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Data and Modeling Tools for Assessing Landscape Influences on Salmonid Populations: Examples from Western Oregon

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Abstract.—Most studies addressing relationships between salmonids, their freshwater habitats, and natural and anthropogenic influences have focused on relatively small areas and short time periods. The limits of knowledge gained at finer spatiotemporal scales have become obvious in attempts to cope with variable and declining abundances of salmon and trout across entire regions. Aggregating fine-scale information from disparate sources does not offer decision makers the means to solve these problems. The Salmon Research and Restoration Plan for the Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative (AYK-SSI) recognizes the need for approaches to characterize determinants of salmon population performance at broader scales. Here we discuss data and modeling tools that have been applied in western Oregon to understand how landscape features and processes may influence salmonids in freshwater. The modeling tools are intended to characterize landscape features and processes (e.g., delivery and routing of wood, sediment, and water) and relate these to fish habitat or abundance. Models that are contributing to salmon conservation in Oregon include: (1) expert-opinion models characterizing habitat conditions, watershed conditions, and habitat potential; (2) statistical models characterizing spatial patterns in and relationships among fish, habitat, and landscape features; and (3) simulation models that propagate disturbances into and through streams and predict effects on fish and habitat across a channel network. The modeling tools vary in many aspects, including input data (probability samples vs. census, reach vs. watershed, and field vs. remote sensing), analytical sophistication, and empirical foundation, and so can accommodate a range of situations. In areas with a history of salmon-related research and monitoring in freshwater, models in the three classes may be developed simultaneously. In areas with less available information, expert-opinion models may be developed first to organize existing knowledge and to generate hypotheses that can guide data collection for statistical and simulation models.

Introduction

Data and modeling tools that describe multiple spatial and temporal scales are increasingly useful to inform decisions related to salmon sustainability. Most studies addressing relationships between salmonids, their freshwater habitats, and factors that affect these have focused on relatively small areas (10^1–10^2 m^2) and short time periods (<2 years). The limits of knowledge gained at finer spatiotemporal scales have become obvious as society copes with variable and declining salmon populations across entire regions. Other pervasive problems, such as decreasing water quality and quantity (e.g., Carpenter et al. 1998; Postel 2000) and loss of aquatic biodiversity and integrity (e.g., Hughes and Noss 1992; Stein et al. 2000), have also elicited calls to broaden the extent of freshwater assessment, management, and research (e.g., Fausch et al. 2002; Rabeni and Sowa 2002; Hughes et al 2006). These complexities require integrated landscape research over extended periods. Considering larger extents often does not alleviate the need for fine-grained (high-resolution) information, which is facilitated by geographic information systems (GIS), availability of spatially explicit field and remotely sensed data, and analytical modeling tools (Hughes et al. 2006).

Modeling can be especially useful to the study and management of salmon across spatiotemporal scales, up to and including landscapes or riverscapes (>10^2 km^2 and 10^2–10^3 years). Broad-scale analyses present difficulties in designing replicated, controlled ex-

periments and in obtaining field data on in-channel characteristics over large areas. The Salmon Research and Restoration Plan for the Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative (AYK-SSI) (2006) explicitly recognizes the contribution of modeling in sustaining salmon and salmon fisheries. The Plan highlights models for analyzing and synthesizing information and for identifying and predicting key variables and patterns.

Our goal in this paper is to summarize numerous examples of data collection methods and modeling tools that are contributing to understanding, restoring, and managing salmon and their habitats across western Oregon. A long and productive history of salmon-related data collection and modeling justifies our focus on western Oregon. Given similarities in certain social and ecological characteristics between western Oregon and the AYK region, some data and modeling examples presented may have immediate utility in accomplishing the goals of the AYK-SSI. Other examples may yield opportunities for adaptation and collaboration, while others may stimulate ideas and offer a point of departure. We provide a general overview, rather than specific details, of each example and identify resources beyond this paper to guide the reader interested in further information.

Biophysical and Management Context of Salmon in Western Oregon

Our focus area covers approximately 58,274 km^2 of western Oregon (Figure 1). It includes the Coast Range, Willamette Valley, and Cascades Level-III Ecoregions (Pater et al. 1998). Elevations extend from sea level along the coast of the Pacific Ocean to 4,390 m in the mountainous inland areas. The terrain is varied, consisting of two mountain ranges, rolling hills, floodplains with productive soils, coastal plains punctuated by headlands, and alluvial and coastal terraces. Rock types are predominately marine sandstones and shales or volcanics that in the Cascade Range are affected by alpine glaciation. The climate is temperate with wet winters and warm dry summers. Mean annual precipitation ranges from 56 cm to 544 cm (Thornton et al. 1997). Precipitation transitions from primarily rain to primarily snow along a west-east gradient. The majority of lowland areas are now managed for agriculture or urban uses but consisted of wetlands, salt marshes, prairies, or oak savannahs before European settlement. The majority of upland areas are managed for timber harvest or recreation. Forested areas are in highly productive pure conifer stands or mixed conifer and hardwood stands; the latter is true particularly along streams. Uplands are characterized by high densities of small, steep streams and lowlands by a few large rivers with historically complex channel patterns.

Streams and rivers support five species of Pacific salmonids: coho salmon *Oncorhynchus kisutch*, Chinook salmon *O. tshawytscha*, chum salmon *O. keta*, rainbow trout/steelhead *O. mykiss*, and coastal cutthroat trout *O. clarkii*. Coho and Chinook salmon are targeted in commercial and recreational fisheries, whereas steelhead and cutthroat trout are primarily taken by sport anglers. Steelhead are listed under the U.S. Endangered Species Act (1973) as a Species of Concern in the Oregon Coastal Evolutionarily Significant Unit (ESU) and as a Threatened Species in the Upper Willamette ESU. Coho salmon are listed as Threatened in the Lower Columbia ESU and in the Oregon Coastal ESU.

Data

Management agencies and research institutions have invested in a wealth of salmon-related biophysical data for western Oregon (Table 1). These data were collected using different designs and methods

