C is sensitive to the sampling procedure.

Life History Diversity from Trajectories.

Let us assume that there exists a set of life history trajectories, $\{t \in T\}$, that meets the condition that they are consistent with the genetic limitations of the modeled species. If the productivity, P_t , for trajectory t is greater than one, then spawners that choose this trajectory will make a positive contribution to the next generation (i.e., more than one offspring will return to spawn). If, on the other hand, P_t is less than one, the net contribution of those spawners will be a population loss. We define trajectories where P_t is greater than one as sustainable. We define the percentage of all trajectories within T that are sustainable as the Life History Diversity Index, D .

$$D = \frac{(\#t \in T : P_t \geq 1)}{(\#t \in T)}. \quad (\text{Equation 11})$$

The computations so far have been based on the assumption that we can estimate the cumulative (i.e. full life cycle) productivity, P_t , and capacity, C_t , for a life history trajectory. Next we describe how the model estimates these trajectory parameters.

Estimating Trajectory Productivity and Capacity from Habitat Ratings

A life history t trajectory consists of a sequence of segments, like beads in a chain. Each segment consists of one time, space and life stage stratum. Within each segment we assume that environmental conditions and the induced biological responses are constant. Each segment thus meets the conditions of the basic survival model described above.

The computation of productivity and capacity for a trajectory requires two main steps: first, the computation of productivities and capacities for each segment; and second, combining the segment parameters into full life cycle or cumulative values. We will describe the second step first.

Assume that trajectory t can be partitioned into N uniform segments, and let $p_{t,i}$ and $c_{t,i}$ be the productivity and capacity parameters for segment i of trajectory t . From Equations 2 and 3 we have:

$$P_t = \prod_{i=1}^N p_{t,i}, \quad (\text{Equation 12})$$

and

$$C_t = \frac{P_t}{\sum_{i=1}^N \frac{P_{t,i}}{c_i}}, \quad (\text{Equation 13})$$

where

$$P_{t,i} = \sum_{j=1}^i p_{t,j} \quad (\text{Equation 14})$$

Now the question remains: how do we estimate the segment p 's and c 's? We are now looking at a uniform stream reach, over a time period when no significant change in habitat conditions occurs, and we are considering one fixed life stage. The productivity parameter for the segment is the low-density survival over the duration of the segment. We assume that this density independent survival parameter is strictly a function of the *quality* of habitat perceived by the given species and life stage. Specifically, the productivity is given by:

$$p_{t,i} = r_{i,j} b_i, \quad (\text{Equation 15})$$

where b_i is a "benchmark" (reference) productivity value for the life stage obtained from the literature adjusted for the duration of the current trajectory segment³. The benchmark values represent optimal survival conditions for the species. The factor $r_{i,j}$ is a relative productivity multiplier that adjusts the benchmark value to the habitat quality conditions of segment t,i . This multiplier is computed from:

$$r_{i,j} = \prod_a (1 - h_a / 4)^{2.7}, \quad (\text{Equation 16})$$

where h_a is a rating for habitat quality attribute a . The model captures habitat quality in terms of 18 such attributes. Each is given a rating between 0 and 4, where 0 implies no effect (no

³ Appendix A includes a set of algorithms used in the model to adjust productivity and capacity values for the varying durations of the trajectory segments. Note that while the habitat data have discrete (monthly or weekly) time steps, the trajectory durations are continuous variables. A trajectory segment may last a fraction of a week or many weeks.

contribution to the multiplier) and 4 implies a lethal effect (multiplier becomes zero).

The capacity parameter for the trajectory segment is computed from reach width, percent of key habitat (within the reach), a food quantity rating, segment productivity, and benchmark productivity and density for the life stage. The calculation is iterative. First the weekly benchmark density at the beginning of the segment is back calculated, correcting for change in size of fish during the life stage (the model includes a size vs. density function). Segment capacity is then calculated as the cumulative capacity for the segment duration using Equation 3 above, including a multiplicative adjustment for percent of key habitat, reach width and food factor (see Appendix A for details).

Data Translation

Biological attribute ratings (h_a above) are derived from observed environmental conditions based on the accumulation of information and knowledge available from the scientific literature and or from experts in the field of habitat and fish biology. The model captures this knowledge in the form of a set of *biological rules*. The most efficient way to generate biological attribute ratings is to apply the rules directly to observed data. Earlier versions of the EDT, accomplished the data translation through a “manual” process, where the ratings were supplied by a panel of experts familiar with the watershed and with the biology of the diagnostic species. Biologists would summarize data and reports and then rate habitat, by reach and month, for each of the attributes – relative to benchmark conditions by life stage. The “manual” data translation process has educational value for the participants.

Appendix B Diagnostic Species

Watershed management actions should be built on, or be consistent with, ecosystem-directed strategies that promote or maintain ecologically healthy watersheds. A management strategy based on an ecosystem perspective provides a scientific basis for evaluating, coordinating, and prioritizing watershed actions in a consistent manner. An ecosystem strategy is holistic; it recognizes that biotic and abiotic components of a watershed are interconnected. Hence, it must consider the long-term and collective consequences of many activities throughout a watershed.

An ecologically healthy watershed may be defined as one capable of supporting and maintaining a balanced, integrated, adaptive biological system having the full range of elements and processes expected in the natural habitat of the region (Angermeier and Karr 1993). This definition of ecological health underscores the importance of planning that considers the entire biotic community and emphasizes sustainability.

