CONSERVATION

Shifting habitat mosaics and fish production across river basins

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Watersheds are complex mosaics of habitats whose conditions vary across space and time as landscape features filter overriding climate forcing, yet the extent to which the reliability of ecosystem services depends on these dynamics remains unknown. We quantified how shifting habitat mosaics are expressed across a range of spatial scales within a large, free-flowing river, and how they stabilize the production of Pacific salmon that support valuable fisheries. The strontium isotope records of ear stones (otoliths) show that the relative productivity of locations across the river network, as both natal- and juvenile-rearing habitat, varies widely among years and that this variability is expressed across a broad range of spatial scales, ultimately stabilizing the interannual production of fish at the scale of the entire basin.

The generation and maintenance of biological complexity over ecological and evolutionary time scales ultimately depend on processes that generate habitat heterogeneity across landscapes (*1*). Such heterogeneity is produced from interactions between local geomorphic features (e.g., topography) and environmental forcing (e.g., regional climate). Habitat can be described as a mosaic of environmental conditions arranged across landscapes but, importantly, the spatial configuration of habitat patches shifts through time as prevailing environmental conditions interact with geomorphology, successional processes, and the biological responses of locally adapted populations (*2*–*4*). This concept—the shifting habitat mosaic—has been empirically tested at small scales (*5*, *6*), but how these dynamics play out across a range of spatial scales has never been quantified, specifically in terms of how they influence the reliability of ecosystem services.

The argument to conserve biodiversity often focuses on ecosystem stability and how biologically diverse communities tend to spread the risk of collapse or poor performance (*7*–*9*). Less common, however, is to consider the continuum of spatial and temporal scales dictating the processes that generate ecosystem heterogeneity, its hierarchical structure, and thus, resilience. The concept of shifting habitat mosaics integrates how different dimensions of ecological diversity (e.g., habitat variation, locally adapted populations, and variable life histories) interact to contribute to resilience as ecosystems respond to a heterogeneous and ever-changing environment over a continuum of spatial and temporal scales. The persistence of biological communities at short (*5*, *6*) and long (*10*) time scales is ultimately linked to whether organisms have the ability to exploit shifting mosaics of environmental conditions in space and time. Thus, understanding how shifting habitat mosaics influence the reliability of ecosystem services is crucial, especially in the current era of rapid industrial and urban growth threatening biodiversity worldwide (*11*).

We quantified how shifting habitat mosaics influence the reliability of Chinook and sockeye salmon fisheries at the mouth of the Nushagak River flowing into Bristol Bay, Alaska by reconstructing production and migratory patterns of

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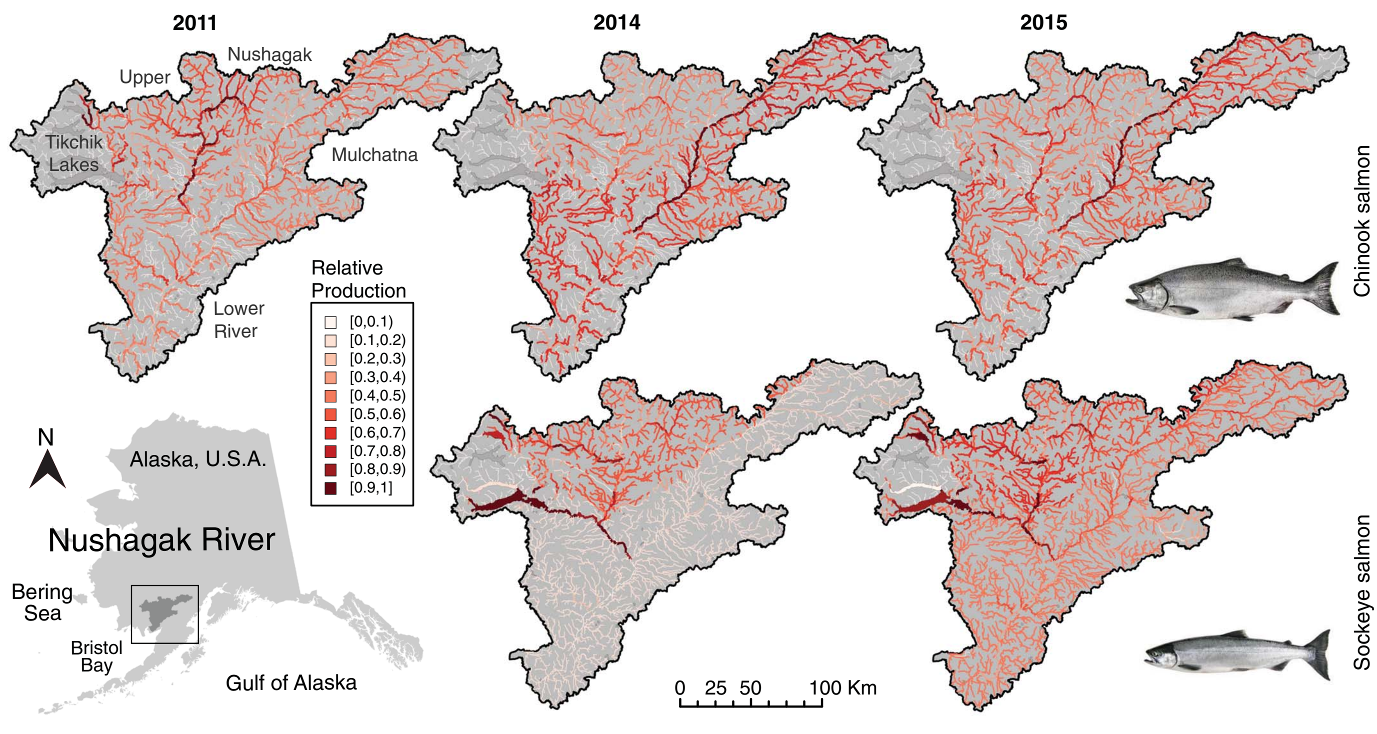

