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Guest Editorial, part of a Special Feature on Pathways to Resilient Salmon Ecosystems

Reconnecting Social and Ecological Resilience in Salmon Ecosystems

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ABSTRACT. Fishery management programs designed to control Pacific salmon (*Oncorhynchus* spp.) for optimum production have failed to prevent widespread fish population decline and have caused greater uncertainty for salmon, their ecosystems, and the people who depend upon them. In this special feature introduction, we explore several key attributes of ecosystem resilience that have been overlooked by traditional salmon management approaches. The dynamics of salmon ecosystems involve social–ecological interactions across multiple scales that create difficult mismatches with the many jurisdictions that manage fisheries and other natural resources. Of particular importance to ecosystem resilience are large-scale shifts in oceanic and climatic regimes or in global economic conditions that unpredictably alter social and ecological systems. Past management actions that did not account for such changes have undermined salmon population resilience and increased the risk of irreversible regime shifts in salmon ecosystems. Because salmon convey important provisioning, cultural, and supporting services to their local watersheds, widespread population decline has undermined both human well-being and ecosystem resilience. Strengthening resilience will require expanding habitat opportunities for salmon populations to express their maximum life-history variation. Such actions also may benefit the “response diversity” of local communities by expanding the opportunities for people to express diverse social and economic values. Reestablishing social–ecological connections in salmon ecosystems will provide important ecosystem services, including those that depend on clean water, ample stream flows, functional wetlands and floodplains, intact riparian systems, and abundant fish populations.

Key Words: *fishery management; Pacific Northwest; Pacific salmon; resilience; salmon ecosystem*

INTRODUCTION

In an open letter to the Oregon State legislature in 1875, U.S. Commissioner of Fish and Fisheries Spencer Baird painted a grim future for Pacific salmon (*Oncorhynchus* spp.) in the Columbia River (Baird 1875). Based on the collapse of Atlantic salmon (*Salmo salar*) in Northeast American rivers decades earlier, Baird predicted that Columbia River salmon would suffer a similar fate for the same reasons: habitat loss, excessive harvest, and dams and other impediments to fish migration. The Commissioner enthusiastically endorsed hatchery technology as the means to maintain a stable salmon supply and to avoid the highly unpopular regulatory alternatives. Numerous state and federal fishery management agencies were established thereafter, and Baird’s simple formula—artificial fish propagation to compensate for habitat loss and intensive harvest—was institutionalized, setting the priorities for U.S. fishery management for the next century (Bottom 1997).

Despite such early knowledge of the principal threats, Baird’s predicted collapse of Columbia River salmon proved quite accurate. The total annual run of all anadromous salmon in the basin, estimated at 10 to 16 million fish before European settlement (Northwest Power Planning Council 1986), has declined to around one million fish, of which approximately 80% or more are now produced artificially in hatcheries (Northwest Power Planning Council 1992, National Research Council 1996, Genovese and Emmett 1997). Of the estimated 385 historical Columbia River populations of five salmon species—chum (*O. keta*), coho (*O. kisutch*), sockeye (*O. nerka*), Chinook (*O. tshawytscha*), and steelhead (*O. mykiss*)—212

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(55%) are now extinct, and 13 evolutionarily significant groups have been added to the U.S. federal list of threatened or endangered species (Gustafson et al. 2007). Recalling both Baird's early warning and his proposed solution, contemporary status assessments now list habitat loss, excessive harvest, dams, and hatcheries among the primary causes of salmon population decline in the Columbia River basin (National Research Council 1996, Williams 2006).

The history of Pacific salmon conservation is a classic case of "command-and-control" management of renewable resources (Holling and Meffe 1996). Fishery management developed from an agricultural model of conservation (Bottom 1997). It devised methods to stabilize fish production at optimum levels by controlling or removing presumed limitations to survival and yield. Biologists selected salmon spawning partners and controlled rearing conditions in hatcheries; dictated the sizes, times, and locations for releasing hatchery fish; established predator control programs to eliminate threats from other fishes, birds, and mammals; and regulated harvest levels to achieve the maximum yield.

Ironically, the long-term effort to stabilize salmon ecosystems for optimum production has created greater uncertainty for salmon and the people who depend on them (e.g., Lichatowich 1999). Throughout the western United States, approximately 29% of nearly 1400 historical salmonid populations (including the five species listed above and pink salmon, *O. gorbuscha*) are now extinct (Gustafson et al. 2007), and 27 salmonid stock groups are formally listed as threatened or endangered (http://www.nwr.noaa.gov/ESA-Salmon-Listings/). Widespread fish population decline in turn has caused severe economic hardships for many coastal communities (Martin 2008) and has led to season and area restrictions for local salmon fisheries, culminating in coast-wide fishery closures for Pacific Northwest coho salmon in 1994 and Chinook salmon in 2008.

Yet, salmon populations and coastal communities have not responded uniformly to social and ecological changes in the region. Despite widespread population decline, more than two-thirds of salmon stocks in the Pacific Northwest have avoided Baird's prediction (Gustafson et al. 2007), and many people have demonstrated a strong commitment to salmon protection and restoration in their attitudes (Smith and Steel 1997, Dunlap 2000) and their actions (Kenny 1999, Oregon Watershed Enhancement Board 2007). Fishers have endured shorter seasons, reduced fishing areas, gear restrictions, and blame for stock declines but many have adapted and continue to survive economically.

