ECOSPHERE

Potential for ecological nonlinearities and thresholds to inform Pacific salmon management

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Abstract. Ecology is often governed by nonlinear dynamics. Nonlinear ecological relationships can include thresholds—incremental changes in drivers that provoke disproportionately large ecological responses. Among the species that experience nonlinear and threshold dynamics are Pacific salmon (*Oncorhynchus* spp.). These culturally, ecologically, and economically significant fishes are in many places declining and management focal points. Often, managers can influence or react to ecological conditions that salmon experience, suggesting that nonlinearities, especially thresholds, may provide opportunities to inform decisions. However, nonlinear dynamics are not always invoked in management decisions involving salmon. Here, we review reported nonlinearities and thresholds in salmon ecology, describe potential applications that scientists and managers could develop to leverage nonlinear dynamics, and offer a path toward decisions that account for ecological nonlinearities and thresholds to improve salmon outcomes. It appears that nonlinear dynamics are not uncommon in salmon ecology and that many management arenas may potentially leverage them to enable more effective or efficient decisions. Indeed, decisions guided by nonlinearities and thresholds may be particularly desirable considering salmon management arenas are often characterized by limited resources and mounting ecological stressors, practical constraints, and conservation challenges. More broadly, many salmon systems are data-rich and there are an extensive range of ecological contexts in which salmon are sensitive to anthropogenic decisions. Approaches developed to leverage nonlinearities in salmon ecology may serve as examples that may inform analogous approaches in other systems and taxa.

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Pacific Salmon as Potential Beneficiaries of Management that Leverages Ecological Nonlinearities

Pacific salmon (*Oncorhynchus* spp.) are important, yet imperiled species. Salmon migrate between rivers and oceans, sustaining aquatic and terrestrial ecosystems and providing people with food, identity, place-based culture, and livelihoods (Schindler et al. 2003). Many human activities jeopardize salmon and their ecosystems. Salmon populations, particularly in their native southern range (e.g., CA, ID, OR, WA), are threatened by stressors including habitat destruction and degradation, migration barriers, overharvest, and competition with artificial conspecifics (Nehlsen et al. 1991). Many populations are listed under the U.S. Endangered Species Act (ESA) and Canada Species at Risk Act and are the focus of recovery efforts.

Salmon management is challenging. Many activities stressful to salmon are otherwise beneficial to society and conservation resources are finite. Management actions that aim to benefit salmon are therefore constrained. Salmon life history entails interactions with many habitat types, species, and geographies where natural and anthropogenic drivers affect their performance (e.g., growth, survival; Quinn 2018). Consequently, one management approach is to determine cases where these drivers are stressful and alleviate them. As management actions are typically constrained, it may be particularly useful to appreciate ecological nonlinearities and thresholds—points where incremental changes in drivers provoke substantial ecological responses (Groffman et al. 2006; Fig. 1)—to apply small management adjustments that greatly benefit salmon.

Concepts and potential applications of thresholds and nonlinearities have been discussed broadly in the realms of ecology, fisheries, and conservation (Samhouri et al. 2010, Travis et al. 2014), and they may be particularly informative for salmon. To summarize, the literature argues that ecological relationships are often nonlinear, nonlinear relationships can have clear thresholds, and that identifying the location of these thresholds can guide the selection of reference points that make decisions more efficient (e.g., benefits per unit effort), effective (e.g., highest allowable

stress regardless of economic cost), or prepared (e.g., conditions under which resources are no longer reliable). Scientists are increasingly capable of understanding nonlinearities in salmon ecology. Salmon were listed under the ESA beginning three decades ago (Waples 1991) and have received considerable research and monitoring attention. Time series describing salmon performance and ecological conditions are becoming longer, and novel tools (e.g., remote sensing, environmental DNA) are broadening research questions. As agencies strive for ecosystem-based management, their monitoring has expanded to report on many species and environmental components that interact with salmon. Additionally, we now have many analytical tools to more precisely distill trends from complex datasets and describe the shape of nonlinear relationships. With richer data and increasingly powerful analytical capabilities, we are poised to detect ecological nonlinearities and apply them in salmon management.

While nonlinearities underpin much of ecological theory and some research suggests that these relationships may enhance decisions involving salmon (Levi et al. 2012, Martin et al. 2017, Connors et al. 2020), nonlinearities are not widely used to inform salmon management. This is unfortunate because appreciating nonlinearities may enhance harvest and recovery efforts, especially considering trade-offs, competing human activities, costs, and resources that constrain management. Additionally, life cycles of salmon compared with many other fisheries resources are short (≈2–5 yr), suggesting that people may realize benefits of some enhanced decisions on short time scales. Here, we review nonlinearities and thresholds reported in salmon ecology, describe potential for applications that scientists and managers could develop to leverage nonlinear dynamics, and offer a path toward decisions that account for nonlinearities to improve outcomes. We do not attempt a comprehensive review because the salmon ecology literature is vast and, as we suggest below, is not always explicit about nonlinear relationships. Instead, we drew from a diversity of studies, management arenas, and perspectives that overlap with our expertise, which led to an apparent generality: Appreciating nonlinearities and thresholds in salmon ecology may in many scenarios inform
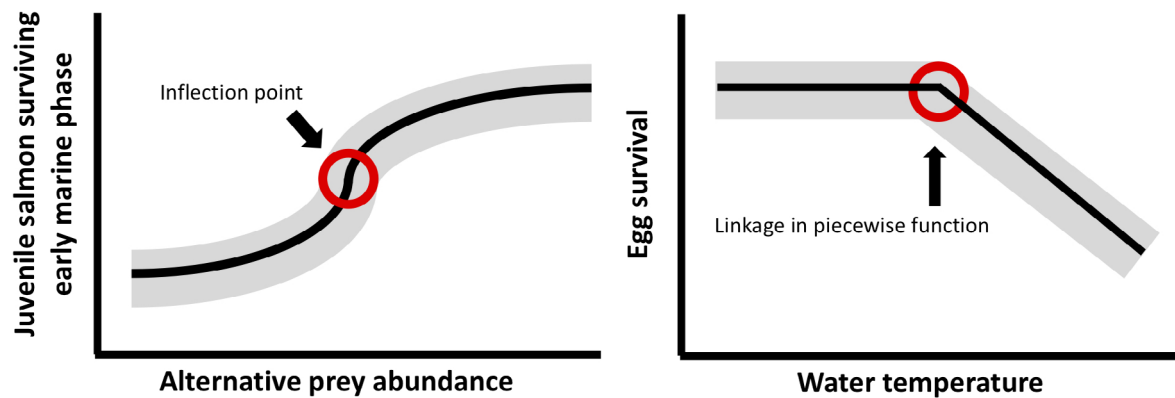
Fig. 1. Hypothetical examples of nonlinear ecological relationships (lines), their uncertainty (shading), and potential reference points (circles). Left panel alternative prey in the ocean buffer juvenile salmon from predation (sensu Wells et al. 2017). A predator prefers to feed on alternative prey that inhabit areas offshore where salmon are uncommon. If alternative prey are above abundance thresholds, predators will forage increasingly offshore and feed on salmon less. Right panel egg survival decreases when water temperature exceeds a threshold (sensu Martin et al. 2017).

more efficient or effective decisions involving salmon.