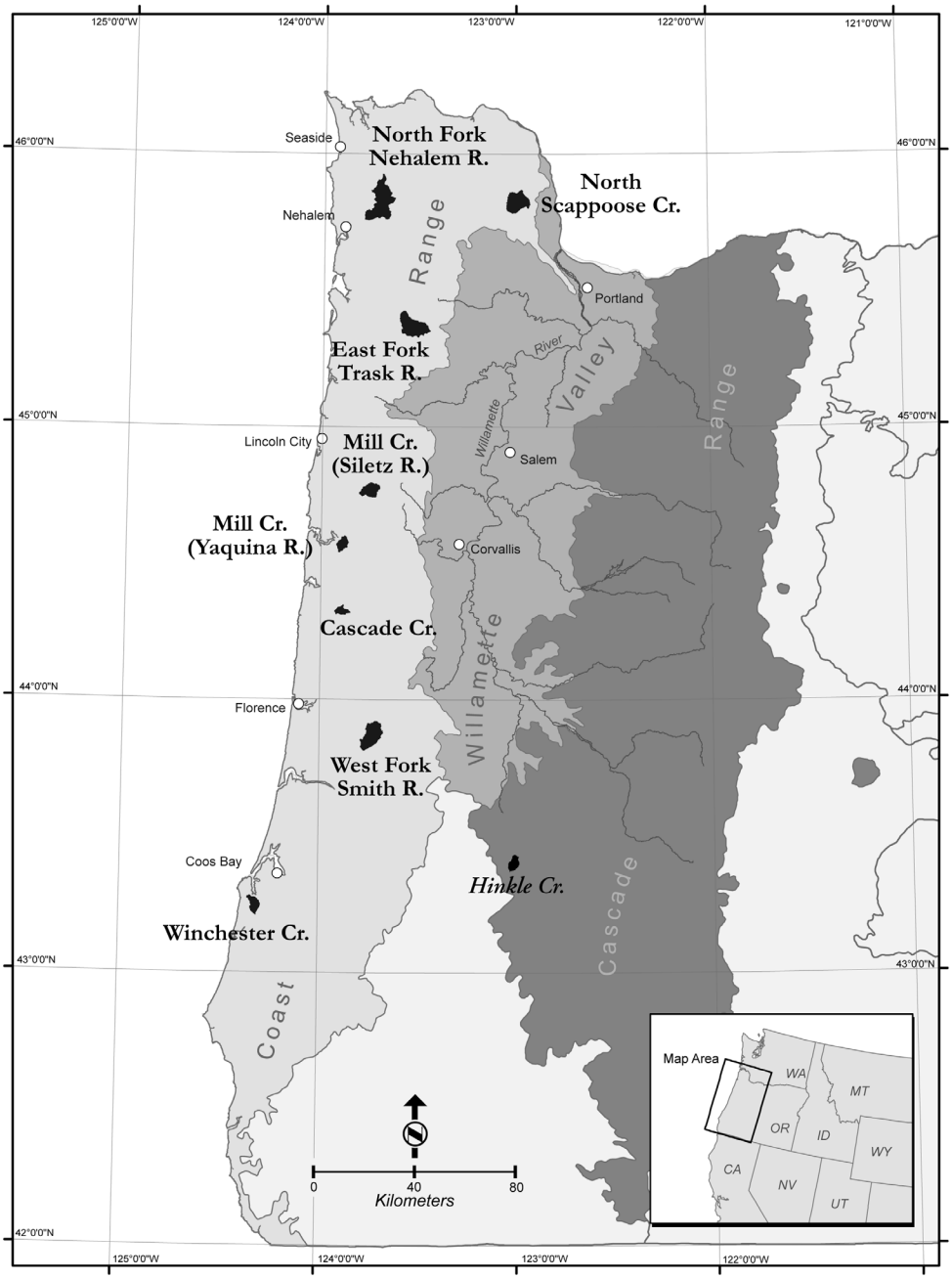

FIGURE 1. Western Oregon as referenced in this paper. Level III Ecoregions (Pater et al. 1998) and intensively monitored basins are highlighted in shades of gray and black, respectively.

TABLE 1. Western Oregon data sets addressed in this paper. Highlighted areas correspond to sub-headings in the text.

Data collection approach	Rationale	Source	Spatial/ temporal resolution	Spatial/temporal extent	Types
Probability-based sampling	Monitor and assess condition of wadeable streams	Environmental Monitoring and Assessment Program (EMAP)	Stream reach /annual	Western OR /2000–2004	Fish, aquatic macro-invertebrates, physical habitat, water quality
	Monitor effectiveness of the Northwest Forest Plan	Aquatic and Riparian Effectiveness Monitoring Program (AREMP)	Stream reaches nested in 6th-code Hydro-logic Units/ 5 yrs	Federal lands western OR, western WA, northern CA/2002–present	Aquatic macro-invertebrates, physical habitat
	Monitor effectiveness of the Oregon Plan for Salmon and Watersheds	Oregon Plan for Salmon and Watersheds	Stream reach/ annual	Western OR/1997–present	Spawning coho, juvenile salmonids, physical habitat
Intensive Basin Monitoring	Life-cycle monitoring	Oregon Plan for Salmon and Watersheds	8 basins ≤ 75 km^2/ annual	Western OR/1997–present	Abundance of migrating adult and juvenile salmonids, physical habitat
	Research juvenile salmonid population dynamics	U.S. EPA Western Ecology Division	Habitat unit–watershed/ seasonal–annual	WF Smith River, 69 km^2/ 2002–2005	Fish abundance and movement, physical habitat, water quality, discharge
	Research timber-harvest effects	USGS	Habitat unit–watershed/ seasonal–annual	Hinkle Creek 19 km^2/ 2002–2010	Abundance and movement of steelhead and cutthroat trout, physical habitat, water quality, discharge

TABLE 1. Continued.

Data collection approach	Rationale	Source	Spatial/ temporal resolution	Spatial/temporal extent	Types
Census	Characterize and monitor	Various agencies and remote sensing technologies	≤25 m/variable	Western OR/variable	Land use/cover
	Monitor and assess	Various agencies with airborne forward looking infrared (FLIR)	1 m/variable	10^1–10^2 m/variable	Water temperature
	Research relationships among watershed, stream habitat, and spatial patterns of cutthroat trout abundance	USGS	Habitat unit/ summer	Western OR/1 yr	Fish and habitat
	Characterize topography	USGS and various remote sensing technologies	≤10 m	Western OR	Digital elevation

to meet a variety of assessment, monitoring, and research objectives. Here we describe in-channel fish and habitat data, as well as landscape data collected using three approaches: (1) probability-based sampling of reaches or watersheds, (2) intensive monitoring of basins, and (3) complete census of an area or stream.

Probability-based sampling to monitor and assess aquatic ecosystems

The ability to assess and monitor trends in aquatic ecosystems over a large area (ESU, ecoregion, or administrative unit such as a National Forest) is of interest to society. Aquatic ecosystems can be characterized using one or more indicators such as a fish species, macroinvertebrate community, or physical habitat feature. A desirable goal might be to describe the abundance and spatial pattern of an indicator. However, conducting a census of these types of indicators across a broad landscape is often impractically expensive. This challenge of characterizing an entirety without a census has been managed in other fields of inquiry by adopting sample surveys (e.g., election polls and health statistics). Textbooks relevant for offering a thorough understanding of the theory and application of sample surveys include Särndal (1978), Cochran (1977), Lohr (1999), and Thompson (1992). The approach relies on selecting and characterizing a statistically representative sample. Unbiased inferences about the entirety are then drawn from measurements on the sample. These survey sampling techniques have been incorporated into a variety of natural resource arenas, including the National Agricultural Statistics Survey, the Forest Inventory and Analysis/Forest Health Monitoring program, and the National Wetlands Inventory. Here we describe three survey sampling programs for monitoring and assessing aquatic ecosystems in western Oregon are described.

Environmental Monitoring and Assessment Program (EMAP).—Responding to a variety of critiques that the nation was able to "assess neither the current status of ecological resources nor the overall progress toward legally mandated goals" at regional and national scales (U.S. House of Representatives 1984), the U.S. Environmental Protection Agency (EPA) initiated the EMAP (Messer et al. 1991). The inland aquatic component (lakes, streams and rivers, and wetlands) began with a survey of the condition of lakes in the northeastern USA. Most recently, a 5-year survey was completed of the condition of streams and rivers in the coterminous western USA, including western Oregon. The national programs, organized and run by EPA's Office of Research and Development (ORD) and Office of Water (OW), are complemented by Regional EMAPs (REMAP). A REMAP is conducted by an EPA regional office along with the states and tribes under their purview, focusing on the condition of inland aquatic ecosystems over smaller areas.

