

Population diversity and the portfolio effect in an exploited species

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One of the most pervasive themes in ecology is that biological diversity stabilizes ecosystem processes and the services they provide to society^{1–4}, a concept that has become a common argument for biodiversity conservation⁵. Species-rich communities are thought to produce more temporally stable ecosystem services because of the complementary or independent dynamics among species that perform similar ecosystem functions⁶. Such variance dampening within communities is referred to as a portfolio effect⁷ and is analogous to the effects of asset diversity on the stability of financial portfolios⁸. In ecology, these arguments have focused on the effects of species diversity on ecosystem stability but have not considered the importance of biologically relevant diversity within individual species⁹. Current rates of population extirpation are probably at least three orders of magnitude higher than species extinction rates¹⁰, so there is a pressing need to clarify how population and life history diversity affect the performance of individual species in providing important ecosystem services. Here we use five decades of data from *Oncorhynchus nerka* (sockeye salmon) in Bristol Bay, Alaska, to provide the first quantification of portfolio effects that derive from population and life history diversity in an important and heavily exploited species. Variability in annual Bristol Bay salmon returns is 2.2 times lower than it would be if the system consisted of a single homogenous population rather than the several hundred discrete populations it currently consists of. Furthermore, if it were a single homogeneous population, such increased variability would lead to ten times more frequent fisheries closures. Portfolio effects are also evident in watershed food webs, where they stabilize and extend predator access to salmon resources. Our results demonstrate the critical importance of maintaining population diversity for stabilizing ecosystem services and securing the economies and livelihoods that depend on them. The reliability of ecosystem services will erode faster than indicated by species loss alone.

The recent focus on ecosystem-based management of renewable resources emphasizes species interactions and how these are affected by human activities within exploited ecosystems. However, there is growing recognition that population diversity within exploited species can contribute to their long-term sustainability and should be incorporated more explicitly into management and conservation schemes^{11,12}. For example, it has been argued¹¹ that population diversity reduced the temporal variability of sockeye salmon fisheries in Bristol Bay because of complementary dynamics in different components of the stock complex. Similar phenomena are now appreciated qualitatively in other marine ecosystems¹². However, at present there are neither quantitative estimates of the strength of portfolio effects produced by population and life history diversity in exploited species, nor an objective assessment of the benefits of population diversity to human economies and ecosystem services in general.

From 1950 to 2008, sockeye salmon supported the most valuable fisheries in the United States (landed value, US\$7,900,000,000), and 63% of the associated revenue came from Bristol Bay (see Supplementary Information for details). The total economic value of this fishery is considerably higher when considering the retail, cultural and recreational value of these fish. Income from sockeye salmon in Bristol Bay is the major source of personal income for most Bristol Bay communities, and landing taxes provide the major funding for local school districts. Thus, the interannual reliability of this fishery has critical and direct consequences for the livelihoods of people in this region.

Population diversity within the stock complex of Bristol Bay sockeye substantially reduces the interannual variability experienced by the commercial fishery, which intercepts sockeye salmon as they enter each of the nine major rivers of this region (Fig. 1a). Each river stock contains tens to hundreds of locally adapted populations distributed among tributaries and lakes (Fig. 1b and Supplementary Fig. 1). This remarkable diversity in sockeye reflects their ability to thrive in a wide range of habitat conditions, the reproductive isolation of populations by precise homing to natal spawning sites, and their capacity for micro-evolution¹³. Thus, the Bristol Bay sockeye fishery integrates across substantial population diversity both within and among watersheds.

Annual sockeye returns to the Bristol Bay stock complex were considerably less variable (coefficient of variation (standard deviation divided by mean), CV = 55%) than those observed for individual rivers (average CV = 77%; Fig. 1c) for 1962–2008. Annual returns to individual populations spawning in streams of the Wood River system, where long-term detailed population assessments are available (Fig. 1b), were more variable (average CV = 95%) than both the aggregate of these streams (CV = 67%) and the total returns to the Wood River (CV = 60%; Fig. 1c). Thus, annual sockeye returns become increasingly more stable across the complexity hierarchy ranging from individual spawning populations to stocks associated with the watersheds of major rivers and, eventually, to the regional stock complex of Bristol Bay.