ECOLOGICAL NONLINEARITIES AND THRESHOLDS AS MANAGEMENT TOOLS

Nonlinearities are ubiquitous ecological features that may be leveraged by natural resource management. Nonlinearities underpin fundamental phenomena such as effects of temperature and consumption on growth (Brett 1971), prey abundance on predation rates (Holling 1965), and population density on population growth (Ricker 1954). Some nonlinearities are characterized by thresholds. Threshold definitions include linkages in piecewise functions (e.g., toxicological no observed effect levels), inflection points in sigmoidal or curved functions, or points where slopes of response-driver relationships change fastest (Kroes et al. 2005, Samhouri et al. 2010). Nonlinearities are often management-relevant, including harvests that maximize sustainable yield (Punt and Smith 2001), nutrient levels that lakes tolerate before turning turbid (Schindler 1974), toxicant levels that species tolerate without succumbing (Kroes et al. 2005), population loss that ecosystems tolerate without transitioning states (Estes and Palmisano 1974), or diminishing returns in conservation efforts (Wu and Boggess 1999, Wu and

Skelton-Groth 2002). Nonlinearities and thresholds may therefore suggest targets or strategies whereby management actions may be disproportionately beneficial (Box 1).

Nonlinearities suggest at least two opportunities to inform natural resource management. First, thresholds may describe points where anthropogenic or biophysical drivers cause disproportionate responses in ecological states (Samhouri et al. 2011). For example, seabird productivity decreases markedly when availability of their forage fish prey falls below abundance thresholds (Cury et al. 2011). Management seeking to harvest fish while minimally impacting seabirds may thus attempt to maintain fish abundances above thresholds. To avoid crossing

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Box 1

Nonlinearity: a relationship between an ecological response and driver that does not follow a straight line.

Threshold: a type of nonlinearity characterized by an incremental change in a driver causing an abrupt change in response.

Reference points: places along response–driver relationships relevant to stakeholders.

Decision trigger: levels of a driver that, when crossed, automatically prompt management actions.

undesirable thresholds, managers may define decision triggers (Link 2005), or specified management actions that they automatically enact when certain ecological conditions are present (Fig. 2). This promotes actions planned in advance, guides decisions via empirical evidence, and increases transparency (Cook et al. 2016). Defining triggers in advance may also avoid delays and stalemates from policymaking and reduce uncertainty for stakeholders (e.g., fishers, tourists). This can increase producer and consumer confidence and incentivize stakeholders to preempt threats before triggering thresholds. Due to these advantages, decision triggers are beneficial in establishing automatic fiscal policies that dampen business cycles and mitigate recession damages (Boushey et al. 2019) and in enacting regulations that stabilize financial institutions and markets during financial crises (McDonald 2013).

Second, nonlinearities may inform resource allocation among alternative conservation investments. Under limited resources, pursuing one investment precludes undertaking others and the

challenge becomes allocating resources effectively. Assuming a linear relationship between conservation investments and benefits implies constant marginal benefits (Wilson et al. 2009). If a set of independent candidate investments exhibited constant returns to marginal benefits, the cost-effective solution is to allocate all resources to the investment with highest marginal benefit. However, ecological nonlinearities imply that marginal benefits vary across their domains. Allocating conservation investments cost effectively in nonlinear systems then requires consideration of whether investments require a minimum investment before they elicit benefits or if further investments become ineffective (Fig. 3; Wu and Skelton-Groth 2002, Wu et al. 2003).

POTENTIAL MANAGEMENT APPLICATIONS OF LEVERAGING NONLINEARITIES IN SALMON ECOLOGY

Salmon research has documented many instances where response–driver relationships are nonlinear, suggesting nonlinearities in salmon ecology are not uncommon (Fig. 4, Table 1). This section describes nonlinear relationships in salmon ecology that suggest potential for management decisions to leverage nonlinearities to improve salmon outcomes. In many instances, it appears that scientists and managers could develop reference points grounded in these nonlinear relationships to help achieve management goals. In other instances, there appear to be nonlinearities underlying complex systems that suggest a more complete understanding of a managed system could eventually inform such decisions.

Fig. 2. Hypothetical example of a management decision triggered by conditions exceeding thresholds. Here, salmon benefits are linked to flow according to a threshold relationship and water is diverted to support human activities. Under baseline flow conditions, salmon benefits are high, but stressful conditions (e.g., drought; black arrows) exacerbated by diversion drop flows below the threshold, resulting in marked declines in salmon benefits. Managers plan a water pumping moratorium when flows fall below the upper limit of a confidence interval quantifying the threshold location. Alternatively, managers may set a more conservative trigger considering risk tolerance.