An EMAP or REMAP project consists of two components. The first is a survey design that addresses the need to obtain a statistically representative sample of the targeted resource. The survey design identifies where to sample (e.g., which lakes or which locations in a stream network). The second component is a response design (Stevens and Urquhart 2000; Stevens 2001) consisting of several parts, including which biological, chemical, and physical indicators to measure at each sample location, field protocols for measuring these indicators, and methods to convert the measurements into quantitative indicator scores. The biological condition of aquatic resources is assessed through multi-metric indices of biotic integrity (e.g., Hughes et al. 2004) or through the ratio of taxa at a site to taxa expected if the site were in "reference condition" (e.g., Van Sickle et al. 2005). In combination with the survey design, results are used to infer the frequency distribution of

resource conditions and the fraction of the resource that is in various quality classes (e.g., good, fair, poor). Changes over time can be evaluated with repeated sampling.

Statistical foundations supporting the current survey designs are in Stevens (1997), Stevens and Olsen (1999, 2003, 2004). Implementation of the design procedures is available at www.epa.gov/nheerl/arm, as written in a public domain statistical computing language (R Development Core Team 2006). Typical EMAP and REMAP field protocols are documented in Peck et al. (2006). Examples of assessment reports include Herger and Hayslip (2000), Hayslip and Herger (2001), and Stoddard et al. (2005). The survey design component of EMAP was used to select watersheds and stream sites in the following two assessment programs. The response designs are specific to each of those programs.

The Aquatic and Riparian Effectiveness Monitoring Program (AREMP).—As part of the Northwest Forest Plan (NWFP) for federal forestlands in the range of the northern spotted owl *Strix occidentalis caurina* (USDA and USDI 1994), effectiveness monitoring programs were developed for plan components. One of the NWFP components, the Aquatic Conservation Strategy (ACS), is designed to restore and maintain the ecological integrity of watersheds and their aquatic ecosystems on public lands. The AREMP is responsible for monitoring the ACS by evaluating the condition of sixth-code (12-digit) U.S. Geological Survey (USGS) hydrologic units using a combination of upslope, riparian, and in-channel physical and biological indicators (Reeves et al. 2004). Given that 2500–3000 of these hydrologic units comprise the NWFP area, conducting a census is impractical for most of the chosen in-channel indicators. Instead, a statistically representative sample of hydrologic units to be assessed on a five-year cycle was selected using a survey design.

For each year, indicator measurements on each selected hydrologic unit are combined through a knowledge-based logic model to produce a watershed condition score (Gallo et al. 2005; Reeves et al. 2006). The frequency distribution of these scores for sampled hydrologic units in each year is a snapshot of the condition of watersheds across the NWFP area. The expectation is that if the NWFP is working, the frequency distribution of scores will shift over time in a direction indicating watershed conditions are improving. The field phase of monitoring began in 2002; however, landscape-level indicators were estimated from historical remote sensing data (e.g., aerial photography) beginning with implementation of the NWFP in 1994. A 10-year summary of the effectiveness of the ACS is published in Gallo et al. (2005).

Oregon Plan for Salmon and Watersheds.—Dramatic declines in populations of coastal coho salmon led the State of Oregon in 1997 to implement a plan for restoring native populations and the aquatic systems that support them. This plan, called the "Oregon Plan for Salmon and Watersheds," featured an innovative approach to estimate and monitor habitat conditions and total numbers of coho salmon adults and juveniles. These objectives could not be met with census techniques. From the 1950s until implementation of this new approach, fish and habitat monitoring relied on handpicked "index" sites that were not necessarily representative of the larger landscape for which monitoring information was needed. Because the surveys were biased, it was impossible to derive a reliable, statistically rigorous estimate of Oregon coastal coho salmon and their habitats. The new survey design for the Oregon Plan is a spatially balanced, random sample that produces unbiased estimates for which precision can be calculated (Stevens 2002). The surveys feature a rotating panel design, based on the 3-year life cycle of coho

salmon, wherein one quarter of the sites are sampled each year, one quarter every 3 years, one quarter every 9 years, and one quarter only once. The rotating panel design is intended to balance the need to estimate status (precision improves with more sites sampled) and the need to detect trends (power improves with more revisits to each site). Although sampling universes of the separate habitat, spawner, juvenile, and water quality surveys that comprise this program vary, the forced coincidence of survey sites where sampling universes overlap enables analyses of habitat and fish relationships across scales (from reach or site to ESU or population).

The information gathered by these surveys, as well as the existence of a monitoring program, was considered by NOAA Fisheries during the listing process for Oregon coastal coho salmon under the Endangered Species Act. The Oregon Department of Fish and Wildlife (ODFW) routinely publishes statistical summaries of the results of these surveys; a published synthesis of results is also available (OWEB 2005a, 2005b). More information on the Oregon Coastal Coho Salmon Assessment and how the Oregon Plan survey information was used in the assessment can be obtained at: http://nrimp.dfw.state.or.us/OregonPlan/.

Intensive basin monitoring

The goal for intensively monitored basins (IMB) is to focus research and monitoring efforts in a particular location. These can be locations for descriptive or experimental research, such as in paired watershed studies. Data may be collected over long periods on many indicators, including water quality and quantity, fish population abundances at different life cycle stages, food-web interactions, and movement of individual fish. Intensively monitored basins are typically selected based on practical rather than statistical consideration. Thus, the scope of inference for results is not always clear. Landscape classification can help place intensively monitored basins into a broader context and thus help approximate how likely are fine-scale research or monitoring results to represent a larger area.

Life Cycle Monitoring.—In 1998, as part of the Oregon Plan, the ODFW began intensive monitoring in eight basins across western Oregon (Figure 1). The specific objectives of this monitoring are to: (1) estimate abundances of returning adult salmonids and downstream migrating juvenile salmonids, (2) estimate marine and freshwater survival rates for naturally produced coho salmon, and (3) evaluate relationships between freshwater habitat conditions and salmonid production. Although the Life Cycle Monitoring basins were "hand picked" based on the feasibility of trapping upstream migrating adults and downstream migrating juveniles, the basins do represent an array of Oregon coastal landscapes. Work is progressing to identify those that are under- or un-represented by the current Life Cycle Monitoring network and to add new basins. This will allow extrapolation of the findings from the Life Cycle Monitoring basins to most Oregon coastal landscapes. More information about the Life Cycle Monitoring Program can be obtained at: http://nrimp.dfw.state.or.us/crl/default.aspx?pn = SLCMP.

Research on juvenile salmonid population dynamics.—In 2002, the U.S. EPA Western Ecology Division initiated a 4-year study in the West Fork Smith River (W.F. Smith River) to investigate juvenile salmonid population dynamics, specifically focusing on spatial patterns of survival and growth in relation to movement within the basin. The W.F. Smith River is a tributary to the lower Umpqua River draining a 69-km^2 forested basin in the south-central Oregon Coast Range, and is one of the eight Life Cycle Monitoring basins (Figure 1). The study uses a hierarchi-

cally organized, spatially nested sampling design. At various spatial scales throughout the basin, environmental characteristics are monitored, including water chemistry and discharge (stream level), temperature and channel morphology (reach level) and channel unit structure (channel unit level). Biological data are collected seasonally and annually at the individual fish (growth, movement) and population (patterns of abundance, survival) levels. Movement, growth and survival parameters are estimated using a mark–recapture approach, and these biological responses are correlated to environmental characteristics at the appropriate spatial and temporal scales.