The failure of traditional command-and-control approaches to account for social–ecological interactions and to protect or restore many natural resources has stimulated interest in an alternative conservation framework based on ecosystem resilience (Holling and Meffe 1996, Ludwig et al. 2001, Folke at al. 2004). The contributions to this special feature examine that framework as a means for human communities to reconnect with salmon to strengthen social–ecological resilience in variable environments.

The resilience perspective acknowledges that ecosystems continually adapt to disturbances at a variety of scales and cannot be controlled predictably to maintain an optimal condition or level of production. Moreover, because ecosystems have limits in their capacities to reorganize and repair themselves following disturbance, human actions must work within the resilient capacities of salmon to avoid placing important ecosystem services at risk. A resilience-based management approach, therefore, seeks to strengthen the self-repairing capacity of ecosystems to support the services that people value.

We define resilience as the amount of disturbance that an ecosystem can accommodate without shifting to a different regime or stability domain as characterized by a fundamentally different structure, function, and feedback mechanisms (Walker et al. 2004). The resilience concept has been applied broadly to complex and adaptive social–ecological systems (e.g., Walker et al. 2002)—integrated systems of people and the natural environment. We use the term "salmon ecosystem" to define an integrated system of people and environments that are directly linked to anadromous salmon populations or groups of populations within particular geographic areas. Salmon ecosystem resilience then is a measure of whether this integrated and adaptive system can reorganize, renew, and persist following disturbance.

This special feature explores resilience as a goal and rationale for reestablishing social–ecological connections to salmon. Few examples in resource conservation can match the large geographic extent or documented management history of Pacific salmon. As an economic product, cultural icon, and driver of nutrient and energy flow, salmon are the hub in a network of social–ecological interactions that characterize diverse North Pacific environments (National Research Council 1996, Stouder et al. 1997). In this regard, Pacific salmon epitomize Dayton's (1972) characterization of a "foundation species," a species that "defines much of the structure of a community by creating locally stable conditions for other species, and by modulating and stabilizing fundamental ecosystem processes." Salmon ecosystems thus have broad application as case studies for understanding the resilience of social–ecological systems and the implications for natural resource management.

The papers in this volume describe the results of a conference held 3–5 April 2007 in Portland, Oregon to explore salmon ecosystems from a resilience perspective. Together, these papers address three principal questions:

1. What are the social and ecological attributes of resilient salmon ecosystems?
2. What factors have undermined resilience of salmon ecosystems?
3. What changes are most needed to incorporate resilience thinking in fishery management and to strengthen social–ecological connections to salmon?

Salmon ecosystems adapt to changes across multiple scales, including the effects of large-scale shifts in climatic, economic, and geopolitical regimes. Their resilience is a function of the ecosystem services that salmon populations convey and the diversity of habitat and socioeconomic opportunities that allow both salmon and people to respond to variable conditions. As context for the papers that follow, this introductory essay examines these attributes of salmon ecosystems that have been overlooked by traditional command-and-control approaches: cross-scale interactions, climatic regime shifts, ecosystem services, and response diversity.

CROSS-SCALE INTERACTIONS

The failure to account for various scales and cross-scale interactions in natural resource management frequently has undermined resilience of social–ecological systems (Cash et al. 2006). Cash et al. (2006) defined "scale" as spatial, temporal, jurisdictional, or other dimensions and "levels" as the various units within a particular scale. Interactions across scales (e.g., spatial vs. jurisdictional) and across levels (e.g., local vs. global, national vs. international) create difficult management challenges that traditional resource management approaches have been unable to resolve.

Many of the case studies used to develop resilience theory have depicted the dynamics of relatively discrete and stationary ecosystems with well-defined spatial boundaries such as lakes (Carpenter 2003), forests (Dublin et al. 1990), savannas (Anderies et al. 2002, Rietkerk et al. 2004), wetlands (Gunderson 2001), coral reefs (McCook 1999, McManus and Polsenberg 2004), and kelp forests (Simenstad et al. 1978, Steneck et al. 2002). By comparison, the ecosystems of Pacific salmon are open systems with fluid boundaries that encompass vast distances across multiple spatial levels and environments. Like migratory marine species, anadromous salmon raise fundamentally different management problems compared with those for fixed resources or localized, community-based users (Berkes 2006). The spatial extent and complexity of salmon ecosystems raise important issues of spatial scale and scale mismatches (Cash et al. 2006) that have contributed to the failures of traditional fishery management approaches (Crowder et al. 2006, Francis et al. 2007).

Salmon ecosystems are defined by the long chain of freshwater, estuarine, and marine habitats that individuals in a population must navigate to complete their anadromous life cycles. Salmon may spawn and rear in a diversity of freshwater habitats from small headwater streams and lakes to larger rivers and estuaries, and feed for months or years in coastal and open marine waters of the North Pacific Ocean (Fig. 1). Salmon migrations thus cut across the steep environmental gradients often used to distinguish river, estuary, and ocean systems and the narrow disciplinary boundaries (i.e., stream ecology, limnology, estuarine ecology, and oceanography) that compartmentalize data collection and reporting in fisheries science and management.

The collapse of many Pacific salmon populations in part has resulted from ignorance of cross-level dynamics: fishery biologists with backgrounds in stream ecology long assumed that salmon populations were regulated entirely by freshwater variables at early life stages that could be controlled in hatcheries (Bottom et al. 2005b, 2006). Large-scale climatic and oceanographic influences on salmon survival were not considered before a biological crisis generated interest in other cross-disciplinary and cross-level explanations (Nickelson 1986, Johnson 1988, Pearcy 1992, Francis and Hare 1994).