The degree of temporal covariation among portfolio assets controls the strength of portfolio effects^{8,14}; the buffering effects of asset diversity on variability of the aggregate portfolio become weaker as asset dynamics become more synchronous. Analysis of the covariation among river stocks and among stream populations (that is, the analogues of assets in an investment portfolio) showed that annual sockeye returns were only weakly synchronous (and some negatively correlated) both within and among the watersheds of Bristol Bay. This lack of synchrony among populations of Bristol Bay sockeye occurred despite many commonalities in their migration corridors, nursery habitats and seasonal timing of migrations between freshwater and marine environments. Furthermore, strong shifts in climatic conditions

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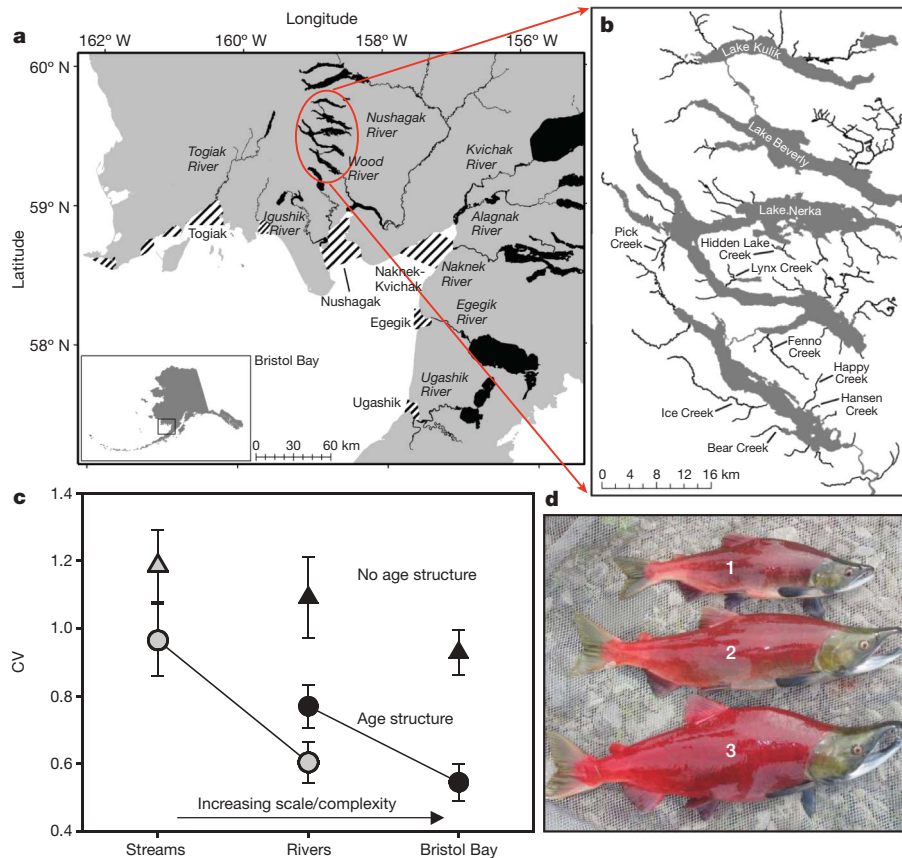


Figure 1 | Bristol Bay sockeye habitat and associated change in variability of returns at different spatial scales and levels of life history aggregation. **a**, Map of Bristol Bay, southwest Alaska. Sockeye salmon nursery lakes are shown in solid black. Fishing districts associated with major rivers are highlighted as striped areas. **b**, Map of the Wood River system showing streams supporting anadromous salmon populations. **c**, Interannual variability in total returns to sockeye populations and stocks at three spatial scales and two levels of life history aggregation. Grey symbols are for the