Fig. 1. Productive habitats for salmon shift across river basins. Areas of high Chinook salmon production in 2011 shifted from the upper Nushagak River to the Mulchatna River in 2014 and 2015. Sockeye salmon production was concentrated in Tikchik lakes in 2014 but was more evenly distributed in 2015 including across riverine habitats.

these species using strontium isotopic ($^{87}Sr/^{86}Sr$) variation across this watershed. Natal origins and movement patterns of juveniles were inferred from profiles of $^{87}Sr/^{86}Sr$ ratios recorded in otoliths of each species (*12*). Production and habitat-use patterns were reconstructed by calculating the most likely geographic locations of 1377 returning adult salmon (>250 fish per species per year) at each snapshot in time recorded by the otolith during each fish's juvenile freshwater residence (*12*). To do so, we quantified conditional probabilities of $^{87}Sr/^{86}Sr$ ratios, geomorphic habitat preferences, prior locations, and directional movements (*12*). Because otoliths grow proportionately with the length of fish, we could infer how habitat mosaics contribute to the total growth of fish before entering the ocean (*12*). By analyzing otoliths collected from individuals captured at the river's coastal terminus during annual returns in 2011, 2014, and 2015, our analysis spanned spatial scales ranging from the entire basin to individual streams (stream orders 3 to 9), and temporal scales including interannual variability in returns, the age structure of each year, and the months to years of habitat use during freshwater residence. This breadth of spatial and temporal scales provides a test of how shifting habitat mosaics influence fish-production patterns in free-flowing rivers.

The Nushagak River (35,000 km^2) flows into Bristol Bay, which is distinctive in the region for its vast riverine habitats in addition to large lakes. It is remote, pristine, and defined by substantial landscape heterogeneity. Physiographically, the basin is composed of four regions: the Tikchik lakes and the upper Nushagak, Mulchatna, and lower rivers. These are geologically and geomorphically distinct, generating variations in $^{87}Sr/^{86}Sr$ ratios, temperature, precipitation, and hydrology. Variation in how this landscape heterogeneity filters overriding climatic conditions generates a mosaic of habitats that contribute to the production of salmon. Furthermore, precise natal homing of adult salmon leads to a hierarchical, locally adapted population structure. Because $^{87}Sr/^{86}Sr$ ratios vary widely across the basin (fig. S1) and are temporally stable (*12*), the Nushagak River provides an ideal system in which to test how shifting habitat mosaics influence landscape patterns of fish production.

Chinook and sockeye salmon exhibited heterogeneous production patterns across the basin during each return year, and patches of high and low production shifted between years (Fig. 1). Regions of high Chinook salmon production in 2011 were in the upper Nushagak River in the northwest portion of the watershed. These shifted eastward to the Mulchatna River in 2014 and 2015. Similarly, the production of sockeye salmon shifted from being concentrated in the Tikchik lakes in 2014 to being more evenly distributed across both lake and riverine habitats in 2015. Spatial production patterns of both species also differed among the contributing age classes within return years (Fig. 2 and fig. S2). In 2014 and 2015, the production of freshwater age 0 sockeye salmon (salmon that spent <1 year in fresh water, i.e., "sea-/river-type" sockeye) primarily originated from riverine habitats compared with those fish that spent at least 1 year in fresh water, which are typically associated with lake habitats (i.e., "lake-type" sockeye salmon) (Fig. 2).