Water regulation

Many watersheds are modified by dams, reservoirs, and water diversions that impose flow and temperature regimes and create traumatic environments. In these regulated systems, management options include adjusting flows, sourcing water releases from reservoir thermoclines to adjust downstream temperatures, and spilling water over dams rather than through turbines. These actions may provide appropriate flows and temperatures for spawning adults, eggs, and juveniles and allow outmigrating juveniles
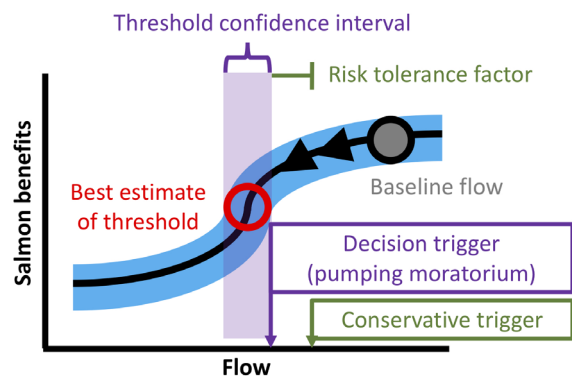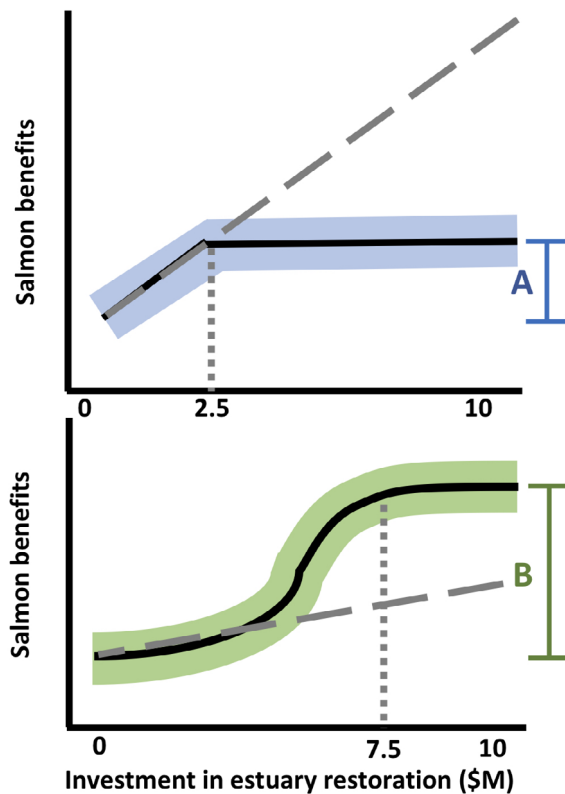
Fig. 3. Hypothetical scenario where appreciating thresholds leads to efficient resource allocation. Managers can invest $10M on water leases (top) or estuary restoration (bottom). Curved, solid lines show true threshold relationships. Straight dashed lines show erroneous linear relationships assumed by extrapolating from smaller investments. Knowledge of thresholds indicates that the optimum allocation is $2.5M in water leases and $7.5M in estuary restoration (vertical lines). This leads to achieving salmon benefits A plus B. Assuming constant marginal benefits suggests an inefficient recommendation: invest all $10M in water leases because salmon benefits per investment is higher (i.e., its linear relationship is steeper). This achieves salmon benefits A but forgoes B.
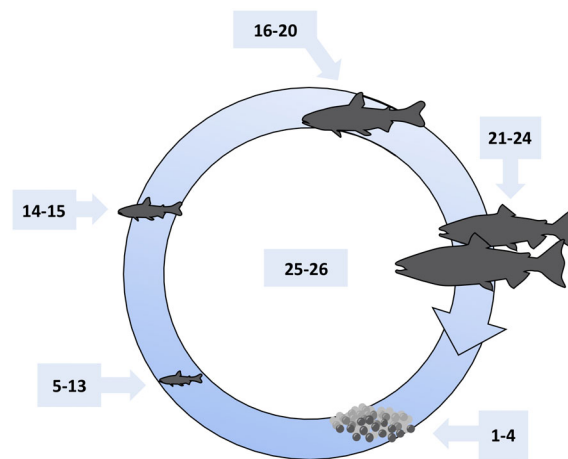
Fig. 4. Examples of ecological nonlinearities and thresholds that influence salmon dynamics across their life cycle (25 and 26 occur across life cycles). Numbers refer to studies in Table 1.

to avoid swimming through harmful dam machinery.

Flow can provoke nonlinear responses in salmon. For example, a flow threshold tips the Eel River (CA) from a state dominated by toxic cyanobacteria to habitats that support salmon (Power et al. 2015). In the Central Valley (CA), juvenile habitat occupancy falls precipitously when flows fall below thresholds (Munsch et al. 2020) and smolt-to-adult survival increases nonlinearly, with increasing returns, with flow (Michel 2019). In addition, threshold flow levels inundate floodplains, resulting in lateral expansion of rearing habitats. For example, the Yolo Bypass (CA) floods at a flow threshold determined by the elevation of the weir at the head of the bypass and salmon that can access this floodplain benefit from enhanced feeding and growth (Sommer et al. 2001). On the edges of the Columbia River plume, piscivorous seabirds aggregate when the plume exceeds threshold sizes of 1500–4000 km^2 (Phillips et al. 2018). Researchers hypothesize that the birds inhabit these boundary areas because they attract forage fish prey, suggesting plumes exceeding threshold sizes protect outmigrating salmon within the plume. Additionally, high levels of flow in the Klamath River scour fine sediments and remove parasitic *Cyratomyxa shasta* (Fujiwara et al. 2011). However, also at higher levels of flow, the physical forces of water surpass thresholds of gravel bed scour, inducing floods that can destroy salmon redds (May et al. 2009). Water regulation in some cases may thus provoke nonlinear responses in salmon ecology via flow.

Salmon also respond nonlinearly to temperature. In the Central Valley, salmon embryo survival falls precipitously when, under typical flow conditions,

Table 1. Examples of nonlinear and threshold salmon ecology.

Reference	Findings	Studies
1	Embryo mortality increases when water temperature exceeds threshold	Martin et al. (2017)
2	Egg mortality, but also subsidy of salmon eggs to stream consumers, increases nonlinearly when increasing densities of spawners compete for nesting space or purposefully superimpose nests	McNeil (1964), Essington et al. (1998), Moore et al. (2008)
3	Egg mortality increases when fine sediment proportions exceed thresholds	Tappel and Bjornn (1983), Chapman (1988), Jensen et al. (2009)
4	High flows scour egg nests	WRIA 8 Technical Committee (2007), May et al. (2009)
5	Juvenile mortality increases when water temperature exceeds threshold	Baker et al. (1995)
6	Juvenile territory sizes increase when prey availability decreases below thresholds	Dill et al. (1981)
7	Juvenile habitat occupancy decreases when flow decreases below threshold	S. H. Munsch et al., *unpublished manuscript*
8	Smolt-to-adult survival increases nonlinearly, with increasing returns, with flow	Michel (2019)
9	Low exploitation rates on predators substantially increases juvenile salmon survival	Beamesderfer et al. (1996)
10	River transitions from ecosystem favoring salmon to ecosystem favoring bacteria following chronic low flows	Power et al. (2015)
11	Floodplains benefit juveniles, provided inundation by threshold flows	Sommer et al. (2001)
12	Reaction distances of salmon to prey decrease when light and turbidity thresholds are exceeded	Hansen et al. (2013)
13	Juvenile growth rates plateau when zooplankton saturate salmon	Edmundson and Mazumder (2001)
14	Salmon harmed when contaminant concentrations exceed thresholds	Meador et al. (2002)
15	Foraging performance of juveniles declines with increasing conspecific densities, but only in systems below threshold levels of historical wetlands	David et al. (2016)
16	Smolt survival decreases nonlinearly when alternative prey for common predator are less abundant	Emmett and Sampson (2007)
17	Avian predators aggregate on the edge of a river plume when plume size exceeds threshold, potentially reducing spatial overlap with smolts	Phillips et al. (2018)
18	Seabirds prey on salmon when alternative prey availability decreases below thresholds	Wells et al. (2017)
19	Survival increases nonlinearly with increasing availability of copepod prey	Peterson et al. (2006)
20	Subadult body condition decreases when contribution of krill in diet falls below threshold	Wells et al. (2012)
21	Proportion of adult salmon killed by bears decreases nonlinearly with increasing salmon abundance	Quinn et al. (2017)
22	Salmon fishery forecasts overpredict returns when poor ocean conditions during salmons' final year at sea exceed thresholds	Satterthwaite et al. (2020)
23	Pre-spawn mortality increases when temperature exceeds threshold	Bowerman et al. (2018)
24	Migration rate to spawning grounds declines when river velocity exceeds threshold	Martin et al. (2015)
25	Salmon growth is governed by nonlinear functions of feeding and temperature	Brett (1971)
26	Simulated portfolio performance of salmon stocks decrease when the number of salmon populations decreases below a threshold	Moore et al. (2010)