Wood River, highlighting the watershed for which continuous long-term data on stream populations (1962–2007, $n = 8$) exist. Black symbols are for rivers (including the Wood River, $n = 8$) and the Bristol Bay aggregate (1958–2008). Circles show average variabilities for populations and stocks with their observed age composition, and triangles show average variabilities for the dominant age classes at each spatial scale. Error bars, 1 s.e. **d**, Three age classes of reproductively mature male sockeye salmon from the Wood River that have spent one, two or three years at sea, as indicated.

of the North Pacific Ocean during the past century^{15,16} should also have induced synchrony in the population dynamics of the stock complex, but had little effect (Supplementary Fig. 2). Thus, the portfolio effects observed in Bristol Bay sockeye, both among major rivers and within individual watersheds, are derived from the weakly synchronous population dynamics among the components of this stock complex. If portfolio components in Bristol Bay fluctuated fully independently of one another, the expected CV would be only marginally lower (42% for rivers, 38% for Wood River tributary populations) than is currently observed (55% for rivers, 67% for tributary populations).

Life history diversity further buffers the variability of the sockeye stock complex. Most Bristol Bay sockeye spend one to two years rearing in fresh water and one to three years in the ocean as they complete their life cycles (Fig. 1d). This staggered age structure reduces variation in recruitment because it reduces the probability that all individuals in a cohort of siblings will encounter unfavourable environmental conditions over the course of the life cycle. To assess the effect of age structure diversity on variability, we compared the CV of total annual returns (above) with the CV observed within the two dominant age classes at each level of spatial aggregation considered earlier (Supplementary Fig. 3). The CVs of the dominant age classes in stream populations, river stocks and the Bristol Bay stock complex were respectively 44%, 42% and 69% higher than the variabilities observed at these spatial scales for the diversified population age structure (Fig. 1c). In sum, if the dynamics of Bristol Bay sockeye returns were characterized by the most simplified spatial and life history portfolio (that is, dominant age classes in the average stream population), they

would be about 2.2 times more temporally variable ($CV = 119\%$) than is currently observed for the Bristol Bay stock complex with its full complement of population and life history diversity.

To illustrate the value to commercial fisheries of population and life history diversity in Bristol Bay sockeye, we considered alternative hypothetical stocks characterized by the same long-term average return (30,000,000 fish) but with different interannual CVs. Furthermore, we assumed that fishery management would resemble the current system, in which the management goal is to allow approximately 10,000,000 fish onto the spawning grounds per year; returns in excess of 10,000,000 are harvested, and no fishing is allowed in years when fewer than 10,000,000 sockeye return. Given the current variability of the Bristol Bay stock complex, this picture translates into a complete fishery closure less than four times per century (Fig. 2). If Bristol Bay sockeye lacked the dampening effects population and life history diversity provide, complete fishery closures would occur every two to three years (Fig. 2). Thus, the net result of losing population and life history diversity could be a tenfold increase in the frequency of fishery closures, generating considerable hardship for people who rely on consistent annual returns for their livelihoods. A full assessment of the economic implications of such increased interannual variability resulting from loss of population and life history diversity would be valuable, but the necessary livelihood and economic data are lacking at present.

In addition to sustaining a valuable marine fishery, sockeye also support a diverse array of well-documented ecosystem processes and services in the watersheds where they spawn^{17,18} (Supplementary

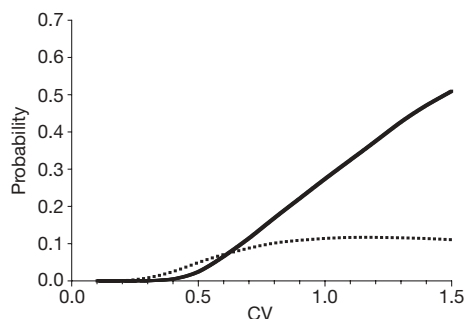


Figure 2 | Effect of interannual variability on the probability of fishery closures or capacity-swamping returns. Probability of total annual return being less than 10,000,000 (solid line) or greater than 60,000,000 (dotted line) as a function of the coefficient of variation in the overall distribution of returns. No fishing is allowed when total returns are less than about 10,000,000. Returns in excess of 60,000,000 swamp the capacity of the fishing fleet and processing industry to capture their allocation of the resource. Stock abundances were assumed to be characterized by log-normal distributions. Current Bristol Bay returns have a CV of about 0.55 and the simplest component of the stock dynamics is about 1.2.