Key findings from the study include the understanding that habitat configuration and availability can change in response to natural and anthropogenic disturbance. For example, while overwintering habitat may be limiting at most times, summer habitat can be limiting during extreme low summer flows, especially in streams underlain by sandstones. Ebersole et al. (2006) found that summer conditions, including high water temperatures and reduced scope for growth, were associated with reduced overwinter survival of juvenile coho salmon in the W.F. Smith River following a relatively warm, dry summer. Summer habitat could become locally limiting also following restoration of overwintering habitat or improved access to existing winter habitats. In the W.F. Smith River, the potential importance of intermittent tributaries to overwintering juvenile coho salmon was assessed with mark–recapture experiments. Ebersole et al. (2006) found that overwinter growth and survival were enhanced in an intermittent tributary relative to nearby mainstem habitats, and that individual fish moving into the intermittent stream experienced a distinct survival and growth advantage. Intermittent streams in the W.F. Smith River were also important to adult coho salmon, as a disproportionate number of spawners used intermittent streams over several years of study (Wigington et al. 2006).

These findings highlight the importance of considering the dynamic nature of stream habitats for salmon, and the ability of salmon to "track" suitable habitats. Field-derived estimates of movement and survival will be used to parameterize scenarios of dynamic habitat configurations and accessibility that can be compared via simulation models. These scenario-based analyses will allow exploration of the potential implications of habitat changes due to restoration, land use, or stochastic environmental events.

Research on timber-harvest effects.— The response of headwater fish assemblages to contemporary timber harvest practices on private industrial land has not been described at the stream-network scale. Hypothetically, changes in habitat, water quality, or food supply associated with timber harvest affect fish in a dynamic way, but the following questions remain unanswered: (1) How do changes in physical and biological characteristics of tributaries without fish seasonally influence habitat quality in other portions of the stream network? (2) How do seasonal hydrologic changes in headwater streams affect fish behavior and distribution? and (3) Do life history expression, behavior, or diversity of fish fauna vary in response to changed habitat quality, or do organisms redistribute to areas where habitat quality remains unaltered? Sampling, to address these questions, began in Hinkle Creek in 2001 (Figure 1). The Hinkle Creek Study, along with the more recent Alsea Watershed Study and Trask River Watershed Study, comprise the Watershed Research Cooperative (http://watershedsresearch.org/) for examining effects of contemporary forest harvest practices.

Fish abundance has been estimated annually since 2002 in all pools and cascades of Hinkle Creek, with electrofishing as the primary means of fish collection. During each

sampling period, all coastal cutthroat trout and steelhead ≥100 mm (fork length) were implanted with a passive integrated transponder (PIT) tag prior to release. Stationary receiver antennae were placed to continuously monitor fish movement at the stream segment scale. Additionally, tagged fish were located with portable sensors during subsequent field visits, typically during winter, spring, and early summer. This information is being used to detect fine-scale shifts in fish distribution and movement patterns (e.g., timing, direction, and distance) that can be compared with reach-scale stream discharge, substrate composition, water temperature, food availability, and geomorphic structure. Fish sampling at a variety of temporal and spatial scales is providing the opportunity to analyze natural variation at multiple scales. Ultimately, terrestrial and aquatic habitat conditions for coastal cutthroat trout demographics will be available for five years before timber harvest (2001–2005) and five years following harvest (2006–2010).

Census

The challenge with census data lies in describing an entirety at a grain size that resolves the desired level of detail without sampling and without overwhelming the ability to collect, process, and store the information. Field and remote sensing techniques have been applied to collect census data on fish, their habitat, and the surrounding landscape. Census data are available for western Oregon describing aquatic and terrestrial characteristics that can change over time and are relatively static.

Land use and land cover.—Land use and land cover are temporally variable characteristics for which census data are commonly collected. Attributes in these layers are monitored directly as indicators of anthropogenic effects on salmon ecosystems (e.g., Gallo et al. 2005) and used as explanatory or predictive variables in salmon-related models (e.g., Steel et al. 2004; Burnett et al. 2006). In addition to describing current conditions, land use and land cover data offer a baseline for projecting landscape attributes into the future under different management scenarios, via models such as those for the Oregon Coast Range (Bettinger et al. 2005; Johnson et al. 2007) or the Willamette River basin (Hulse et al. 2004).

Land use and land cover are typically derived from remotely sensed imagery (e.g., 1.1 km advanced very high resolution radiometer [AVHRR] or 30 m resolution Landsat Thematic Mapper [TM]) in visible or other wavelengths. High-resolution (<1 m) data can now be obtained from airborne laser mapping such as red waveform light detection and ranging (lidar) (Lefsky et al. 2001, 2002). Despite key advantages offered by the high resolution of lidar, the data are relatively expensive to obtain, process, and store for large areas.

The National Land Cover Database (NLCD 1992, 2001) (e.g., Homer et al. 2004; Wickham et al. 2004) provides "current" land cover for western Oregon and is planned for the AYK region. The NLCD is appropriate for generalized characterizations in that it aggregates land cover from TM imagery into about 15 broad classes and classifies forest cover based on only over-story features. An alternative to the NLCD is available for much of western Oregon (e.g., Ohmann and Gregory 2002; Ohmann et al. 2007). It represents forest over- and under-story characteristics as gradients instead of discrete classes and was developed by linking remotely sensed imagery to field-based ground plots (e.g., Forest Inventory and Analysis (FIA); Ohmann and Gregory 2002).

Water temperature.—Stream temperature, a temporally dynamic freshwater characteristic, is one of the most critical environmental

determinants of habitat quality for salmon and has been the focus of extensive research and water quality monitoring efforts in the Pacific Northwest (USA) (e.g., Poole and Berman 2001; Poole et al. 2004). Recent technological advances led to widespread deployment in streams of automated monitoring stations, which record water temperature at a fine temporal resolution (~15-min sampling intervals) over multiple months. These data helped to increase awareness of temporal variation in stream temperature and raised new questions about the biological consequences of such thermal heterogeneity. However, this work also highlighted that "temporally continuous" temperature data from in-stream recorders are still spatially limited. The use of airborne forward-looking infrared (FLIR) sensors arose out of the need to map variation in stream temperature at a fine spatial resolution (<1 m) over $10^1 – 10^2$ km.

Thermal infrared remote sensing of stream water temperature, initially explored in Washington and Oregon during the early 1990s, has advanced rapidly. Airborne applications of FLIR from a helicopter were first used to identify groundwater inputs and thermal refugia for salmon (Belknap and Naiman 1998; Torgersen et al. 1999). After the approach was validated for accuracy (Torgersen et al. 2001), applications in water quality management and fisheries increased dramatically. Thermal infrared imagery has been used extensively by management agencies to characterize longitudinal thermal profiles for streams and rivers and to examine sources of cold- and warm- water inputs (ORDEQ 2006). Quantitative models of stream temperature and stream-aquifer interactions use thermal infrared imagery to identify thermal anomalies and to increase the spatial accuracy of stream temperature predictions (Boyd 1996; Loheide and Gorelick 2006; ORDEQ 2006).

Researchers have also investigated the utility of high-altitude air- and space-borne thermal sensors for mapping surface water temperature in rivers of the Pacific Northwest (Cherkauer et al. 2005; Handcock et al. 2006). These approaches hold promise for mapping water temperature synoptically throughout large, remote watersheds. However, the coarse spatial resolution (>5 m) of high-altitude and satellite-based imagery confines its use to larger rivers.