temperatures exceed 12°C (Martin et al. 2017). Other nonlinear temperature responses include survival of seaward-migrating juveniles declining rapidly when water temperatures exceed 20°C (Baker et al. 1995) and pre-spawn mortality rising rapidly when temperatures exceed ≈18°C (Bowerman et al. 2018). Fundamentally, growth is governed nonlinearly by temperature because salmon metabolisms are faster in warmer waters, increasing food assimilation capabilities but also maintenance costs (Brett 1971). Thus for some actions (e.g., improving rearing conditions), optimal temperatures depend on local feeding opportunities (Cooke and Suski 2008). Temperature is therefore another factor through which water regulation may provoke nonlinear responses in salmon.

Nonlinearities may also guide decisions to spill water at hydroelectric power dams. Juveniles experience greater survival when they swim through spillways rather than turbines (Haeseker et al. 2012). However, excessive spilling can supersaturate water with nitrogen and cause gas bubble trauma (Beiningen and Ebel 1970). Salmon survival can decrease when total dissolved gas surpasses thresholds allowed under state laws (Brosnan et al. 2016, Elder et al. 2016). A total dissolved gas threshold lethal to salmon is widely acknowledged, but there is uncertainty in its exact levels and in the levels of spill that would be most beneficial to survival. Relationships among spill, flow, and salmon survival across life stages are complicated; however, thresholds such as mortality responses to total dissolved gas suggest that a more complete understanding of regulated systems may eventually inform management.

An example of managers leveraging their knowledge of thresholds to target improved salmon outcomes via flow regulation occurs in the Sacramento River. ESA-endangered Sacramento River winter run Chinook salmon spawn during California's warm, dry summers but dams prevent the population from reaching historical, spring-fed spawning grounds at higher, cooler elevations. By appreciating in situ temperature thresholds across flow levels (Martin et al. 2017) and selectively releasing cold water from deeper reservoir elevations (Danner et al. 2012), managers attempt to maintain appropriate temperatures on spawning grounds.

Habitat restoration and conservation

Restoration and conservation can rehabilitate habitats impacted by destruction, degradation, and fragmentation, which are major stressors that have led to salmon declines (Nehlsen et al. 1991). There are many facets to protecting and repairing habitats, and habitat improvement efforts typically aim to facilitate functional rearing habitats for juveniles in fresh, estuarine, and nearshore marine waters and spawning habitat in fresh water. Considerable resources have been invested in restoring salmon habitat. Especially over the past three decades, people have also invested in monitoring salmon responses to restoration at the watershed scale (Bennett et al. 2016). These coupled restoration and monitoring programs conducted at the watershed scale reflect the need and capability (Bouwes et al. 2016) of researchers to achieve an ecosystem-level understanding of restoration benefits to salmon. In addition, researchers have tracked and assembled meta-data (e.g., location, type) describing several thousand restoration actions across the Pacific Northwest (Katz et al. 2007). We may expect such programs to shed light on potential threshold responses of salmon to restoration, especially at scales relevant to management (e.g., populations, evolutionarily significant units).

Geomorphology.—Salmon habitat capacity in watersheds is governed by nonlinear relationships with its physical attributes. Landscape, geomorphic, and hydrologic thresholds determine the stream network and associated stream channel types and patterns that are the foundation for riverine aquatic habitats. Seven primary controlling variables including stream channel slope, stream discharge, valley confinement, sediment supply, sediment caliber, bank strength, and wood loading help to determine a stream network (Beechie and Imaki 2014). Abrupt spatial changes to these controlling variables in a stream network result in rapid transitions in channel pattern. These effects act in a nonlinear fashion and are thresholds for spatial pattern change (Schumm 1973, Church 2002, Wohl 2017). Transitions in the hierarchical controls of stream channel morphology such as valley confinement and slope form a spatial threshold that determines how the inputs of water, sediment, wood and energy determine stream channel characteristics. Thus alluvial channel patterns are prone to occur where river networks transition from relatively confined steeper valleys to less confined, lower gradient sections due to changes in stream power (Schumm 1973). These nonlinear changes also change the potential types, amount, and overall spatial distribution of aquatic habitats, providing additional habitat capacity across salmon life stages (Beechie et al. 1994, Cluer and Thorne 2014). Additional inputs such as wood can also result in threshold effects that change non-alluvial reaches to alluvial reaches (Montgomery et al. 1996).