Information). Sockeye release substantial quantities of productivity-limiting nutrients following their post-spawning death¹⁹, and are the dominant food source for a community of mobile predators and scavengers in freshwater and terrestrial ecosystems. These species perform important ecosystem functions such as dispersing salmon-derived nutrients from spawning sites to the broader landscape^{20,21}. Like commercial fisheries, many of these consumers are mobile and can capitalize on spatial variation in sockeye resources associated with the dynamics of individual populations within each river system. Using data on the number of spawning fish observed on the spawning grounds (the 'escapement'), the average CV observed for streams was 82% whereas that for their aggregate was 46% and that for the entire Wood River was 50%. Thus, consumers able to capitalize on high-density sockeye populations experience substantially less interannual variation in salmon resources than they would if they focused on individual stream populations or if population dynamics within the stock were highly synchronous.

The life history diversity observed in the seasonal timing of migration and spawning among populations further enhances many ecosystem services by extending the seasonal availability of salmon resources to the fishery and watershed food webs (Fig. 3). For example, in a typical commercial fishing season 90% of the catch is taken in about 16 days, yet the midpoints of sockeye migration to the respective fishing districts vary over a range of about 13 days (Fig. 3a). This variation in migration timing allows the fishing fleet to assess relative abundance of sockeye among districts and redirect effort to capture fish from multiple districts within a season. If seasonal migration timing were more synchronous among rivers, the window of opportunity to capture sockeye would be more constrained and the capture and processing fleet more easily saturated at the peak of the run. Seasonal access to sockeye by mobile predators is similarly extended because of staggered spawn timing among tributary and lake populations (Fig. 3b and Supplementary Fig. 3). Most sockeye populations are vulnerable to predators and scavengers in individual spawning habitats for approximately one month each year. However, salmon are present for over 2.5 months in spawning habitats throughout the Wood River watershed (Fig. 3b), owing to variation in the spawn timing among populations. Thus, watershed consumers of salmon and the ecosystem services they provide (for example trout fishing and wildlife viewing) also benefit from the variation in spawn timing, which represents one of many dimensions of life history variation in this species¹³.

Although most large-scale fisheries probably integrate across considerable intraspecific diversity in a manner similar to that described here, this 'stock structure' is usually ignored by management focused