The extended migrations of salmon create difficult scale mismatches with the many state, federal, tribal, and international jurisdictions that regulate fisheries and habitats. Although salmon require the entire freshwater-estuarine-ocean habitat continuum to complete their complex life cycles, most management jurisdictions and laws apply to much smaller segments of that chain. For example, by one estimate, a Chinook salmon hatched in the Lochsa River in Idaho, a tributary system of the Columbia River basin, crosses at least 17 separate international, federal, state, and tribal jurisdictions during the later stages of its life cycle (Wilkenson 1992).

The National Research Council (National Research Council 1996) concluded that fragmentation of institutional responsibilities and a mismatch between the spatial scales of salmon habitats and management jurisdictions severely undermine salmon conservation throughout the Pacific Northwest. Although state, federal, tribal, and international working groups allocate harvest among jurisdictions, the ecological complexity across jurisdictions is not adequately addressed in fisheries policy. Fishers harvest salmon within the jurisdictions of both the Pacific and the North Pacific Fishery Management councils. Salmon important to United States fisheries spawn in Canadian rivers, and fish important to Canadian fisheries spawn in the United States. Treaties and interstate compacts have tried but have not resolved fully these jurisdictional complexities (National Research Council 1996, Hanna 2008, Martin 2008).

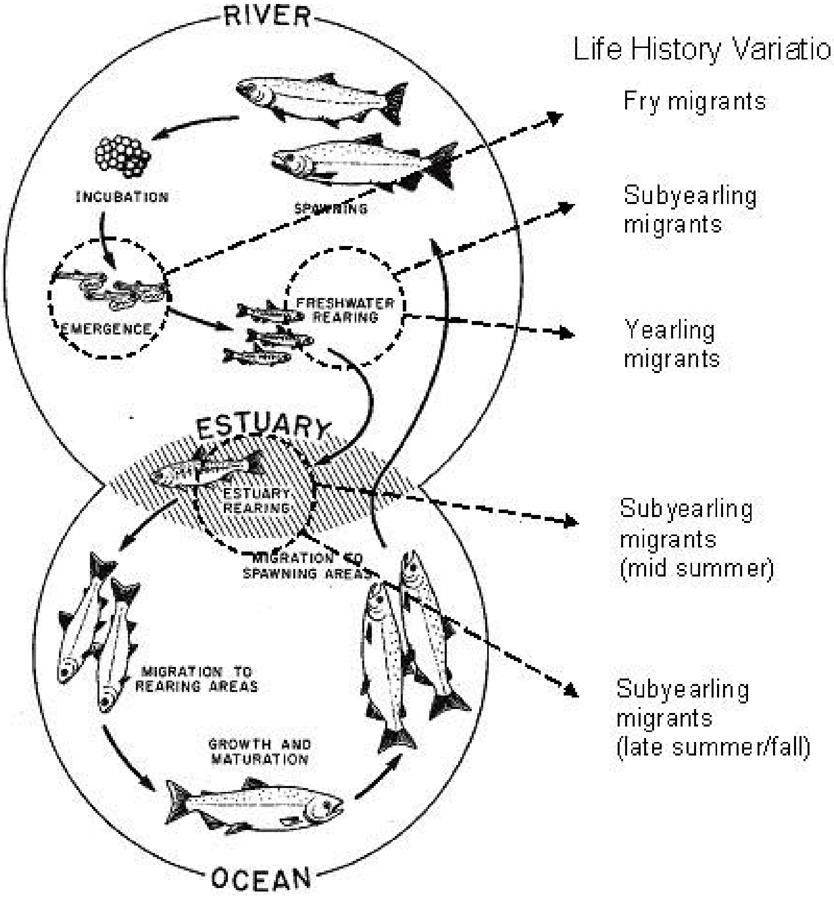
The spatial structure of salmon populations and the varied ocean migration patterns of individual salmon stocks create additional ecological complexity that does not map neatly onto existing management jurisdictions or the scales of ocean fisheries. Because salmon return to their natal streams to spawn, populations adapt to local watershed conditions, creating a geographic matrix of uniquely adapted and self-perpetuating populations within species. Salmon homing behavior and local adaptations argue for a fine-grained management approach that recognizes the individual population and its associated watershed as a fundamental conservation unit (Rich 1939, Lichatowich 1999). Yet, despite improved genetic discrimination and other technological advancements, the resolution of fishery management remains relatively coarse, unable to discriminate the population- and stream-specific origins of individual salmon harvested at sea.

Historically, the cultural practices and harvest methods of native fishers were adapted to local watersheds and the seasonal spawning migrations of local salmon populations (e.g., McEvoy 1986, Lake 2007; V. L. Butler and S. K. Campbell, unpublished data). However, motorized vehicles and other advanced technologies of the last century extended fishing activities to the open ocean, where numerous stocks from distant river basins congregate and can be harvested simultaneously. Despite the expanded scale of salmon fisheries, contemporary fishers must continue to adapt locally as they seek other fishing opportunities and economic options to maintain year-round employment (Ecotrust 1995, National Research Council 1996, Smith and Gilden 2000, Martin 2008).