People may alter some physical attributes of watersheds to markedly change salmon habitat capacity. Alterations to mutable variables

including stream channel geomorphic features such as stream channel slope, stream discharge, channel confinement, sediment supply, bank strength, and wood loading can result in a change in aquatic habitat condition or quantity (Nilsson et al. 2005, Anlauf et al. 2011, Wohl 2019). Habitat loss occurs through alteration of channel slope and confinement in the form of stream channel levees, dredging, and removal of obstructions such as wood, boulders, and beaver dams (Naiman et al. 1988, Roni et al. 2002, Wohl 2005). This can have pronounced effects on the amount and quality of aquatic habitats that are needed for various salmonid life stages (Beechie et al. 1994, Pollock et al. 2004). These impacts result in legacy effects that lead to a simplified riverine landscapes for decades to centuries (Bartz et al. 2015, Wohl 2019). These alterations can be restored to a better condition than what exists if basic principles are implemented with respect to river management and restoration. First, there is a need to identify the ecological and physical processes that maintain and create riverine landscapes and flows (Beechie et al. 2010, Whipple and Viers 2019). Second, understanding and modeling restoration alternatives that take such processes into account, at the appropriate temporal and spatial scale is critical. Lastly, evaluating alternatives and associated metrics that allow resource managers to understand the potential integrated impacts and benefits of their actions can result in better riverine planning and management (Beechie et al. 2010, Whipple and Viers 2019).

Scaling.—Habitat function is mediated by spatial scaling—the emergence of ecological properties with increasing system size. For example, the stability of water temperatures and flows, and thus appropriate environments for salmon, increases sharply with increasing catchment size (Moore et al. 2015). Similarly, fish mortality during drought can rise precipitously in systems below threshold sizes (White et al. 2016). More generally, salmon exploit habitat heterogeneity (e.g., temperature, prey availability; Armstrong et al. 2010), a system-level trait that emerges in large, intact systems. Growth in particular can shift from positive to negative with a gradual increase in temperature (Brett 1971) and salmon can employ fine-scale, adaptive feeding strategies given their metabolic requirements (e.g.,

Rosenfeld et al. 2020), but this requires adequate distributions of food and temperature resources underpinned by habitat complexity at larger scales. Thus, broad-scale habitat simplification may reach thresholds beyond which conditions at the system level more readily transition between desirable and undesirable states. We may therefore expect relationships between salmon outcomes and restoration or conservation scale to be nonlinear. Indeed, ecologists advocate for restoration efforts to match the spatial scale of fish activities (e.g., foraging behavior, spawning) and large-scale habitat restorations are typically required to restore self-sustaining ecosystem functions (Beechie et al. 2010). Watershed-level evaluations of salmon responses to habitat restoration are rare, but ecologists have documented that large-scale restoration to reconnect floodplains increases juvenile productivity (Ogston et al. 2014).

One challenge in restoration is that it is logistically simpler to design and implement massive (and thus expensive) restoration projects on large rivers. However, due to the geometry of river networks, where the length of channel by stream order increases geometrically with decreasing size, the investment of a fixed restoration budget on fewer large (expensive) projects has a dramatically reduced spatial footprint than when many small projects on lower order streams are implemented instead. Due to the ability to change channel state (sensu Cluer and Thorne 2014) in lower order streams, the marginal return on restoration is dramatically higher. Thus, there is a trade-off in managing many small vs. a few large projects, which raises the question of whether there is a most efficient project size, especially considering, as discussed above, that we may expect biologically relevant responses to emerge at scale or if smaller vs. larger projects are likely to disproportionately rehabilitate habitats for certain species or associated life history types.

Connectivity.—Connectivity is another habitat attribute governed by nonlinearities. In the watershed, connectivity falls precipitously with increasing numbers of movement barriers (McKay et al. 2013). Habitats also become inaccessible when currents exceed thresholds determined by fish size (Beamish 1978). In coastal ecosystems, fish performance (e.g., abundance,

mortality) falls rapidly when habitat fragmentation exceeds thresholds (Boström et al. 2011). These thresholds in coastal systems are evident in biogenic habitats including eelgrass that provide prey and predator refuge for juvenile salmon (Semmens 2008).

There are many threats to connectivity that habitat improvements may address. Threats to connectivity include dams, constricted areas that create high flows (e.g., narrowly breached dikes), submerged infrastructure (Moore et al. 2013), and overwater structures that shade nearshore migratory corridors (Munsch et al. 2014), which can be mitigated by removing dams, planning wider dike breaches, minimizing submerged infrastructure, or incorporating light penetrating materials into overwater structures (Cordell et al. 2017, Munsch et al. 2017). In the case of serial dam removal, it is important to appreciate that connectivity may not markedly improve until the number of semi-passable dams in a watershed falls below threshold numbers (McKay et al. 2013). Plans to benefit salmon via restoring habitat connectivity may therefore be more effective if they consider nonlinearities governing habitat connectivity.

Density dependence.—Density dependence, manifestation of limiting habitat attributes as populations approach carrying capacities, is another nonlinearity often overlooked in recovery efforts. Competition is pervasive in salmon ecology and can limit populations. For example, per capita reproductive success can fall as populations increase because adults superimpose their nests on top of their competitors' (Essington et al. 1998). In another example, foraging performance of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) declined with increasing population density, but only in estuaries that had lost >50% of their wetlands, suggesting restoration may be most beneficial in systems degraded beyond thresholds (David et al. 2016). Importantly, current carrying capacities, and therefore density-dependent population growth, may also reflect degraded habitat states. This is relevant for imperiled populations where depressed abundances may experience density-dependent limitations due to diminished carrying capacities (Achord et al. 2003). Notably, density dependence may also trigger beneficial thresholds, depending on management goals. For example,

growth opportunity for resident salmon increases sharply when spawning salmon densities exceed thresholds and superimpose nests, releasing consumable eggs into the stream (Moore et al. 2008).

Density-dependent competition for food can also interact with nonlinear bioenergetics. As discussed above, salmon can grow faster in warmer waters provided adequate food, but will grow slower or lose mass when food is scarce (Brett 1971). Consequently, salmon densities can tip the relationship between temperature and growth from negative to positive when competition is greater (Crozier et al. 2010).

Appreciating density dependence may therefore suggest how to prioritize management actions. For example, curtailing harvest may be more effective in recovering populations that are less limited by competition, and restoring habitat may be more effective in recovering populations constrained by competition. Likewise, life-stage-specific density dependence will dictate where habitat restoration will have the most immediate benefits (Greene and Beechie 2004).

Life history diversity.—A corollary to restoration and conservation is population and life history diversity. In functional, heterogeneous watersheds, salmon evolve locally adapted, reproductively isolated populations, and diverse life histories. Their ecological experiences and outcomes vary asynchronously, imparting stability and protracted availability of composite stocks (Greene et al. 2010, Schindler et al. 2010).