A primary management goal is to ensure the sustainability of valued renewable natural resources. The most important challenge facing environmental management is to foster a balance between short-term human needs and ecosystem sustainability (Ruckelshaus 1989; Lee et al. 1992).

Sustainability is defined as the process of change in which the continued exploitation or protection of resources, the direction of investment in land and water, and associated institutional changes are consistent with future as well as present objectives for perpetuating environmental qualities and socioeconomic functions of ecosystems (WCED 1987). Human communities generally desire that resource-based values and objectives associated with the water and land of a watershed be sustainable, even within the context of watersheds that have undergone major changes to accommodate human needs.

The concept of sustainability must also recognize that ecosystems are constantly evolving. The management concern we raise when we worry about sustainability is the direction

and rate of this evolution. All valued natural resources may not be concurrently sustainable in all watersheds.

Certain species or populations that are dependent on the relative stability of ecological processes over a large portion of a watershed can be used to help diagnose conditions for sustainability. The shift toward ecosystem management that has occurred in recent years is a move away from a conventional, single-species approach to a whole system, multi-species framework (Grumbine 1994). This shift poses a problem: How do we assess the condition of ecosystems, given their inherent complexity? The use of appropriately selected indicator or diagnostic species provides a way of coping with this complexity (Soule 1987; Karr 1992; Lee 1993).

Instead of trying to understand all dimensions of an ecological whole, the use of indicator organisms that are sensitive to an important cross-section of those dimensions gives needed focus for an assessment (Lee 1993). Implicit in this concept is the assumption that a species that is sensitive to a wide variety of ecosystem conditions is useful as a pulse on the system.

Desired conditions for the entire ecosystem may be achieved through actions guided by the needs of populations that fill representative (umbrella species) or key (keystone species) functional roles within the ecosystem (Walker 1995). This approach may currently be the most effective way to achieve ecosystem sustainability (Olver et al. 1995; Walker 1995). The EDT method uses the term *diagnostic species* to emphasize that it is a device to aid in diagnosing and treating watershed conditions.

Migratory salmonid species, like salmon, are highly suited as diagnostic species. Their freshwater life history depends upon streams, the arterial system of the watershed. Streams are generally regarded as a good reflection of overall watershed condition since water drains downhill, bringing with it characteristics created by conditions upstream. Salmonids are sensitive to these characteristics (Bjornn and Reiser 1991). Because fish are often primary determinants of ecosystem structure (Brooks and Dodson 1965; McQueen et al. 1986), conditions shaping their survivability and life history are important to that structure.

Certain salmonid species (e.g., chinook, coho, and steelhead) utilize extensive portions of the watershed, from the mouth of the river to the headwaters of many of its connected branches. To complete their life cycles, individuals of these species

experience the condition of the river from the spawning grounds, often located high in the watershed, to the estuary.

Hence the completion of their life cycle depends upon the connectivity of the stream network over various life stages (Lichatowich and Moberg 1995). These life stages, which can number seven or more (e.g., prespawning, spawning, incubation, colonization, active rearing, inactive, and juvenile migration), have different habitat requirements (Bjornn and Reiser 1991); therefore, sustainable life history patterns require the existence of diverse habitats.

Migratory salmonids have another important, unique role—they connect ecosystems through their extensive migrations. For example, chinook that spawned historically in the upper Cispus subbasin (as in Yellowjacket Creek) utilized not just this stream, but the lower Cispus, the mainstem Cowlitz River, and the Columbia River before moving into the Pacific Ocean. There, they traveled extensively for several years prior to the return to their natal stream. The concept of ecosystem management ultimately must recognize that watersheds (or ecosystems) are not isolated (Maser and Sedell 1994); conditions in one can have profound implications for the sustainability of resources in another. Moreover, salmon are among the few species that cycle nutrients between all these environments (Kline et al. 1993; Bilby et al. 1995; Willson and Halupka 1995).

The potential magnitude of nutrient cycling by salmon and its role in ecosystem function have long been acknowledged (Juday et al. 1932; Donaldson 1967); but, in general, their importance has received scant attention by scientists (Willson and Halupka 1995). Recent findings suggest that nutrient cycling may be very important to the structure and stability of some watersheds, supporting the conclusion that salmon should be considered a keystone species in these systems (Bilby et al. 1995). A keystone species is one that plays a critical role in maintaining the biological integrity of the ecosystem to which it and many other species belong; the loss of such species leads to cascading changes in ecosystem structure (Paine 1969; Paine 1995).

This potential keystone role is seen in the importance that anadromous salmonids have had historically, and continue to have in many areas, as critical nutrient sources to numerous species (Willson and Halupka 1995). The enormous influx of biomass to freshwater systems that can occur through anadromous adult salmonids and their progeny can be heavily

exploited by mammal, bird, and fish species, affecting the distribution, survival, and reproduction of these non-salmon species.

The findings by Bilby et al. (1995), and their on-going work, provide evidence that the capacity of salmon streams to support fish may be progressively declining due to reductions in nutrient loading caused by diminishing numbers of spawning salmon.

In addition to serving as indicators of the quality of watersheds, salmon species symbolize the vitality of the Pacific Northwest to human communities (Jay and Matsen 1994). Salmon are integral to the heritage and present-day values of people throughout the region. In a sense, they are an icon of the quality of life in the area.