Fish and habitat.—An integrated research program was initiated by the USGS to explore relationships among upslope watershed characteristics, physical stream habitat, and spatial patterns of coastal cutthroat trout abundance during summer low-flow conditions (Gresswell et al. 2006). Variation was evaluated at two spatial scales: (1) across western Oregon (spatial extent) using watersheds as sample units (resolution), and (2) within watersheds using as sample units, the individual elements in the stream habitat hierarchy (channel units, geomorphic reaches, and stream segments). Watersheds were selected at the coarser spatial scale with probability-based sampling, and data were collected on fish and habitat characteristics at the finer scale using a census approach.

Data from the fine-scale censuses were summarized for each watershed to examine variation in cutthroat trout abundance across western Oregon. Because data were collected in a spatially contiguous manner in each watershed, it was possible to evaluate spatial structuring in cutthroat trout abundance (see discussion in Modeling Tools—Spatial Models). It appears that cutthroat trout move frequently among accessible portions of small streams (Gresswell and Hendricks 2007). Individuals congregate in areas of suitable habitat and may form local populations with unique genetic attributes (Wofford et al. 2005). Those that move into larger downstream portions of the network may contribute to the genetic structure of anadromous or local potamodromous assemblages. Viewing habitats as matri-

ces of physical sites that are linked by movement is providing new insights into the study of the fitness and persistence of cutthroat trout populations.

Digital elevation data and its processing.—Census data are available for western Oregon on many characteristics that may be considered temporally invariant, particularly over short periods in salmon-related studies. Depending on the temporal extent, these characteristics can include topography, rock type, and climate. Although relatively static, such characteristics may affect spatial and temporal variability in salmon distribution and their habitats. Spatial layers for some of these data types have been, or could be produced, for the AYK region. Predictions of long-term mean annual surface temperature and precipitation are available for Alaska from two sources: the Spatial Climate Analysis Service (SCAS) and the Alaska Geospatial Data Clearinghouse (AGDC) (Simpson et al. 2005). Digital elevation data have been some of the most important for western Oregon and so are highlighted here. These data have been essential in delineating and describing streams and watersheds (Benda et al. 2007); developing and implementing landscape models, such as those of salmon habitat potential (Burnett et al. 2007) and of processes affecting sediment and wood delivery to streams (e.g., Miller and Burnett 2007); and for landscape classification and inference.

The western Oregon digital elevation data are available as gridded 10-m digital elevation models (DEMs). These were created (Underwood and Crystal 2002) by interpolating elevations at DEM grid points from the digital line graph (DLG) contours on standard 7.5-min topographic quadrangles (USGS 1998) and by drainage enforcing to hydrography on the DLG data. The relatively high resolution is essential for representing streams and hillslopes in the complex and heavily dissected, mountainous terrain of western Oregon. However, inaccuracies in the 10-m DEMs, arising from the base DLG data, can affect landscape characterization and modeling results (e.g., Clarke and Burnett 2003).

Very high-resolution DEMs can be obtained from lidar data. Such DEMs can be derived by classifying the "last return" or "bare earth" from multiple-return red waveform lidar data. Hydrography can be mapped directly from this lidar. The red laser pulses are absorbed by water, rather than reflected and returned to the sensor; thus water is identified by "no data." Green waveform lidar, which penetrates water and reflects back to the sensor, is commonly used for bathymetric mapping in coastal areas (e.g., Wozencraft and Millar 2005). The Experimental Advanced Airbone Research lidar (EAARL) is a full waveform lidar that can simultaneously map surface topography, in-channel morphology, and vegetation (McKean et al. 2006) and holds great promise for characterizing river networks in both western Oregon and the AYK region.

Digital data on hydrography (1:63,000-scale National Hydrography Dataset [NHD]) and elevation (e.g., 1:63,000-scale National Elevation Data [NED] and 90-m DEMs below 60 degrees, North Latitude) are available for the AYK region; however, the spatial resolution and extent of these data are questionable for much salmon-related landscape modeling. Higher resolution topographic and hydrographic data can be obtained by processing remotely sensed imagery (e.g., Japanese Earth Resources Satellite [JERS-1] Interferometric Synthetic Aperture Radar [SAR] L-band, and Advanced Land Observing Satellite [ALOS] PRISM and SAR data).

The availability of DEMs, together with powerful and inexpensive computers, has prompted development of tools that facilitate terrain analysis or geomorphometry (Pike 2002). Digital elevation models are processed by specialized computer software such as the Terrain Analysis System (TAS) (Lind-

say 2005) or NetMap (Benda et al. 2007) to automate and visualize spatial analyses of hill slopes and stream networks. Numerous outputs are produced at the spatial grain of the DEM, including surface-flow direction, gradient, and aspect. Linkages among DEM pixels allow derivation of outputs such as synthetic stream networks, catchment boundaries, drainage area, topographic convergence, tributary junction angles, and valley widths. Outputs from these types of terrain analysis are highly relevant to studies of geomorphology, hydrology, and salmonid ecology.

Modeling Tools

Although a large amount of high-quality data is available for western Oregon, information about the components of salmon ecosystems and their complex interactions will never be complete. Thus, models have been developed to help fill data gaps as well as to simplify, abstract, and project conditions in salmon ecosystems (Table 2). Accuracy and precision of modeled outputs are important ways to measure the success of these models. Another measure is utility—does the model help explain, predict, or organize understanding about how salmon interact with their biotic and abiotic environments? Here we focus on three classes of models: expert opinion models, statistical and spatial models, and simulation models (Figure 2).

Expert-opinion models

An expert-opinion model is a transparent and repeatable means to organize existing knowledge. Such models can help when assessing current conditions, projecting likely outcomes, and making decisions when empirical data or relationships are incomplete or uncertain. In addition, an expert-opinion model can be a framework to expose and document knowledge gaps and assumptions, and thus catalyze and generate hypotheses and guide future data collection. Therefore, models of this class can be extremely informative in early phases of study.

Expert-opinion models typically consist of a user interface, a database, and a rule base. The rule base is expressed in the architecture, relationships, and distributions of variables in the model. The rule base may be developed with information from a single expert or small group of experts or may be elicited from a larger group of experts through a systematic process (e.g., Schmoldt and Peterson 2000). Expert-opinion models have been developed for a variety fields, including medicine, business, and natural resources management (e.g., Kitchenham et al. 2003; Marcot 2006a; Razzouk et al. 2006). We present three expert-opinion models that are informing natural resources management in western Oregon and that may have relevance to the AYK region.

Bayesian belief networks.—The first example is a nonspatially explicit set of Bayesian belief networks (BBNs) developed by Marcot (2006b) to help implement the Northwest Forest Plan (USDA and USDI 1994). These BBNs predict habitat quality and potential survey sites for several relatively rare species associated with late-successional or old-growth forests. At its most basic, a BBN rule base is an influence diagram that represents probabilistic relationships (arcs) between variables (nodes). Input variables can be represented in various ways; one common form being discrete states with the prior probability of each state based on empirical evidence, expert judgment, or a combination. Expert opinion played a large role in developing influence diagrams and prior probabilities for the western Oregon BBNs. These models were built in the software package Netica (Norsys, Inc.; http://www.norsys.com) but several other packages are available (e.g., BNet.BUILDER, OpenBayes, and SamIam). More information on BBNs for

TABLE 2. Western Oregon models addressed in this paper.