Fishery rules applied independent of scale considerations have reduced salmon biocomplexity and eroded social–ecological resilience (Nehlsen et al. 1991, National Research Council 1996, Hanna 2008). For example, regulations applied broadly to large stock aggregates have eliminated salmon populations too small to withstand harvest rates set for the most productive stocks, including stocks produced in hatcheries (Hilborn 1992, Wright 1993, Lichatowich 1999). Broad-based regulations also have eliminated various economic niche opportunities that otherwise might allow local salmon fishers to diversify their incomes (Smith and Gilden 2000, Martin 2008).

Today, resource managers face the possibility that, regardless of the management scales applied, external drivers far beyond the spatial extent of regulatory jurisdictions could undermine ecosystem resilience (X. Augerot and C. Smith, unpublished

Fig. 1. Generalized Chinook salmon life cycle and the associated environments of the salmon ecosystem. Salmon may complete their life cycles through a variety of alternative pathways, illustrated here by five juvenile life-history types reported in Sixes River, a small coastal watershed in southwest Oregon (Reimers 1973). Each life-history type represents a different pattern of freshwater or estuarine residency before ocean migration. Figure adapted from Nicholas and Hankin (1988).



data). In Bristol Bay, Alaska, for example, the adaptability of fishers to resource availability has complemented ecological resilience at a regional scale, but falling prices from expanded global production of farmed salmon have reduced economic resilience for the industry as a whole (Hilborn et al. 2003, Hilborn 2006, Robards and Greenberg 2007). Rapid changes in global climate could overwhelm resilience of many salmon ecosystems, particularly at the southern range of salmon distribution in the Pacific Northwest (Bottom et al. 2006, Battin et al. 2007). Salmon ecosystems thus epitomize the difficult cross-scale challenges of natural resource management and reinforce the conclusion that no single scale or level adequately characterizes the dynamics of social–ecological systems (Berkes 2006, Cash et al. 2006).

REGIME SHIFTS

For most of its history, fisheries management assumed that aquatic ecosystems exist in a constant equilibrium (Bottom 1997), unaware that ecosystem regime shifts could suddenly alter the underlying conditions for salmon survival. Numerous studies have described the theoretical basis for ecosystem regime or phase shifts when resilience thresholds are crossed (Holling 1973, May 1977, Scheffer et al. 2001, Scheffer and Carpenter 2003), and others have presented evidence of such shifts in a wide variety of ecosystem types (Gunderson 2001, Steneck et al. 2002, Folke et al. 2004, Knowlton 2004, McManus and Polsenberg 2004). Salmon ecosystems are embedded within a trans-Pacific ocean and climate system that similarly exhibits sudden nonlinear fluctuations from one set of physical and biological conditions to another. Such oceanic and atmospheric changes, which can last for periods of decades, have been termed “regime shifts” (Francis and Hare 1994).

Although the mechanisms are poorly understood, large-scale climatic changes test the resilience of social–ecological systems. Climatic regime shifts alter aquatic conditions at all salmon life stages, including effects on inland precipitation, stream flow, and temperature patterns (Redmond and Koch 1991, Melack et al. 1997) and on ocean species composition, productivity, and food webs (Francis et al. 1998). Moreover, the effects of shifting climatic regimes vary among regions of the North Pacific: climatic regimes characterized by enhanced salmon production in the Gulf of Alaska have coincided with periods of reduced production in the Pacific Northwest, and vice versa (Francis and Hare 1994, Francis et al. 1998). Salmon populations offer instructive lessons in resilient strategies for coping with unpredictable North Pacific environments (Healey 2009).

Regime shifts often are attributed to human actions that have undermined ecosystem resilience (Folke et al. 2004). For example, shifts in ecological, economic, and geopolitical conditions beyond the jurisdictions or control of management institutions influence salmon ecosystem resilience (National Research Council 1996, Hanna 2008). The value of currencies, economic markets, and population and economic growth policies of other nations all modify the social–ecological state of salmon ecosystems.

Unlike regime shifts in many systems, oceanic and climatic shifts have occurred independent of direct human influence. Paleoecological studies have documented large fluctuations in abundance and shifts in the dominance of pelagic marine fish species in the North Pacific well before intensive fisheries had any impact on fish stocks (Soutar and Isaacs 1969, 1974). A 2200-year reconstruction of Alaska sockeye salmon abundances demonstrated dramatic jumps from high to low productivity that lasted for centuries even without any anthropogenic influence (Finney et al. 2002). Langdon (2007) describes how native populations may have adapted to this type of change. Recent archeological studies suggest that native Northwest societies adapted to changes for thousands of years without compromising salmon ecosystem resilience (V. L. Butler and S. K. Campbell, unpublished data).

More frequent regime shifts in the North Pacific have been linked to interannual scales of the El Niño/Southern Oscillation (ENSO) in the tropical Pacific (Mysak 1986), and to interdecadal climatic changes described as the Pacific Decadal Oscillation (PDO) (Mantua et al. 1997). Climatic regimes are marked by oscillations in the areas of high and low productivity around the Pacific Ocean basin in response to changes in the global heat balance (Barber 1988). Whereas characteristic ENSO events may last 6 to 18 months, shifts in the PDO can persist for 20 or 30 years. The ENSO and PDO cycles in the last century have been associated with marked changes in the productivity and abundance of marine organisms at all trophic levels (e.g., Francis et al. 1998, McGowan et al. 1998). The ecological conditions that the individuals in a salmon population might encounter in a particular year thus may vary considerably depending on the climatic regime and its interactions with regional and local scales of variation (Bottom et al. 2006, Bisson et al. *in press*).