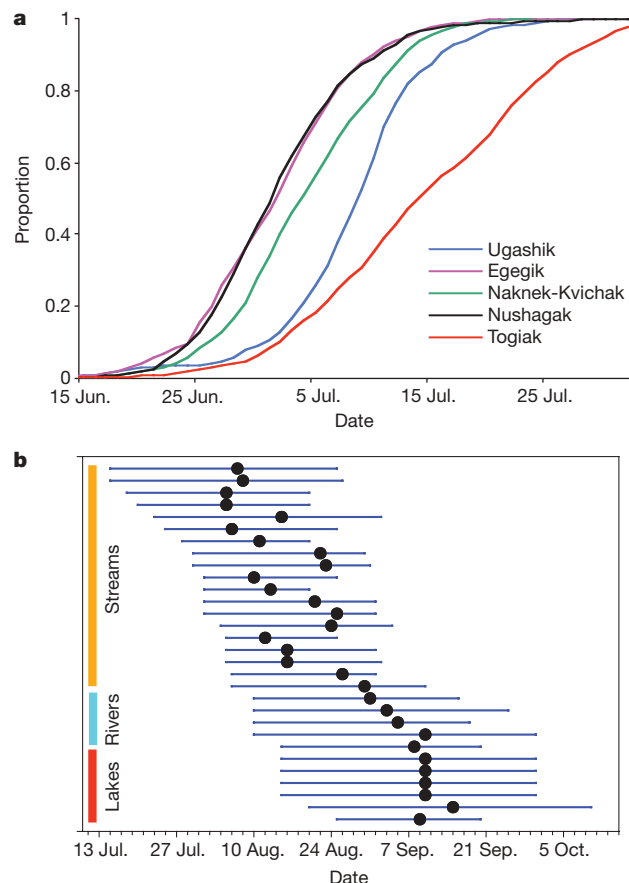


Figure 3 | Annual run timing to fishing districts and streams. **a**, Cumulative returns (catch plus escapement) to each of the major fishing districts in Bristol Bay for 2000–2007. The Bristol Bay fishery can currently process about 2,000,000 fish per day; on days with total returns above this level, the industry cannot capture their allocation of the resource. Between 1978 and 2007, the daily catch plus escapement was >2,000,000 fish on about seven days per season, on average. However, if all the fish had arrived at the fishing grounds with exactly the same timing, as determined by the distribution observed in any single fishing district in a given year, the length of the peak fishing season would have been reduced on average by 20% (range, 8–34%). **b**, Comparison of the dates of occupancy (dot, peak; line, occupancy period) in spawning habitats where sockeye salmon are available to predators and scavengers for 30 populations in the Wood River system (Supplementary Fig. 1).

on numerically dominant stock components¹². Variation in the population dynamics of Bristol Bay sockeye is easy to monitor because of spatial separation among stock components resulting from the homing tendencies within populations. However, similar population diversity, although more cryptic, may exist and be equally important in other species²², a possibility supported by the growing recognition of homing tendencies in marine and freshwater fish stocks^{23,24}. There is no reason to believe that population and life history diversity are any less important in other aquatic or terrestrial species that are focuses of exploitation or conservation.

The portfolio effects in the Bristol Bay sockeye stock complex are a characteristic of a landscape with a largely undisturbed habitat, natural hydrologic regimes and neither invasive species nor artificial propagation of salmon in hatcheries, combined with sustainable fishery exploitation. In contrast, in the southern end of their range, Pacific salmon populations have declined substantially owing to the cumulative impacts of heavy exploitation, habitat loss, climate change, hatchery dependence and hydropower development. Recent assessments show that 29% of 1,400 populations of Pacific salmon in the US Pacific Northwest and California have been extirpated since European contact²⁵. What is underappreciated is that extant stocks in highly

affected watersheds have also lost some of the stabilizing portfolio effects that we observe in Bristol Bay^{26,27}.

Although ecosystem management schemes commonly map the habitat requirements of individual species, it is rare to consider the heterogeneity and disturbance regimes that maintain population and life history diversity in ecosystems. In the case of fisheries management, minimizing the homogenizing effects of hatcheries on genetic diversity and protection of weak stocks from overharvesting in mixed stock fisheries will be required to maintain the diversity that stabilizes variance in returns. Without this broader framework for conserving the roles of individual species, the resilience biodiversity provides to ecosystems²⁸ will deteriorate well before individual species are extirpated.

METHODS SUMMARY

Annual sockeye escapements to rivers were enumerated visually from towers on each of the Bristol Bay rivers by the Alaska Department of Fish and Game²⁹. Age composition of sockeye was estimated by subsampling approximately 50,000 fish from the fisheries and the escapement towers in each year. Total returns to each river were calculated as the sum of fisheries catch and the escapement to the spawning grounds. In fishing districts that capture fish from neighbouring rivers, age composition comparisons between the fishery catch and the escapement towers was used to assign harvested fish to the total annual return to each river²⁹. Stream-spawning populations of sockeye salmon in the Wood River system were monitored by two to four people who surveyed the entire extent of habitat suitable for sockeye spawning at least once per year at the peak of spawning activity. Otoliths were sampled annually from up to 220 fish from each stream to determine the age composition of the escapement. The total stream production for eight streams was calculated by accounting for the age- and year-specific vulnerabilities to the fishery and then adding estimated fishery interceptions back to the stream-spawning populations on the basis of the stream age composition in each year³⁰. Interannual variability was calculated as the CV for all situations considered.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