Juvenile Chinook and sockeye salmon also exhibited a variety of habitat-use strategies among return years to achieve growth in fresh water before migrating to the ocean (Fig. 3, A and E). For Chinook salmon, these different strategies resulted in patchy spatial patterns of juvenile growth, which shifted interannually (Fig. 3, I to K). In some return years, the distribution of total growth across the riverscape differed markedly from the natal production pattern that same year. For example, production of Chinook salmon in 2011 was concentrated in the upper Nushagak River (Fig. 1); the spatial pattern of total freshwater growth, however, was more evenly distributed with the Mulchatna River (Fig. 3I). The amount of growth achieved in the lower river was also much higher in 2014 relative to other years (Fig. 3, I to K).

We also quantified how individuals and populations differentially used the lower river as rearing habitat for accumulating growth as well as a migratory corridor to the ocean (*12*) (movie S1). Depending on the return year, between 8 and 20% of Chinook and sea-/river-type sockeye salmon exhibited forays in the lower river (e.g., Fig. 3, A to C), where they achieved between 10 and

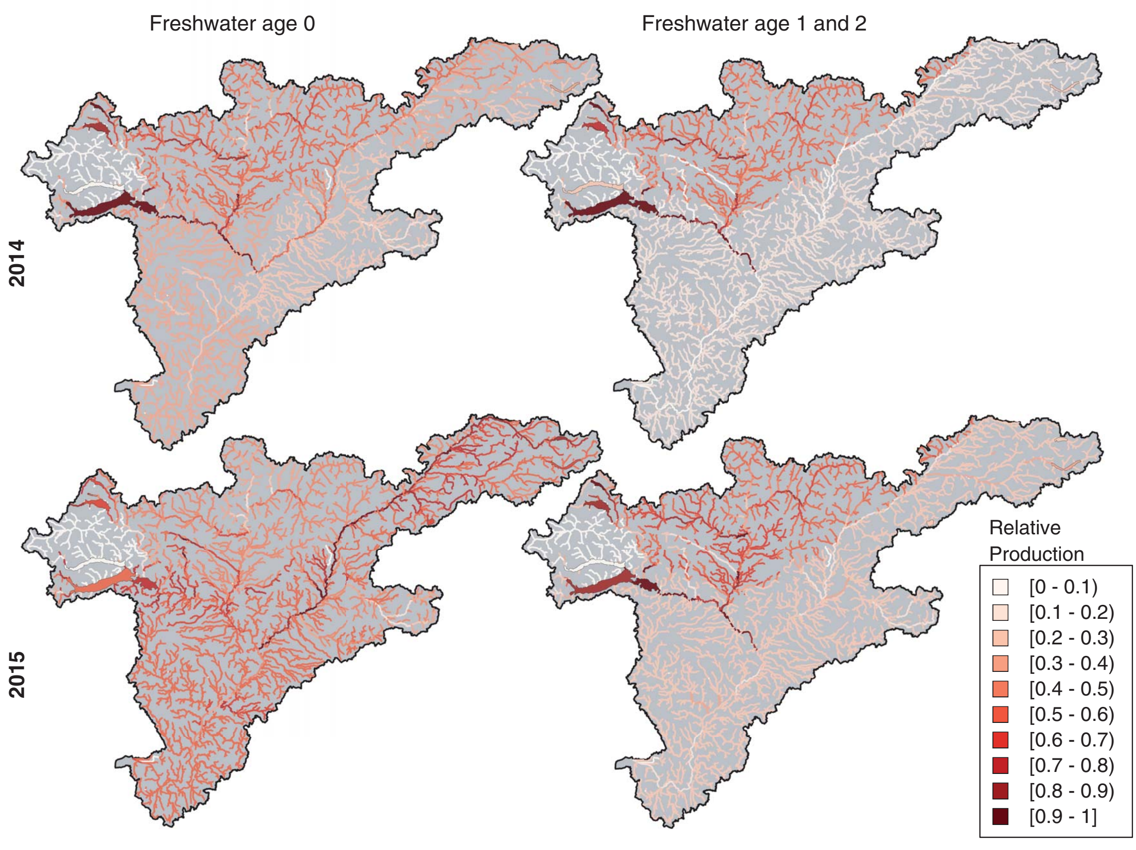

Fig. 2. Habitat and life history diversity interact to shape spatial production patterns. In 2014 and 2015, there was relatively high production of freshwater age 0 fish from riverine habitats.