Model class	Type	Objective for use in western Oregon
Expert Opinion	Bayesian belief network	Predict habitat quality and potential survey sites for relatively rare late-successional or old-growth forest associated species
	Knowledge-based logic model	Monitor effectiveness of the Northwest Forest Plan
	Habitat potential model	Describe the intrinsic potential of streams to provide high-quality habitat for salmonids
Statistical and spatial	Statistical models of fish and habitat	Explain or predict variation in biotic, physical-habitat, or water-quality characteristics from landscape characteristics
	Spatial interpolation of probability-based sample data	Predict the spatial pattern of coho salmon abundance on the Oregon coast
	Spatial analysis of census data	Quantify and explain the degree of spatial structure within and among headwater basins in cutthroat trout distribution
Simulation	Coho salmon life cycle	Evaluate potential outcomes of management scenarios and climate change on coho salmon in freshwater and marine environments.
	Disturbance and stream habitat	Evaluate potential outcomes for fish habitat of management scenarios and climate change that affect sediment and wood delivery from fires, storms, and debris flows.

western Oregon and on other BBN applications is available at http://www.spiritone.com/~brucem/bbns.htm.

Knowledge-based logic models.—The second example is a knowledge-based logic model (Gallo et al. 2005) that uses the survey data collected by the Aquatic and Riparian Effectiveness Monitoring Program (AREMP). The logic model was designed to assess and monitor watershed conditions in the area managed under the Northwest Forest Plan (USDA and USDI 1994). This model was constructed with Ecosystem Management Decision Support (EMDS) software (Reynolds et al. 2003) and is linked to a GIS. It was designed to evaluate the proposition that conditions in a watershed are "suitable to support strong populations of fish and other aquatic and riparian-dependent organisms" (Gallo et al. 2005). Truth of this general proposition is evaluated for a watershed by aggregating evaluation scores for model attributes (e.g., road density, channel gradient, percent pool area) according to the hierarchical architecture of the logic model. Each evaluation score is derived by comparing data for the attribute against a curve that expresses the contribution to overall watershed condition. As with any knowledge-based logic model, the shape of the curves may vary by attribute. However, the curves share a common scale (–1.0 to + 1.0) that expresses the strength of evidence for a proposition (Zadeh et al. 1996). This scale describes uncertainty about the definition of events rather than uncertainty about

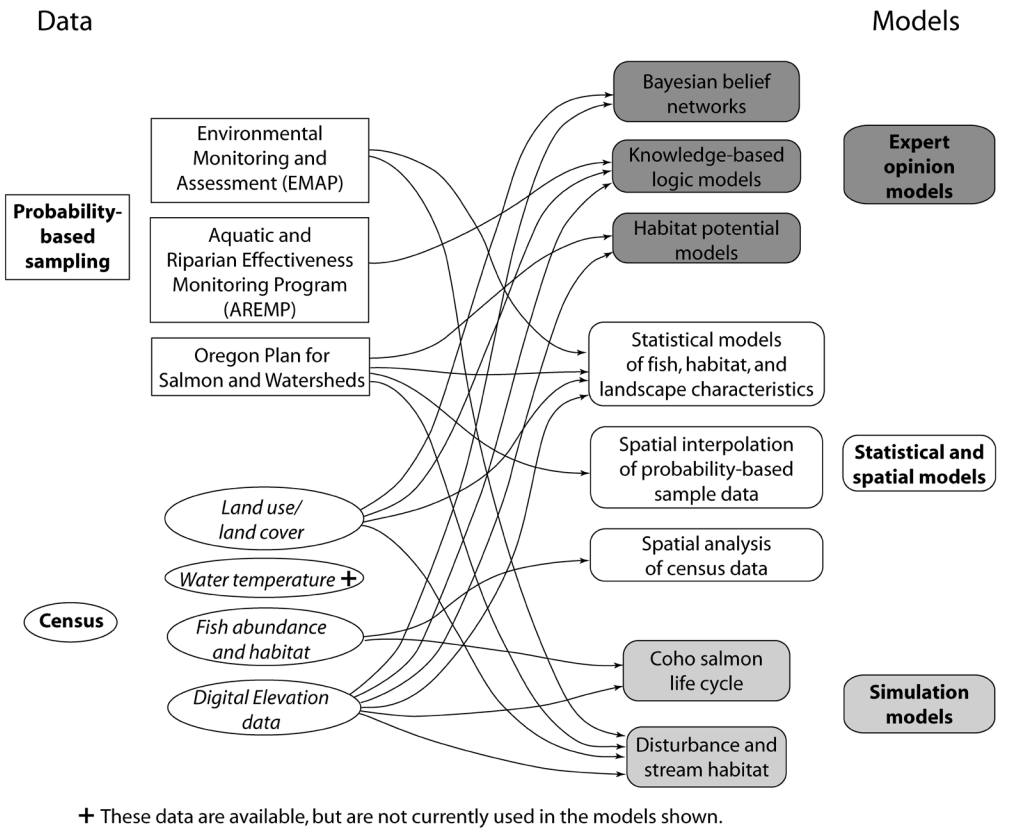

FIGURE 2. Relationships between collected data and developed models for western Oregon.

the likelihood of events as with BBNs. In the AREMP knowledge-based logic models, the overall model structure and the attribute curves were based on expert opinion.

Habitat potential models.—The third example focuses on models describing the potential of streams to provide high-quality habitat for salmonids (Steel and Sheer 2002; Burnett et al. 2007). Steel and Sheer (2002) modeled spawning habitat potential for chinook salmon and for steelhead from channel gradient. Burnett et al. (2007) modeled habitat potential for juvenile coho salmon and juvenile steelhead from mean annual stream flow, valley constraint, and channel gradient. In both studies, stream attributes were calculated from climate data and terrain analysis of DEMs, during automated production of a digital stream network (Miller 2003), and habitat potential was interpreted from these stream attributes based on empirical evidence in published studies. Outputs were data layers and GIS maps depicting species-specific habitat potential for modeled stream networks across 36,000 km in the Willamette and Lower Columbia River basins (Steel and Sheer 2002) and 96,000 km in the Oregon Coast Range (Burnett et al. 2007). Once habitat potential was estimated, these studies answered a variety of questions relevant to conservation, including required spawner densities to meet population viability thresholds (Steel and Sheer 2002), what land covers are adjacent to reaches with high habitat potential (Burnett et al. 2007) and how much high-quality habitat has been lost above anthropogenic barriers (Sheer and Steel 2006).

Outputs of the habitat potential models for the Oregon Coast Range have also been used to estimate fish production potential assuming relatively little human disturbance (Lawson et al. 2004), and to evaluate fish passage and restoration projects (Dent et al. 2005). The model for the Oregon Coast Range was adapted and applied to other areas and to other salmonid species with established relationships to topographic characteristics (e.g., Agrawal et al. 2005; Lindley et al. 2006).

Statistical models

A large amount of high-quality data has allowed western Oregon to become a laboratory for exploring statistical relationships of relevance to understand and manage salmon.