Regime shifts in many ecosystems have been attributed to reduced resilience through gradual modification of slowly changing ecological variables such as soils, nutrients, or biodiversity (Carpenter et al. 2001, Folke et al. 2004). The collapse of coho salmon populations in the Pacific Northwest followed a similar pattern. In this case, gradual losses of freshwater habitat and depletion of diverse wild salmon stocks were masked for decades by a productive ocean regime and a continued subsidy of fish produced in hatcheries. The failure to account for ocean fluctuations reinforced faulty assumptions about management successes during favorable ocean regimes and undermined ecosystem resilience (Lawson 1993, Bottom 1997, Lichatowich 1999). Incremental habitat and fish population losses set the stage for regional fishery collapse when the climate regime shifted, causing severe hardships for commercial and recreational fishers and their communities (Hanna and Hall-Arber 2000, Smith and Gilden 2000). It is uncertain whether degraded salmon ecosystems in the Pacific Northwest remain sufficiently resilient to respond positively to ongoing restoration programs or have shifted to a stable, low-productivity state that may persist regardless of the climatic regime.

Ocean and freshwater conditions for salmon in the region have become increasingly uncertain, and past climatic cycles may not be a useful indicator of future trends. For example, some studies suggest that the PDO was not a prominent feature before the last two centuries, and others question whether it will continue as a major source of interdecadal change (Francis et al. 2007). Warming of the world's oceans, reduced snow packs, and other effects of global climate change are creating new uncertainties about the adaptive capacities of salmon populations in the region (Mote et al. 2003). Such trends suggest a need to strengthen ecosystem resilience as a strategy to cope with unpredictable social–ecological changes (Carpenter and Folke 2006).

ECOSYSTEM SERVICES

The traditional fishery management goal to maximize commercial and recreational harvest did not recognize the importance of salmon as a foundation species in aquatic ecosystems (Dayton 1972) and competed with other ecosystem services that benefit human well-being (Gresh et al. 2000, Schindler et al. 2003). Salmon populations are directly responsible for conveying three of the four categories of ecosystem services defined by the Millennium Ecosystem Assessment (2005): provisioning, cultural, and supporting (Fig. 2). The reliable delivery of these services depends on tens of thousands of component populations (Luck et al. 2003), each supplying services to a localized area within the broad distribution of Pacific salmon species.

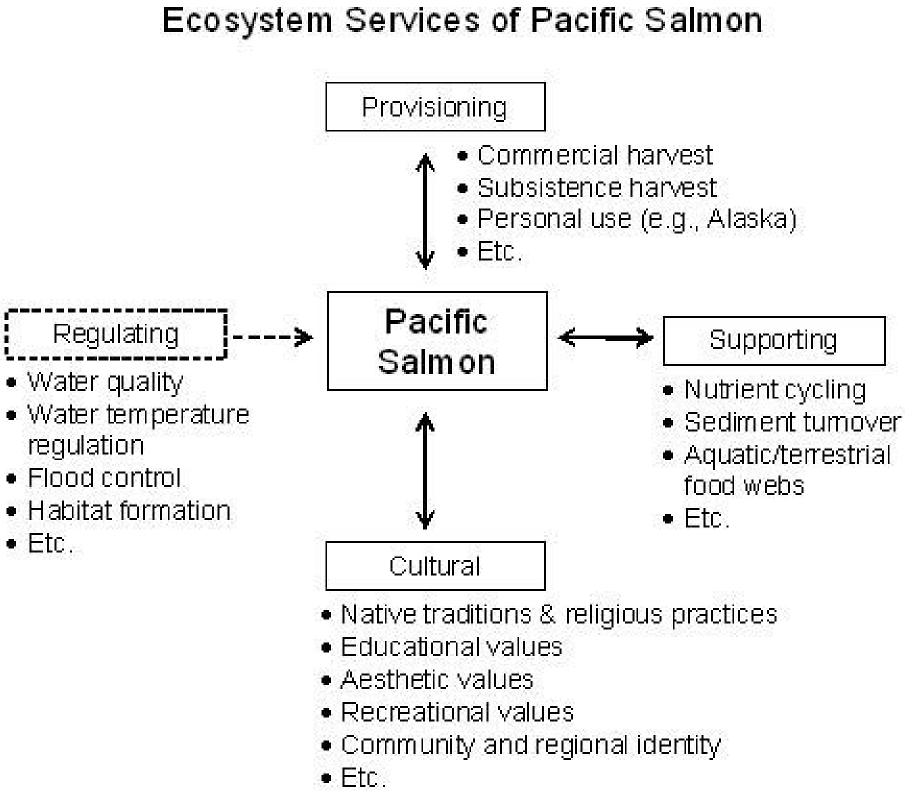
The most obvious service is the provisioning role of salmon ecosystems, which produce highly valued food products harvested in various commercial, subsistence, and personal-use fisheries across the North Pacific. Historically, salmon species were not only a major component of native fisheries for thousands of years (V. L. Butler and S. K. Campbell, unpublished data). They also were a principal focus of the spiritual and cultural lives of diverse native communities from northern California to the Gulf of Alaska (Drucker 1963, Matson and Coupland 1995). Today, salmon are a cultural icon for people of all races in the region, providing diverse cultural services through the support of educational, recreational, spiritual, and community values (Columbia River Inter-tribal Fish Commission 1994, Smith and Steel 1995, Smith and Berg 1998, Wolf and Zuckerman 1999).