50% of their total body mass before migrating to the ocean (Fig. 3, D and H). Furthermore, the infrequent use of the lower river by lake-type sockeye salmon (Fig. 3, D and H) illustrates how the strategy of using the lower river was not species specific, but rather was more related to the general life history of locally adapted salmon populations.

Interannual variability in the production of salmon from the Nushagak River ecosystem was maintained across the spatial hierarchy of the river network, indicating that a range of spatial scales contributes to variance dampening of salmon resources observed at the river basin scale (Fig. 4, A and B). For both species, we observed variance dampening from fine through aggregated spatial scales (stream orders 3 to 9). Deviations of these observations from a simulation of independent population dynamics (*12*) (Fig. 4, A and B) indicated that production dynamics are not random across the basin. Both species exhibited such deviations at intermediate stream orders, suggesting a strong interaction between the environment (Fig. 4, C to E) and large-scale habitat features that produced independent dynamics among their populations.

Habitat conditions conducive for survival and growth of salmon throughout the Nushagak basin likely vary as a function of how local geomorphic features filter prevailing environmental forcing. This heterogeneity enables the opportunity for juveniles to find suitable growth conditions among the array of habitat options that mosaics provide. Similarly, fisheries in Nushagak Bay benefit from favorable conditions persisting somewhere in the basin for at least one of the age classes exhibiting a particular habitat-use strategy. Freshwater habitats are linked to marine survival not only through the body size achieved by juvenile fish, but also through variation in the timing of their entry to the ocean and whether they meet favorable conditions (*13*, *14*). Correspondence among the spatial scales of environmental variation and shifts in production (Fig. 4, C to E) suggests that environmental heterogeneity plays an important role in shaping how growth and production of salmon vary among locations through time.

Our results demonstrate how multiple dimensions of biocomplexity operating across a continuum of nested spatial and temporal scales integrate to stabilize salmon production and fisheries at the scale of the Nushagak River watershed. Furthermore, we show that shifting habitat mosaics play out at large and intermediate scales in addition to the well-documented cases on small spatial scales for providing resiliency to ecosystem services.

Ultimately, entire landscapes are involved in stabilizing biological production. For conservation, and management more broadly, this makes it difficult to prioritize some habitats over others and emphasizes the critical role of evaluating multiple landscape-use scenarios in the face of increasingly uncertain futures (*15*). For the restoration of affected areas, it emphasizes the need to coordinate efforts across large spatial