Received 21 October 2009; accepted 24 March 2010.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

Acknowledgements We thank the Gordon and Betty Moore Foundation, the US National Science Foundation, the University of Washington, the Alaska salmon processing industry and the H. Mason Keeler Professorship for support for this work. N. Baron, L. Neeley and S. Sethi provided feedback and comments on the manuscript, and P. Lisi and G. Holtgrieve helped prepare the figures.

Author Contributions D.E.S. designed and coordinated the project; R.H., B.C. and L.A.R. contributed to the analyses; M.S.W. helped design the project; and all authors contributed to the writing.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of this article at www.nature.com/nature. Correspondence and requests for materials should be addressed to D.E.S. (deschind@u.washington.edu).

METHODS

River escapements were estimated by visual counts from towers located on either side of each of the Bristol Bay rivers by the Alaska Department of Fish and Game²⁹. Migrating sockeye were counted for 20 min each hour, split equally between the two sides of each river, and these figures were extrapolated into daily escapement estimates. Nine major rivers contribute to the Bristol Bay fishery. For the analyses in this paper, we have not included the populations in the Nushagak River, as these have only been enumerated for the past two decades. Ages (numbers of years in fresh water and in the ocean) of fish were determined by visual examination of scales or otoliths sampled in the escapement and in the fishery catches.

Stream-spawning populations of sockeye salmon have been monitored by the University of Washington since 1956 throughout the Wood River system. Stream surveys were conducted by two to four people who walked the entire extent of habitat suitable for sockeye spawning at least once per year at the peak of spawning activity, counting the live and dead sockeye. Otoliths were sampled annually from up to 220 fish from each stream to determine the age composition of the returns. The total stream production for eight streams was calculated by accounting for the age- and year-specific vulnerabilities to the fishery on the basis of samples collected in the fishery, and then adding estimated fishery interceptions back to the stream-spawning populations on the basis of the stream age composition in each year³⁰.

The interannual variability in total returns to Bristol Bay was compared with the variability observed in the total returns to each of the major rivers. The variability in the annual returns to each of the eight streams in the Wood River for which we had detailed age composition data, which could be used to apportion fishery catches to total annual returns, was compared to the interannual variability observed in total returns to the Wood River system as a whole. When considering services provided by sockeye in freshwater ecosystems, we assessed variability only for sockeye abundance in the spawning grounds for the eight stream populations (that is, not including fishery interceptions).

We calculated covariations among the numbers of sockeye that returned to each of the rivers or streams (Supplementary Fig. 2) as the Pearson correlation among all pairwise combinations of stocks or populations with a minimum of ten years of concurrent data. Because the time series were often positively autocorrelated, we used the method of ref. 31 to adjust the degrees of freedom in tests of significance for each pairwise correlation. Tests of statistical significance were two-tailed, with $\alpha = 0.05$.

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SUPPLEMENTARY INFORMATION

Value of sockeye salmon resources in Bristol Bay.