However, habitat degradation and homogenization and artificial propagation threaten salmon biodiversity and associated portfolio benefits (Moore et al. 2010, Carlson and Satterthwaite 2011). Indeed, simulations suggest that portfolio benefits decrease markedly when salmon population numbers fall below thresholds (Moore et al. 2010). Similarly, a diversity of salmon phenologies maintained by heterogeneous, intact landscapes may often be more important than prey abundance in determining overall prey availability to predators (e.g., charismatic megafauna). This occurs because salmon can saturate their predators on short time scales, but predators can prolong feeding seasons by foraging across the landscape over time, provided that different salmon populations are present at different times (Armstrong et al. 2020). Thus,

conserving threshold levels of population diversity may contribute to maintaining stock stability.

Toxics.—Exposure to toxic chemicals, and the degradation of aquatic ecosystems through chemical pollution, is a modern reality for salmon across many systems (Scholz and McIntyre 2015). Relating salmon health to toxic chemical exposure is challenged by limited data and complex interactions, and often requires modeling to link the exposure to adverse health outcomes. Often, assessment tools consider health effects from exposure to toxics in a dose–response relationship. This relationship may be linear, implying a continuous response proportional to dose, or described using a complex biological or ecological based model that includes nonlinear relationships. Threshold concentrations of toxics are commonly extrapolated to estimate acceptable levels of risk. For example, aquatic life criteria in surface waters are established by the U.S. EPA to reflect the collective scientific knowledge of single chemical impacts on the mortality, growth, and reproduction of aquatic species. These values establish chemical determinants of water quality. An extension of this includes threshold criteria based on reductions in predator avoidance behavior (i.e., survival) from contaminant-mediated changes in fish olfaction (namely metals and pesticides; Hecht et al. 2007, Tierney et al. 2010). Tissue and sediment thresholds that are protective for aquatic species have also been established. For example, thresholds for tissue concentrations in fish species, including salmonids, have been estimated for PCBs and DDTs (Meador et al. 2002, Beckvar et al. 2005, Berninger and Tillitt 2019) based on reported effects of growth, reproduction, and immune impairment. Together, data from surface waters, sediments, and tissue may be used to consider contaminant levels across the ecological system and how these compounds may be impacting salmon.

To protect salmon ecosystems from chemical pollution, potential management considerations extend beyond applying thresholds for known chemicals of concern. Established thresholds can serve as a guide to estimate acceptable levels of risk but should be applied with caution. Water quality standards and tissue thresholds are lacking for nearly all chemicals of emerging concern, including pharmaceuticals and personal care products. Similarly, threshold determination is complicated by the complexity of the chemical mixture. Mixed exposures may magnify the level of toxicity and thereby question the level of protection based on the analysis of a single compound (Laetz et al. 2009). In addition, salmonid life history and life-stage determine chemical exposure and toxicity. For example, juvenile Chinook salmon rear in streams for up to two years before outmigrating (Quinn 2018). Extended residency may increase their likelihood of consuming contaminated prey such as small invertebrates, which are an established exposure route for multiple contaminants. Conversely, prey may be limited due to pollutants disrupting the food web, thereby compromising prey availability during a phase when growth is critical (Macneale et al. 2014, Goertler et al. 2015). Lastly, during outmigration through multiple habitats and jurisdictions, juvenile Chinook salmon may repeatedly exceed the aquatic life criteria threshold for individual compounds and increase exposure likelihood to unmonitored contaminants. In all, a screening-level evaluation with consideration specific to salmon life history and life-stage would help define chemical exposures and health impacts to make decisions beneficial to salmon populations. Moving forward, these evaluations may prioritize new scientific assessments to reduce resource management uncertainty regarding habitat quality, salmon health, and pollution.

Fine sediment.—Salmon eggs diffuse gasses between their membranes and the environment and egg mortality occurs when fine sediment levels in water exceed thresholds (Jensen et al. 2009). Fine sediments can be released via practices such as logging and building roads, suggesting that regulating to avoid these sediment loads may be especially beneficial to salmon.

Stream evolution.—Streams nonlinearly evolve across states that determine their ecology (Cluer and Thorne 2014). These states include stages of anastomosing, sinuous single thread, channelized, degradation, degradation and widening, aggradation and widening, quasi equilibrium, and laterally active streams, which vary widely in their hydrogeomorphic attributes (e.g., longitudinal and planform complexity, hyporheic connectivity) and habitat and ecosystem benefits (e.g., temperature amelioration, drought refugia).

Because people may constrain or enable these states by introducing or restoring disturbances (e.g., channelization, alteration of flow, and sediment regimes), conservation and restoration plans may consider explicitly targeting stream conditions under which streams can achieve greater habitat function for salmon.

Fisheries

A goal of fisheries management is to maximize long-term yield, subject to conservation constraints and needs to protect co-occurring weaker stocks. Typically, harvest regulations attempt to achieve spawning escapement corresponding to estimates of maximum sustainable yield, given the forecasted pre-fishing abundance and exploitation rates expected under proposed regulations (PFMC 2016).

Thresholds may inform salmon fisheries by improving abundance forecasts or incorporating forecast uncertainty. Success of environmental covariates in improving forecast performance has been mixed, sometimes outperformed by models without environmental covariates, and often with changes through time in the specific environmental covariates best explaining productivity (Haeseker et al. 2005, Winship et al. 2015). However, in most cases, environmental covariates have been considered using linear models only and forecast models rarely consider nonlinear model forms that may provide more accurate predictions (Rupp et al. 2012). Additionally, some forecasts are based on the assumption that returns will be proportional to jack (i.e., individuals one year younger than dominant returning age class) returns in the previous year. These forecasts risk-marked inaccuracies if nonlinear ecosystem dynamics, such as poor ocean conditions, reduce survival in the final year at sea (sensu Satterthwaite et al. 2020).

In addition, harvest may mediate nonlinear ecological trade-offs and small adjustments to harvest may provoke substantially more desirable outcomes. For example, increasing escapement from low to medium levels may substantially increase grizzly bear density—a proxy for ecosystem function—while in some cases also increasing fisheries yields (Levi et al. 2012) and policies resulting in small reductions (−20%) to mixed stock harvest may greatly increase equitable access to salmon resources

(+84%) and virtually eliminate the risk of weak stock extirpation (Connors et al. 2020).

Hatcheries

Many populations are supplemented by artificial propagation in attempts to enhance harvest and promote recovery. Among the decisions that hatcheries make are where to release fish and how many fish to release. A key challenge in hatchery operations is to bolster overall salmon abundances, especially without impairing naturally spawned counterparts.