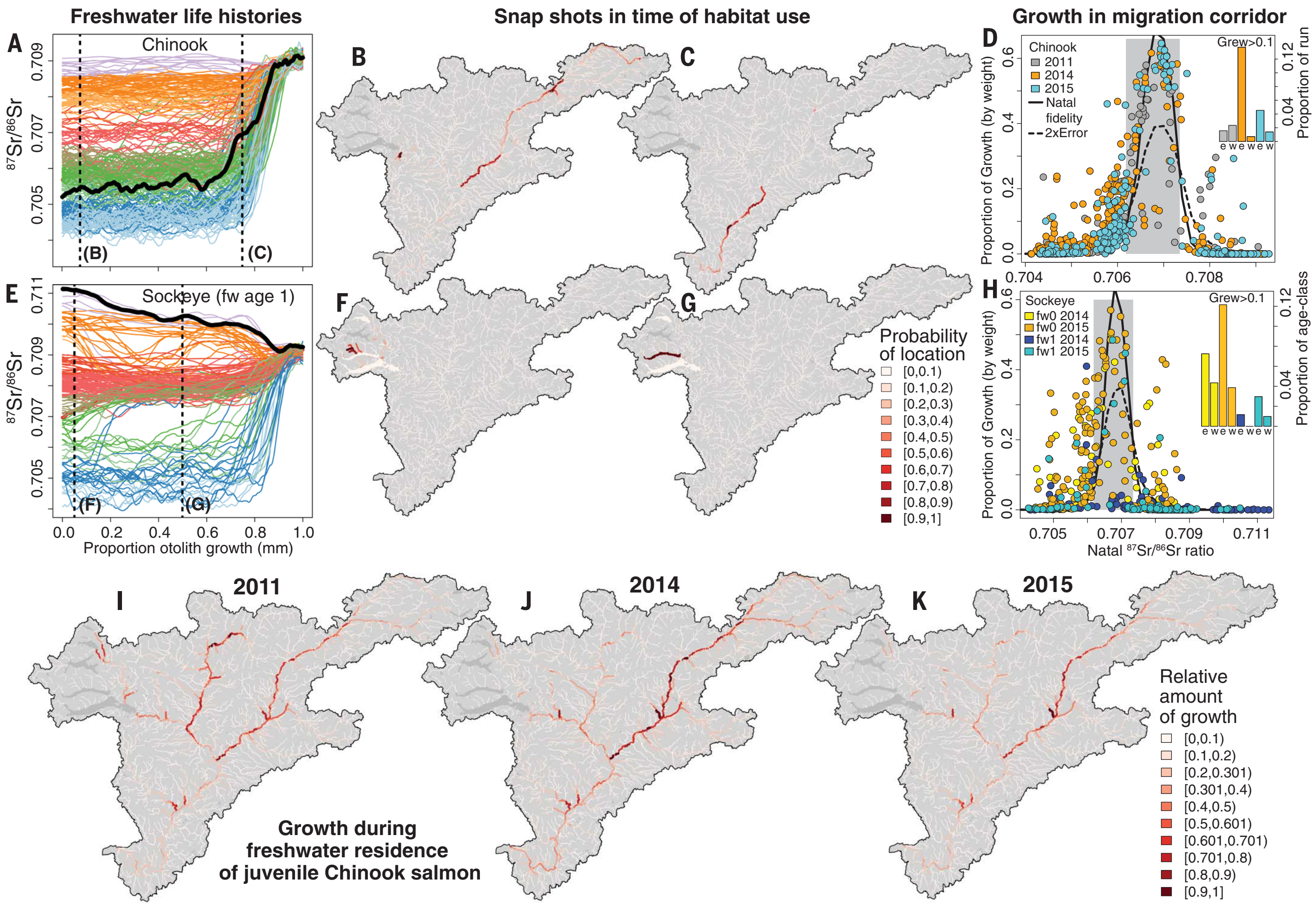

Fig. 3. Diverse freshwater life histories, use of migration corridors, and shifting patterns of growth. Freshwater life histories (**A** to **C** and **E** to **G**) and the amount of growth achieved in the lower river migration corridor of Chinook (**D**) and sockeye (**H**) salmon of the Nushagak River differed among return years ("e" and "w" correspond to fish originating from the eastern or western parts of the basin, respectively). Fish that plot above the black lines and outside of the gray box grew substantially in the lower river but originated elsewhere. Snapshots of habitat use (B and C, F and G) of individual fish [bold lines in (A) and (E)] correspond to positions in the otolith indicated by vertical dotted lines in (A) and (E). Isotope profiles [(A) and (E)] are color coded on the basis of each fish's natal ^{87}Sr/^{86}Sr ratio. (**I** to **K**) Spatial patterns showing how the total amount of freshwater growth (body mass) achieved by juvenile Chinook salmon was distributed across the basin and shifted among return years.