In the last two decades, ecological studies have detailed many ecosystem supporting services also provided by salmon populations. Salmon are the principal food item of many terrestrial wildlife species (Willson and Halupka 1995, Merz and Moyle 2006) and a source of marine-derived nutrients to coastal lakes and streams (Bilby et al. 1996, Cederholm et al. 1999, Finney et al. 2000). They act as watershed engineers that structure streambed habitats and alter sediment composition during spawning (Schindler et al. 2003).

Ecosystem provisioning, cultural, and regulating services ultimately may depend on the supporting services of salmon populations that drive nutrient and energy flows in coastal watersheds. Salmon carcasses, eggs, and sperm left behind after spawning deliver a continuous flow of nutrients and energy from the ocean to small coastal streams, rivers, and lakes. Predation by terrestrial scavengers and nutrient uptake by riparian vegetation transfers marine-derived nutrients to terrestrial plants and animals. Marine-derived nutrients from salmon even provide direct economic benefits through nutrient inputs to agricultural crops in fields near salmon rivers (Merz and Moyle 2006). The growth of riparian trees that shade freshwater systems, regulate stream temperatures, and provide in-stream habitat structure may at least partially depend on healthy salmon populations (Helfield and Naiman 2001, Naiman et al. 2002). Similarly, marine-derived nutrients incorporated into freshwater biota through consumption and decomposition of salmon increases freshwater productivity and fish growth and may constitute a positive feedback loop to salmon survival (Bilby et al. 1996, Gresh et al. 2000, Schindler et al. 2003), even in estuarine ecosystems (Kline et al. 1990).

Salmon also are sensitive indicators of regulating services in coastal watersheds. Because the environmental tolerances of salmon species are

Fig. 2. Local salmon populations provide provisioning, cultural, and supporting ecosystem services that benefit people. These services often involve two-way interactions with feedbacks to salmon. Because salmon populations are sensitive to changes in environmental quality and habitat structure, they also are indicators of important regulating services that people derive from resilient salmon ecosystems.



relatively narrow and habitat requirements at each life stage are very specific, populations are sensitive to water quality and habitat structure throughout a watershed. Thus, many of the same habitats that support robust salmon populations—functional wetlands and floodplains and intact riparian systems, for example—also support regulating ecosystem services (e.g., water purification, flood control, and temperature regulation) that benefit people (Fig. 2).

Fishery management programs that were designed to optimize food production have undermined provisioning as well as many of the other services that salmon ecosystems provide. For example, harvest managers assumed that allowing more adults to spawn than what was needed to attain the maximum sustained yield (MSY) was wasteful and inefficient (Larkin 1977, Finley 2009). Maximum sustained yield took for granted that the aggregate abundance of all salmon populations across a region was predictable and infinitely resilient if annual fisheries took only the “harvestable surplus.” Population models did not consider whether harvested salmon were surplus to the nutrient and energy flows through local ecosystems.

The decline of salmon populations across much of the Pacific Northwest has undermined ecosystem resilience and reduced or eliminated many of the services that salmon historically supplied at a regional scale (Nehlsen et al. 1991, Gustafson et al. 2007; X. Augerot and C. Smith, unpublished data). Population decline has had a serious impact on fisheries, on the economies of coastal communities, and on the livelihoods and cultural identities of native and non-native fishers alike (e.g., Martin 2008). By one estimate, only 6%–7% of the historical subsidy of marine-derived nitrogen and phosphorous now reaches rivers across the Pacific Northwest (Gresh et al. 2000). Widespread salmon decline may affect regional biodiversity of terrestrial-dependent wildlife species (Willson and Halupka 1995). Others hypothesize that disruption of the marine feedback loop to coastal rivers could cause a downward spiral in freshwater ecosystems and a shift to a persistent low-productivity regime that is resistant to salmon recovery (Gresh et al. 2000, Schindler et al. 2003).

Although many recreational and sport fisheries continue to decline, salmon fishery management is evolving to recognize the nutrient-cycling role of wild salmon in coastal watersheds, and salmon farming activities are assuming an increasing role in food production (X. Augerot and C. Smith, unpublished data). A resilience perspective argues for a more explicit accounting of all of the salmon ecosystem services that natural-resource management programs influence and hope to maintain (Carpenter et al. 2001).

RESPONSE DIVERSITY

The resilience of ecosystem services has been linked to the diversity of species within functional groups —i.e., sets of organisms that support similar ecosystem processes (Walker et al. 1999, Carpenter et al. 2006)—and to the diversity within species and populations (Luck et al. 2003). The relationship between resilience and diversity depends on the variation in responses of species and populations to changing conditions. That is, the ecosystem processes supported by a functional group are likely to be maintained over a wider range of conditions if its component species respond independently to environmental fluctuations (Elmqvist et al. 2003, Folke et al. 2004, Norberg 2004, Carpenter et al. 2006). Variation in response to environmental change among species with the same ecosystem function has been termed “response diversity” (Elmqvist et al. 2003).

Diverse life histories within and among Pacific salmon species are a population-level example of response diversity. Diverse behaviors of individuals within salmon populations—all part of the same salmonid functional group—confer resilience to salmon ecosystems as conditions vary. Several papers in this special feature describe examples of diverse salmon life histories (Koski 2009, Healey 2009) that, in turn, promote resilience of the many ecosystem services that people value (Fig. 2).