Statistical models of fish, habitat, and landscape characteristics.—Numerous statistical models have been developed recently for western Oregon to examine relationships among salmonids, their habitats, and landscape characteristics. These models are designed so their users can take advantage of census data on landscape characteristics to predict in-channel characteristics that are otherwise difficult or expensive to collect. Analytical techniques applied in these models include classification and regression trees (Wing and Skaugset 2002), discriminant analysis (Burnett 2001), and linear mixed models (Steel et al. 2004). Model objectives were to explain or predict variation in in-channel characteristics such as the amount of large wood in streams (Wing and Skaugset 2002; May and Gresswell 2003), an index of fish biotic integrity (Hughes et al. 2004), densities of juvenile salmonids (Hicks and Hall 2003), deposition of fine sediment (Sable and Wohl 2006), and nitrogen export (Compton et al. 2003). In-channel responses were found to be related to static characteristics (e.g., geology or stream size) as well as those reflecting natural and anthropogenic disturbance (e.g., percent area in large trees or percent area in red alder *Alnus rubra*). Some of the studies explored mulit-scale relationships by summarizing landscape characteristics across different spatial extents (e.g., buffer and catchment) (e.g., Compton et al. 2003; Van Sickle et al. 2004; Flitcroft 2007). Here the focus is on two of the several studies from western Oregon.

In the first study, Steel et al. (2004) used mixed linear models to identify associations between landscape condition and winter steelhead spawner abundance in multiple watersheds of the Willamette River basin. Their approach identified relationships between landscape conditions and relative redd densities that were consistent over time despite year-to-year fluctuations in fish population size. This general approach has been successful for Chinook and coho salmon in other basins (Pess et al. 2002; Feist et al. 2003). These models explained up to 72% of the spatial variation in year-to-year distribution of spawners. Landscape predictors of redd density included alluvial deposits, forest age, and land use. Predictions of potential redd density from these landscape models were examined along with inventories of known and potential barriers to fish passage. Using this information, barrier removal projects and mitigation for in-stream barriers, common approaches for restoring salmon habitat and populations, were prioritized. The prioritization scheme evaluated the potential quantity and suitability of spawning habitat that would be made accessible by restoration.

The second study explored relationships between landscape characteristics and stream habitat features in the forested, montane Elk River basin (Burnett et al. 2006). The modeled habitat features (mean maximum depth of pools, mean volume of pools, and mean density of large wood in pools) were those found to distinguish between sampled stream segments that were highly used by juvenile Chinook salmon and those that were not (Burnett 2001). Landscape characteristics were sum-

marized at five spatial extents, which varied in the area encompassed upstream and upslope of sampled stream segments. In regressions with landscape characteristics, catchment area explained more variation in the mean maximum depth and volume of pools than any other landscape characteristic, including all those reflecting land management. In contrast, the mean density of large wood in pools was positively related to percent area in older forests and negatively related to percent area in sedimentary rock types. The regression model containing these two variables had the greatest explanatory power at an intermediate spatial extent. Finer spatial extents may have omitted important source areas and processes for wood delivery, but coarser spatial extents likely incorporated source areas and processes less tightly coupled to large wood dynamics. Thus, the multi-scale design of this study suggested the scale at which landscape features are likely to influence stream attributes as well as testable hypotheses for examining influence mechanisms.

Spatial models

These models address the challenges and opportunities presented by spatial autocorrelation among observations. Spatial autocorrelation is a measure of the tendency for points that are close to one another to share more characteristics than points that are farther apart. A high degree of spatial autocorrelation reflects a lack of statistical independence in a dataset, violating the assumptions of standard parametric statistical methods, such as analysis of variance (ANOVA) and least squares regression (Legendre and Fortin 1989). Techniques are available to account for this spatial autocorrelation in standard parametric tests (e.g., mixed models). The fact that most ecological data, and particularly census data, are spatially autocorrelated is viewed simply as a nuisance unless one recognizes that such spatial structure contains information essential to describing and understanding underlying ecological processes (Legendre 1993).

Geostatistical methods provide the means to explicitly identify the presence of spatial structure and to describe these patterns in a quantitative manner (Rossi et al. 1992). Geospatial techniques were developed for, and are typically applied in, settings such as lakes and landscapes that are described by points in two or three dimensions. In these settings, the distance between sample locations can be measured as a straight line between two points, and the effective distance is the same in both directions. However, the effective distance between two points in a stream network may be as the fish swims, not as the crow flies, and may be greater in one direction than the other, depending upon the process of interest. Such issues pertaining to aquatic habitat and organisms within the context of a network topology are increasingly being raised in aquatic monitoring and resource modeling efforts.

Understanding the factors that influence the spatial scale of variation in fish distribution in stream networks is necessary for developing aquatic sampling designs and is widely recognized as a new frontier in studies of river systems (Fagan 2002; Campbell et al. 2007; Flitcroft 2007). Investigation of stream network processes and biological responses may often require census data and models that explicitly consider the configuration of drainage patterns and the juxtaposition of tributary junctions, which play key roles in structuring aquatic habitat and biota in riverine systems (Benda et al. 2004; Kiffney et al. 2006; Rice et al. 2008).

Spatial interpolation of probability-based sample data.—Random process models are important for analyzing environmental data that varies through space and time, especially to predict the value of some environmental variable at an arbitrary point. Kyriakidis and Journel (1999) provide a recent overview and

bibliography. In the last ten years, use of hierarchical models to analyze dependencies among variables has increased. Hierarchical models have been widely applied to environmental data, especially data with space/time components. The basic idea of hierarchical models is that the observed data are modeled as a function depending on unknown parameters and unobserved random errors. The random errors in turn are modeled as dependant on unknown parameters. In the Bayesian version, the unknown parameters are given a prior distribution, and the posterior distribution is calculated from the observed data. These techniques have been used to develop statistical models that accommodate missing data, temporal and spatial dependencies, latent variables, multiple response variables, and nonlinear functional forms. Several years ago, such models were not feasible, because the parameter estimation was too computationally intensive. Several recent theoretical developments have substantially reduced the computational burden, most notably the so-called Gibbs sampler (Geman and Geman 1984; Gelfand and Smith 1990), Markov Chain Monte Carlo (MCMC) techniques (Gilks et al. 1996), and the Metropolis-Hastings algorithm (Metropolis et al. 1953; Hastings 1970). For more details on these algorithms and MCMC, see Robert and Casella (2004), Gelman et al. (1995), and Gelfand (2000). Smith et al. (2005) have applied these techniques to predict the spatial pattern of coho salmon abundance on the Oregon coast.

Spatial analysis of census data on coastal cutthroat trout.—Data from a census of aquatic habitat and coastal cutthroat trout in headwater basins of western Oregon have made it possible to evaluate spatial patterns in fish distribution across multiple scales (Gresswell et al. 2006; Torgersen et al. 2004) as opposed to a single scale predetermined by the sampling design (Schneider 1994; Torgersen et al. 2006). Results of this census for approximately 200 km of stream were mapped in a spatially referenced database (Torgersen et al. 2004). Spatial patterns in the relative abundance of coastal cutthroat trout (Bateman et al. 2005) were examined relative to fine- and coarse-scale habitat features, ranging from substrate characteristics within channel units to landscape patterns in topography and land use (Gresswell et al. 2006). Because the census data could be summarized by different geomorphically defined units (e.g., channel unit, reach, or segment) or by different fixed-length units (e.g., 10 m, 100 m, or 1000 m), investigations into the spatial structure of fish distribution could be addressed in an exploratory manner. Such analyses of census data have revealed unexpected results in which the distribution of an organism was associated with a predictor variable at one spatial scale but not at another (Schneider and Piatt 1986; Torgersen and Close 2004). Moreover, flexibility in the size of the analysis window alleviates concerns associated with calculations of population density, which is highly scale dependent and can be a misleading indicator of the habitat preferences of an organism (Van Horne 1983; Grant et al. 1998).