Thresholds may guide decisions about hatchery release procedures. In some systems, salmon smolts are transported downstream to avoid harmful watershed conditions. However, artificial transportation decreases homing to natal streams because juveniles minimally imprint on local cues en route to sea (Keefer and Caudill 2014). Whether transportation will ultimately improve salmon fitness can depend on ocean conditions, salmon origin (hatchery vs. natural), and migration timing (Gosselin et al. 2018), suggesting that managers could decide to transport fish when these conditions exceed thresholds that favor the fitness of transported salmon over volitionally migrating salmon. For instance, managers transport more hatchery fish to sea during droughts (Sturrock et al. 2019). Decisions based on costs and benefits of this approach could be made more objectively and transparently by quantifying relationships between salmon survival and flow or temperatures and transporting fish when monetary and biological costs of transportation are exceeded by their benefits.

Additionally, hatcheries may account for density-dependent effects of hatchery fish on wild populations. Hatchery and wild fish share common resources, and when these resources are limiting, increasing abundances of hatchery fish can diminish survival or body condition in wild fish (Levin et al. 2001, Cline et al. 2019). Thus, there may be threshold levels of hatchery fish above which competition with wild fish is unacceptable.

Indirect management of ecological processes

An ecosystem-based perspective can reveal important interactions that determine salmon outcomes. For example, juvenile salmon survival

can decline when abundances of other small fish fall below thresholds because their common predator switches to feeding on salmon (Emmett and Sampson 2007, Wells et al. 2017). In another example, body condition declines rapidly when contribution of certain prey to diets fall below threshold levels (Wells et al. 2012). In addition, predation pressure on salmon can decrease markedly with small amounts of fishing that target large individuals of predators (Beamesderfer et al. 1996). This can occur because removing larger predators disproportionately reduces predators with threshold gape sizes large enough to consume salmon and high metabolic needs.

Managers may leverage these indirect processes to enhance salmon outcomes. For example, fisheries regulation may promote abundances of species that buffer salmon from predators or reduce abundances of key predators that disproportionately reduce salmon survival.

MOVING TOWARD SALMON MANAGEMENT INFORMED BY NONLINEARITIES

Ecological nonlinearities are one piece of information among many that scientists and managers can leverage to improve decision-making (Fig. 3). Nonlinearities potentially exacerbate the risk of doing nothing or acting in a cautious or uninformed manner if status quos assuming linearity lead to wasted opportunities or ecological surprises. That is not to say that nonlinearities will simplify decision-making. Even when nonlinearities are well-established, managers must make decisions on a case-by-case basis. For example, managers may employ more or less conservative approaches (Fig. 2) depending on system-specific parameters and constraints. Complicating matters, migratory salmon cross many management jurisdictions, potentially requiring management entities to coordinate to leverage thresholds. Given this reality, in most situations nonlinearities will inform salmon management alongside other considerations. A key benefit is that compared with social, cultural, and political considerations, threshold effects on salmon populations provide objective reference points on which to center discussion. To that end, this section highlights concepts that may increase the future utility of ecological nonlinearities in salmon management.

Bolstering the research that informs management

One step toward leveraging nonlinearities in salmon management is to use existing knowledge to expand our understanding of nonlinearities in salmon ecology. Currently, available data, including previously published studies, can be used to explore salmon outcomes in relation to ecological conditions (Table 2). For example, emergent approaches such as satellite photo analyses allow us to quantify habitat conditions at vast scales commensurate with spatial extents of managed stocks, which we can compare to stock-level metrics of salmon performance (Hall et al. 2018). In addition, oceanographic models of the North Pacific are proving skillful in explaining and predicting variation in survival and recruitment of marine fishes (Tolimieri et al. 2018), and could be similarly aligned to different

Table 2. Examples of pre-existing data that may be used to detect ecological thresholds in salmon.

Data	Source	Availability
Spawner counts	GrandTab	https://wildlife.ca.gov/Conservation/Fishes/Chinook-Salmon/Anadromous-Assessment
	SPS	https://inport.nmfs.noaa.gov/inport/item/17904
Juvenile counts	Delta Juvenile Fish Monitoring Program	https://www.fws.gov/lodi/juvenile_fish_monitoring_program/jfmp_index.htm
Smolt traps	Various	Various
Offshore trawls	NOAA juvenile salmon and ocean ecosystem surveys	https://www.fisheries.noaa.gov/inport/item/18502
Water flow, water temperature, snowpack	USGS	waterdata.usgs.gov
Annual ecosystem indicators	California Current Integrated Ecosystem Assessment	https://www.integratedecosystemassessment.noaa.gov/regions/california-current-region/index.html
Salmon habitat status and trends	NMFS	https://www.nwfsc.noaa.gov/research/datatech/data/salmon_habitat_status/index.cfm

stages of salmon life histories to explain nonlinear responses to conditions in the ocean environment. Researchers recently developed generalizable protocols to detect nonlinear relationships and ecological thresholds that are conducive to exploratory analyses using existing data (Large et al. 2013, Samhouri et al. 2017). This broad-scale, correlative approach may reveal trends that can later be investigated more incisively and mechanistically to quantify nonlinear relationships that can inform stakeholder development of reference or trigger points.

A common challenge in establishing threshold or nonlinear relationships, especially as decision support tools, may be that the supporting data must be conducive to quantifying robust patterns. For example, analyses must be able to detect accurate, precise reference points (e.g., inflections, breaks) in the locations of nonlinearities and we may expect observations that arise from some nonlinear relationships to appear as outliers, especially in limited data (e.g., short time series), and/or when thresholds occur at rarely encountered environmental extremes. A logical approach to address this may be for researchers to begin with a hypothesis or conceptual model of a nonlinear relationship that is supported by exploratory, opportunistic, or correlative studies as well as fundamental, prior knowledge (e.g., "warm water is harmful to salmon eggs and the relationship between egg mortality and temperature is known to be nonlinear based on experimental evidence"), then develop mechanistic relationships or refine monitoring programs to more precisely assess evidence supporting the hypothesis in the field (e.g., "drawing from fundamental approaches in biophysics, we can model a threshold relating salmon egg survival to temperature and flow and test whether this relationship predicts egg survival in situ"; sensu Martin et al. 2017). Overall, quantifying nonlinear relationships intended to inform decisions may require careful attention to design appropriate studies or monitoring efforts, and long time series adequate to cover the full range of environmental conditions.

Additionally, our understanding of nonlinearities in salmon ecology would be enhanced if researchers routinely examine for nonlinear trends alongside conventional linear approaches and report evidence for and against nonlinearities.