Salmon homing behavior and reproductive isolation create a diverse genetic structure of locally adapted populations upon which natural selection can operate. Variation in the types of suitable habitat available, in turn, allows expression of a wide variety of phenotypic traits within and among salmon populations.

Chinook salmon, for example, express a diversity of life histories, including variations in freshwater and estuarine residency, timing of seaward migration, and timing and ages of spawning (Healey 1991). Within one small Oregon coastal river, for example, Reimers (1973) identified five different juvenile life history types that represent alternative strategies for using all available freshwater and estuarine nursery habitats within the basin (Fig. 1). Each life-history variant defines an alternative pathway by which individuals can complete their life cycles. Even the characterization of diverse life-history “types” oversimplifies the broad continuum of behaviors that individuals can express during their migrations through a watershed (Burke 2004, Bottom et al. 2005b).

The life-history diversity of salmon populations has been described as an evolutionary strategy for spreading risk and avoiding brood failure in the presence of unpredictable watershed or ocean conditions (Healey 1991). Life-history diversity provides resilience to salmon populations in variable environments because all individuals do not behave similarly or occupy the same habitats over time. Different timing and sites of juvenile rearing, for example, maintain options for at least some individuals to survive unfavorable conditions or to recolonize areas previously affected by disturbance. For example, a strong El Niño event in 1982–1983 brought warm ocean temperatures and low-productivity conditions across the northeast Pacific Ocean. Chinook salmon stocks that reared locally along the Oregon coast suffered high mortality and very low adult returns during this period, whereas stocks with a northerly distribution pattern in the Gulf of Alaska showed little or no decline in abundance (Johnson 1988).

The response diversity of salmon populations is directly tied to the variety of habitat opportunities that allow individuals to express alternative rearing, migration, and spawning behaviors. For example, a sizeable proportion of the individuals in some Chinook salmon populations migrate to estuaries to rear soon after emergence. Expression of this behavior requires suitable estuarine rearing sites, including floodplain and tidal wetlands or other shallow, low-velocity habitats preferred by salmon fry (Healey 1991, Bottom et al. 2005b).

For example, relatively few Chinook salmon fry reared in Oregon's Salmon River estuary three decades ago, when most of the tidal wetlands were isolated by dikes and tide gates to create pasture for cattle. A long-term dike removal program to reconnect tidal wetlands and restore estuarine functions also reconnected a critical link in the salmon habitat chain. After restoring about 60% of the historically diked wetlands, significant proportions of the salmon population now exhibit diverse estuarine life histories, and juvenile salmon migrate to the ocean at a wider range of sizes and times (Bottom et al. 2005a). Reconnecting estuarine wetlands, therefore, increased juvenile response diversity to changing freshwater and ocean conditions and likely strengthened population resilience.

Among the best examples of salmonid response diversity are steelhead populations along the west coast of Russia's Kamchatka Peninsula, where six different life-history types have been identified (Augerot 2005, Pavlov et al. 2008). The distribution and proportions of each type varies across the region and from year to year within the same river, depending on environmental conditions. Phenotypic variations among Kamchatka steelhead, including anadromous (i.e., those that migrate to the ocean to rear), resident (i.e., those that remain entirely in fresh water), estuarine, and riverine-estuarine forms, reflect the diverse habitat opportunities for expressing different life histories. For example, whereas resident life histories predominate in highly complex and productive rivers with ample feeding opportunities, anadromous forms are prevalent in smaller rivers with simple channels and limited rearing habitat (Pavlov et al. 2008). Remarkably, individual steelhead also exhibit a diversity of responses: under changing environmental conditions, the life-history strategies of a particular individual can change from resident to anadromous forms, and vice versa (Zimmerman et al. 2003, Pavlov et al. 2008).

In the Columbia River Basin, the cumulative effects of dams, hatchery production, intensive harvest, and habitat degradation have reduced salmon rearing and spawning opportunities and eliminated many local populations within the basin (National Research Council 1996, Williams 2006, Gustafson et al. 2007). Not surprisingly, contemporary patterns of salmon migration and rearing through the system appear much less diverse than the complex juvenile life-history patterns that were reported early in the 20th century (Rich 1920, Burke 2004, Bottom et al. 2005b). Reduced response diversity in the Columbia River populations may limit salmon resilience to future environmental changes.

Just as diverse life histories provide resilience to salmon populations, the resilience of social–ecological systems also may depend upon the opportunities for the people in salmon ecosystems to express diverse economic, cultural, and spiritual values (Suttles 1968, Hunn and Williams 1982, Ames 2004). Diverse human values may provide the social response diversity that human communities need to adapt successfully to changing environments (Lake 2007, Langdon 2007, Losey 2007).

Norton (2005) defined the sustainability of human communities as a function of intergenerational opportunities to express human values, which can be eroded by technological and personal choices that people make in the present. He argues that a policy or action is not sustainable if it reduces the ratio of opportunities to constraints for the future. Thus, a generation that overconsumes its local resources and reduces diversity without creating new opportunities eliminates options for the community to adapt when conditions change.

Complex coastal ecosystems that were capable of maintaining robust, self-sustaining salmon populations often provided opportunities for diverse natural resource-based economies, including commercial and sport fisheries, wood products industries, tourism, and recreation. Historically, the high-quality ecosystems and food webs that maintained diverse salmon runs also afforded opportunities for a rich diversity of other aquatic and terrestrial species. These species, in turn, constituted a diverse resource portfolio that sustained native fisheries and Northwest cultures for millennia (Butler and Campbell 2004; V. L. Butler and S. K. Campbell, unpublished data).