The technical hurdles of applying geostatistical tools to the study of spatial patterns of fish distribution were examined by Ganio et al. (2005), using the census data on coastal cutthroat trout in western Oregon. Their work revealed that cutthroat trout distribution exhibited a high degree of spatial structure, that the spatial structure varied among headwater basins, and that this variation could be explained by geology and watershed characteristics, such as elevation, slope, and drainage density.

Simulation models

Simulation models have been developed for western Oregon to assess changes in salmon abundance and habitat characteristics over

time. Simulation models attempt to integrate the many component processes that drive complex dynamic systems. The models may explicitly represent the mechanics of, and relationships between, component processes or derive more from empirical understanding about these. Outputs from one component are typically inputs for the next, and feedback can be incorporated between components. Running a simulation model with different input values can identify components of a system that may be most sensitive to change. Simulation models provide a means to evaluate potential outcomes of management scenarios or climate change on salmonids and their habitats. Such models have been developed for the Willamette Valley in western Oregon (e.g., Bolte et al. 2007; Guzy et al. 2008), and we focus on two examples from the Oregon Coast Range.

Coho salmon life cycle.—A stochastic habitat-based life cycle simulation model for coho salmon on the Oregon Coast was developed from relationships between freshwater habitat characteristics, the capacity of those habitats to support coho salmon at various life stages, and survival rates in those habitats (Nickelson 1998; Nickelson and Lawson 1998). Monte Carlo runs of the model produce likely patterns of coho salmon abundance (and variability in abundance) under a variety of circumstances including variable marine survival. A similar model was developed for coho and chum salmon in Carnation Creek, British Columbia (Holtby and Scrivener 1989). The Oregon Coast model has been used to estimate coastal carrying capacity, to identify under-performing basins, to compare proposed fishery management strategies, and to perform population viability analysis.

The model is based on freshwater reaches of about 1 km, with smolt carrying capacity and parr-to-smolt survival rates estimated from measured habitat characteristics. For each reach, females deposit eggs that hatch into fry. Fry survive to summer parr based on a density-dependent function. Summer parr survive to smolts based on reach-specific survival rates and a maximum capacity. Smolts migrate to the ocean and survive at a variable rate. Most return to their natal reach to spawn, but some migrate to other reaches allowing recolonization of depleted areas. Although the original model did not incorporate a spatially explicit representation of the stream network, newer versions of the model will. These are under development in separate efforts by scientists at the U.S. EPA Western Ecology Division (Leibowitz and White, in press) and at the NOAA NW Fisheries Science Center/Earth Systems Institute.

Landscape disturbance and stream habitat.—Wildfires, landslides, floods, and other natural disturbances are integral to the functioning of aquatic ecosystems (Reeves et al. 1995), but our ability to understand and predict the consequences of altered disturbance regimes is hindered by the large spatial and temporal extents involved. Computer simulations of natural processes can be run over entire regions for millennia, propagating disturbances into and through stream networks and estimating in-channel effects. Integrated simulation models provide baseline outputs for characterizing disturbance regimes unaltered by human activities, and for evaluating future conditions under various management scenarios. A prototype simulation model that integrates multiple processes to estimate stream habitat conditions (USDA Forest Service 2003) has been adapted for western Oregon.

Several component models were necessary to build the integrated habitat simulation model for western Oregon. Regional wildfire models, for example, provide estimates of spatial and temporal variability in stand ages and types under a natural fire regime (Wimberly 2002). An empirical model that relates forest attributes to landslide susceptibility (Miller

and Burnett 2007) is used to predict landsliding associated with changes in forest cover. By relating storm characteristics to landslide rates (Benda and Dunne 1997a), climate variability is incorporated into the modeling. Fires, storms, and landslides affect processes of wood recruitment to streams (Benda and Sias 2003), leading to temporal and spatial variability in simulated wood loading (Benda et al. 2003). In the simulation model, the spatial overlap and temporal sequence of interacting events that deliver and transport sediment and wood create a mosaic of channel and related habitat conditions (e.g., number of pools and amount of large wood) that changes over time (USDA Forest Service 2003). Such predictions reveal potential patterns and relationships that can be difficult to discern empirically. This is due to the fact that cause and effect may be separated in time and space (e.g., fires in the headwaters 100 years ago and an aggraded mainstem channel now [Benda and Dunne 1997a]). The integrated habitat simulation model is now being coupled with a habitat-based coho salmon life cycle model (Nickelson 1998; Nickelson and Lawson 1998). The model will produce possible trajectories of salmon abundance as the landscape changes through processes related to climate or management.

Conclusions

Over the past 50 years, western Oregon has been an active locus for collecting data and developing models (Tables 1 and 2; Figure 2) to help understand and manage salmon. Though these efforts have not always proceeded logically and systematically, we have attempted in this paper to organize this experience through hindsight. The AYK-SSI Salmon Research and Restoration Plan (2006) is a strategic framework to guide research and monitoring in collecting the right data the first time around. The authors hope to contribute to these endeavors by offering managers and scientists working in the AYK region the opportunity to evaluate examples of data and models that have been particularly useful in western Oregon.

Of the many possible lessons to take from the western Oregon experience, some may be readily transferable for meeting objectives of the AYK-SSI Salmon Research and Restoration Plan (2006) and some may not. There are three lessons for designing and initiating data collection that may have particular value for the AYK region. The first is that data are more valuable when their scope of inference is known. Although the scope of inference is determined objectively in the design of a probability-based sampling strategy, it can be approximated through landscape classifications for data collected in intensively monitored basins or case studies. The second lesson relates to striking the right balance between answering the questions of how many and why. Data collected for monitoring and assessment are essential, but may be insufficient, for effectively managing salmon and their habitats. Data collected specifically for research may be necessary to provide critical understanding—to answer the "why" questions about salmon ecosystems. This may be particularly true as populations in the AYK region face new levels or combinations of stressors that are outside the range of recent experience. The third lesson is that upfront integration between interested parties can yield efficiencies in where and what types of data are collected and can increase the utility of any collected data. Meta-analysis of existing data collection efforts and databases can help prioritize information gaps that are critical for meeting regional goals (e.g., Holl et al. 2003). Establishing regular communications among monitoring and research participants will clarify assumptions and expectations and improve opportunities for collaboration, thereby enhancing the likelihood that collected data can contribute to accomplishing multiple objectives.

A key lesson regarding modeling that may prove useful in the AYK region is that all models are "expert opinion" to one degree or another. Consequently, correct predictions should be viewed with a healthy degree of skepticism. Understanding of model precision, which is the potential range of model outputs given known uncertainties in the input data, can aid in the appropriate use of modeled data in a decision-making context (Jones and Bence 2009, this volume. The landscape models we addressed here likely compromise some degree of local accuracy for broad-scale coverage or synthesis. Even so, these models have proven useful. A good model is one that can help explain, predict, or understand salmon and their ecosystems, and the best models are likely to derive from an iterative and adaptive process. Such a process involves organizing existing knowledge and data, collecting data to fill essential gaps, building and running a model, evaluating model outputs against newly collected data or traditional knowledge, and then repeating the entire process.

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