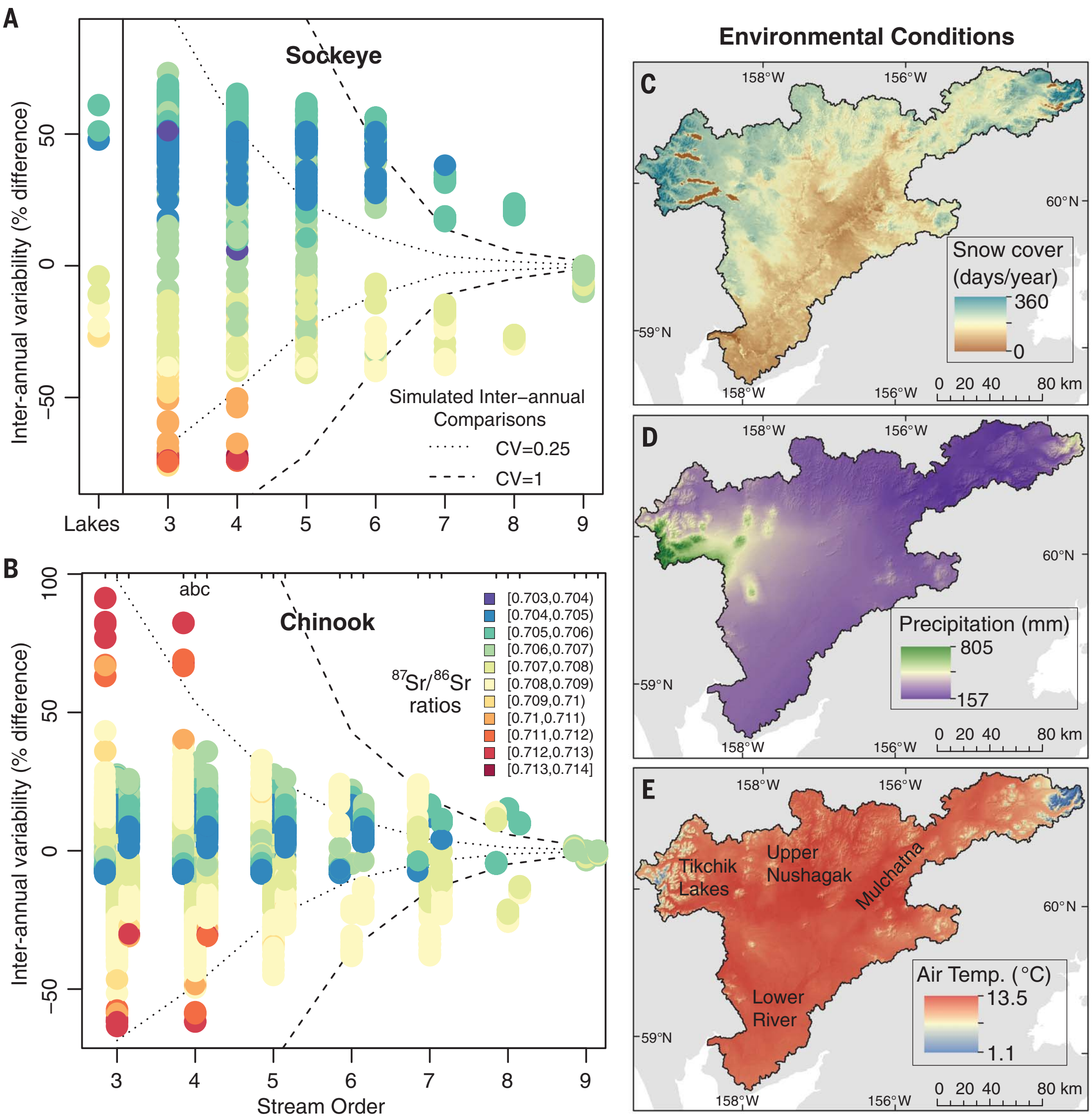

Fig. 4. Shifting habitat mosaics damp variance in production across nested spatial scales. Each spatial scale (stream orders 3 to 9) contributed to the reliability of Nushagak River salmon production. (**A**) Percentage difference in sockeye salmon production of each stream reach among return years aggregated by stream order. (**B**) Comparisons among Chinook salmon return years (a: 2014 versus 2011; b: 2015 versus 2011; and c: 2015 versus 2014). Dotted lines represent simulations in which each unique stream reach is an individual population with independent production dynamics. (**C** to **E**) Multiscale variability in environmental conditions: mean snow cover (days/year from 2011 to 2016) (C), decadal mean summertime precipitation amount (millimeters from 2000 to 2009) (D), and air temperature (°C from 2000 to 2009) (E).

scales and to avoid independent small-scale projects (e.g., tributary by tributary) (*16*, *17*). Such approaches are unlikely to restore a system's resiliency to the levels that we observe across intact landscapes and riverscapes.

Shifting habitat mosaics are a central feature of what makes ecosystems resilient. Because patterns of high and low production, or conditions most suitable for growth, shift among locations through time, the biological performance of a landscape tends to be more reliable at aggregate spatial scales (*1*, *8*). This means that conservation of the processes that generate and maintain heterogeneity and connectivity across landscapes (e.g., fires, floods, and migration) is as important as the biological communities that they support (*10*).

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SUPPLEMENTARY MATERIALS

science.sciencemag.org/content/364/6442/783/suppl/DC1
Materials and Methods
Figs. S1 to S5
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A portfolio of habitats

To conserve species, we must conserve their habitat. This concept is well known, but the reality is much more complex than simply conserving a particular area. Habitats are dynamic and vary across both space and time. Such variation can help to facilitate long-term persistence of species by allowing local movement in search of the best conditions. Brennan *et al.* clearly demonstrate the benefit of the habitat mosaic to Pacific salmon by characterizing how both climate and population productivity vary over time and space in an Alaskan river system.

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