Degradation of salmon ecosystems and industrialization of fisheries have eroded opportunities for resource-dependent economies and other human values that depend on productive watersheds, requiring difficult adjustments by many Pacific Northwest communities (Robbins 1990, White 1995, Hanna and Hall-Arber 2000). To cope with declining salmon harvest, commercial fishers from the Columbia River have diversified by shifting harvest among a variety of marine species and by participating in distant and more robust fisheries in Alaska (Martin 2008). Regional crises often are relieved through similar cross-scale subsidies of natural resources from another region (Carpenter et al. 2001). Although Columbia River salmon communities have participated in Alaskan fisheries for decades, it remains uncertain whether shifting harvest northward to compensate for lost local opportunities will remain a resilient strategy at a broader North Pacific scale. Nonetheless, such changes cannot address the intergenerational or ecological consequences of local fish population loss.

In contrast to the Columbia River, other areas with more resilient salmon populations have maintained resilient fishery institutions and cultures. Bristol Bay sockeye salmon provide a regional example of response diversity sustaining a viable fishery during the last century (Hilborn et al. 2003). In this case, salmon populations in different regions and with different life-history strategies have been major contributors to salmon abundance and fisheries at different times, allowing the population aggregate (Bristol Bay) to remain productive despite major changes in regional climatic conditions. By conserving the full diversity of salmon life-history strategies and not simply focusing management on the most productive stocks, both salmon populations and salmon fisheries have shown considerable resilience (Hilborn et al. 2003).

Traditional command-and-control management tends to reinforce short-term goals and limit opportunities for diversification by resource-dependent communities (Smith and Steel 1995). Single-species management of salmon, for example, can limit response diversity in human systems and undermine the cultural mechanisms by which fishers and their communities adapt to change. A combination of specialist and generalist fishing enterprises may be needed for communities to cope with natural and market fluctuations (McKelvey 1983, Smith and McKelvey 1986). Fishers also can adapt to variations in fish abundance by building diverse portfolios composed of fishing and non-fishing activities (Baldursson and Magnusson 1997, Hanna 1998, 2008). To promote salmon ecosystem resilience, Hanna (2008) proposes institutional changes and establishing incentives to integrate human and ecological systems and account for the inherent resilience of both.

CONCLUSIONS

The resilience of salmon ecosystems has been eroded by human actions that have simplified the complex structure of salmon populations and their habitats. Such changes were supported by a scientific framework of ideas that took for granted that salmon ecosystems are predictable, malleable, and infinitely resilient and, therefore, could be controlled for optimum fish production (Bottom 1997, Lichatowich 1999). In this regard, the history of salmon conservation exemplifies the “pathology of natural resource management” described as the loss of resilience to a system that occurs when its natural range of variation is reduced (Holling 1986, Holling and Meffe 1996, Folke et al. 2004).

At the same time salmon ecosystems have become less resilient, rapid climatic and global economic changes are creating novel environments and greater uncertainties for the future. Such challenges underscore the need to establish new relations in salmon ecosystems that strengthen their resilience. A resilience perspective must account explicitly for the multiple management scales and cross-scale interactions that affect salmon ecosystem dynamics and for the full array of ecosystem services that are conveyed by robust, self-sustaining salmon populations.

Past failures to account for recurring oceanic and climatic regime shifts have reinforced faulty conclusions about the success of hatcheries and other management prescriptions that have eroded ecosystem resilience. Salmon have evolved a variety of resilient strategies (Healey 2009) to accommodate environmental fluctuations, including the sudden climatic shifts that can alter survival conditions across their ecosystems. Salmon adaptations and responses to social and ecological change thus provide a window into the dynamics of large coastal ecosystems whose interactions are difficult to perceive or anticipate. By strengthening social–ecological connections to salmon, people become more aware of the environmental uncertainties beyond their control and can seek more resilient strategies to accommodate them.

Strengthening salmon ecosystem resilience will require expanding opportunities for greater social–ecological response diversity in changing environments. Restoring opportunities for salmon to express diverse life histories also may expand opportunities for local communities to express diverse values and adaptive strategies. For example, reestablishing resilient salmon populations benefits social–ecological resilience by providing adequate stream flows, clean water, functional wetlands and floodplains, intact riparian systems, productive fisheries, and other ecosystem services that are directly linked to robust salmon runs. Management institutions and incentives must support sufficient diversification of human activities, including diverse fishing portfolios and economic opportunities, for communities to respond to changing economic, geopolitical, or other social–ecological conditions.

Clearly, Pacific salmon provide useful insights beyond just the realm of fisheries management. Salmon ecosystems across the North Pacific encompass a diversity of environmental, cultural, and management histories. These offer a comprehensive series of “experiments” to compare the dynamics of social–ecological systems and their implications for natural resource management (X. Augerot and C. Smith, unpublished data). The resilience of Bristol Bay (Hilborn et al. 2003) stocks and the rapid decline of Northwest salmon stocks (Williams 2006, Gustafson et al. 2007), for example, represent stark contrasts in salmon ecosystem dynamics that may hold useful lessons about resilience thresholds. The following papers in this special feature offer insights from a variety of historical and contemporary experiments in salmon ecosystem resilience.

Responses to this article can be read online at:
http://www.ecologyandsociety.org/vol14/iss1/art5/responses/

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