Furthermore, past analyses plausibly used conventional linear analyses when nonlinear analyses may more accurately describe relationships and suggest nonlinear dynamics (e.g., water temperature vs. juvenile survival in the Sacramento River; Kjelson et al. 1982). Overall, we may currently underappreciate nonlinearities in salmon ecology (sensu Hunsicker et al. 2016), suggesting that salmon research with an eye toward nonlinearities may uncover additional opportunities to leverage nonlinearities in management contexts.

Translating knowledge of nonlinearities and thresholds into the complex, multifaceted world of salmon management

Nonlinearities and thresholds may be particularly informative to managers if they can be applied in multivariate, lifecycle contexts (Fig. 4). Many anthropogenic (e.g., fishing) and natural (e.g., competition) drivers impact salmon across their life stages to determine population-level responses (e.g., cohort survival, cohort size). Furthermore, compensatory actions by salmon in later life experiences can mitigate effects of harsh conditions in early life experiences (Al-Chokhachy et al. 2019). Thus, lifecycle analyses that account for these multiple factors and their sequences can more accurately describe the impact of a stressor in the greater context of population-level responses (McHugh et al. 2017). One approach that ecologists may use to develop reference points is to generate ecological indicators and corresponding salmon response surfaces (i.e., expected performance described in multidimensional space) for life stages of lifecycle models. Following efforts in other systems (Large et al. 2015), ecologists may quantify relationships between salmon performance and a tractable number (e.g., 2) of salient indicators to develop surfaces that show critical points at which small changes in a single or multiple driver(s) provoke major responses in salmon. For example, embryo survival could respond nonlinearly to temperature and linearly or nonlinearly to flow (Martin et al. 2017), or the adults returning to spawn may respond nonlinearly to ocean conditions and fishing season length. Such approaches are visualizable in bivariate figures (Large et al. 2015) and the multivariate perspective could align threshold-based recommendations with

ecosystem-based approaches that integrate multiple determinants of ecosystem states to quantify management reference points (Link 2005). Additionally, researchers may incorporate nonlinearities into ecosystem models to evaluate management strategies. Overall, realistic applications of thresholds to inform management will involve researchers and managers appreciating the multidimensional and cumulative nature of experiences acting on salmon performance.

Scientists and managers must work together to develop system-specific approaches. Defining ecosystem indicators and associated control rules, targets, and risk tolerances specific to managed systems presents challenges, albeit not new ones (Link 2005). A major part of overcoming this challenge is to promote a two-way flow of information between researchers and practitioners to appreciate the parameters and constraints of conservation problems, which are often unique to particular salmon populations and associated ecosystems. This approach will facilitate research designs and products that produce actionable science (Enquist et al. 2017). Part of these discussions must address uncertainty. Uncertainty can manifest as prediction uncertainty, parameter uncertainty, model uncertainty, measurement uncertainty, natural stochastic variation, inadequate communication among scientists, outcome uncertainty, and unclear management objectives (Steel et al. 2009, Link et al. 2012). It is especially important to assess confidence in the shape of nonlinearities and thresholds because they describe points where small changes provoke large responses. Working together to avoid these pitfalls, scientists and managers may then weigh the importance of nonlinearities among other criteria in decisions aiming to enhance salmon outcomes.

Moving toward implementing nonlinearities in protocols and planning

Knowledge of nonlinearities may enhance current management arenas. In fisheries management, forecasts of the expected abundance of adults returning to spawn (and also the target of fisheries) help determine annual harvest levels (PFMC 2016). Given recent work demonstrating that bias in these forecasts can change abruptly in relation to environmental thresholds (Satterthwaite et al. 2020), there may be scenarios where

state and federal managers choose precautionary harvest allocations suggested by effects of environmental conditions on forecast reliability. Because stronger stocks often co-occur with weaker stocks, managers would also need to consider appropriate risk aversion in setting fisheries rules in mixed stock fisheries.

Another arena is plans to protect salmon under the ESA. Under the ESA process for listed salmon populations, Biological Opinions can specify trigger criteria (e.g., water quality, habitat integrity) whereby managers declare jeopardy and must revise current actions if they fail to avoid harmful thresholds as planned. Quantitative, empirical identification of ecological thresholds for salmon may bolster confidence in these trigger criteria. Ecological thresholds may also be considered in phases of the National Environmental Policy Act process. For example, Environmental Impact Statements could include alternative objectives to release fish from harmful thresholds (e.g., habitat connectivity limited by dams; McKay et al. 2013). These consultations may also explicitly consider efficient allocation of resources in their alternatives (sensu Wu et al. 2003). For example, managers may pool resources contributed by many mitigation projects into "habitat banks" (NOAA 2016) that scale restoration efforts above threshold levels necessary to benefit salmon populations. Considering that stressors vary widely in complexity (e.g., localized stressors vs. basin-wide habitat function), a practical route at present may be to develop a quantitative understanding of tractable threshold scenarios to serve as reference points in ESA documents.

Conclusion

Human activities increasingly press managers to facilitate desirable outcomes for myriad stakeholders. In addition to current issues, many challenges loom, including watershed development with increasing human populations, warming watersheds forced by climate change (Crozier et al. 2019), water scarcity in California with increasing drought risk (Diffenbaugh et al. 2015), increasing abundances of federally protected salmon predators (Chasco et al. 2017), and co-managing endangered Southern Resident killer whales alongside imperiled salmon that they prey upon (Chasco et al. 2017). However, our

understanding of salmon and their ecosystems has advanced rapidly in the past few decades and current knowledge suggests that salmon ecology is often governed by nonlinearities and thresholds. Additionally, many datasets, especially concerning annual, population-level metrics, are maturing that may allow researchers to uncover additional management-relevant nonlinearities. Despite contrary evidence, the status quo is to by default conceptualize ecological relationships as linear (Hunsicker et al. 2016). However, our increasingly rich understanding of salmon ecology should allow people to more confidently discern nonlinear relationships and quantify reference points that reflect nonlinearities. This enhanced ecological understanding may enable greater conviction in management decisions based on nonlinear dynamics. Indeed, many nonlinearities understood at present implicate opportunities where managers, scientists, and stakeholders may focus on developing targets or strategies to increase salmon benefits despite constraints or allocate resources efficiently. Furthermore, approaches to benefit salmon may also contribute to ecosystem-based goals, for instance by feeding salmon predators or fertilizing nutrient-poor watersheds via spawned salmon remains. Enabling management frameworks that appreciate and leverage ecological nonlinearities and thresholds, alongside other management tools, may promote sustainable relationships between people, salmon, and ecosystems that salmon support.

Acknowledgments

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