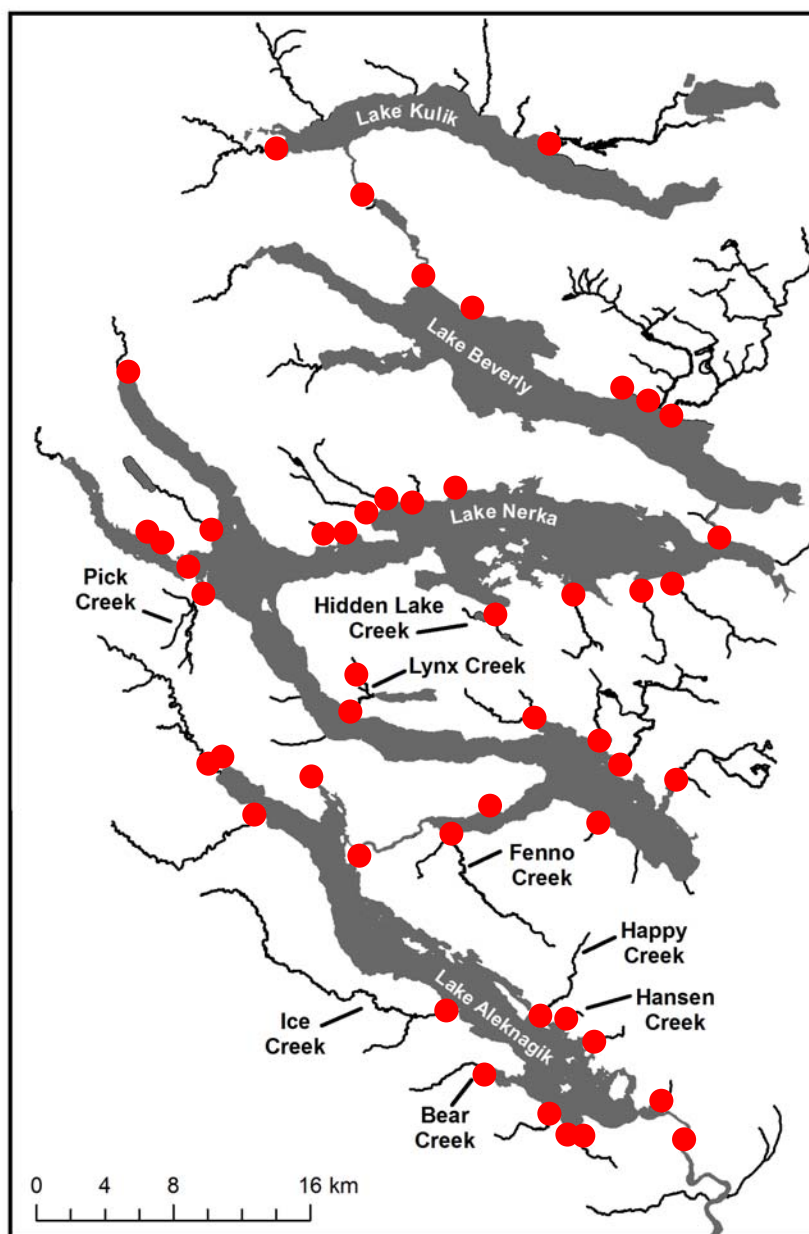
Sockeye salmon were the most valuable fishery in the United States, assessed at 7.9 billion \$US between 1950 and 2008. Bristol Bay produced 63% of this total translating into a cumulative landed value of about 5 billion \$US over this time period (http://www.st.nmfs.noaa.gov/st1/commercial/landings/annual_landings.html). These estimates do not include any of the economic benefits of processing and auxiliary industries, so \$5 billion is an underestimate of the total value of the commercial fishery since 1950. Wholesale values are typically about twice the landed values.

An average of 29M adult sockeye returned to Bristol Bay watersheds between 1958 and 2008, and returns observed in the last two decades (average = 37M) were higher than for any other decade in the last century because of favorable conditions for growth and survival in the ocean. The landed value of the commercial fishery averaged \$US 176 million from 1985-2004³² (adjusted to 2004 \$US). The value of all ecosystem services supported by salmon in Bristol Bay was estimated to be approximately 324 million \$US in 2005, of which 234 million \$US were derived from the wholesale value of salmon caught by the commercial fishery, 61 million \$US were derived from sport fishing, and the remainder from a combination of subsistence expenditures, wildlife viewing, and hunting³³. The Bristol Bay ecosystem supports many ecosystem services in addition to those provided by salmon but these have not yet been valued.

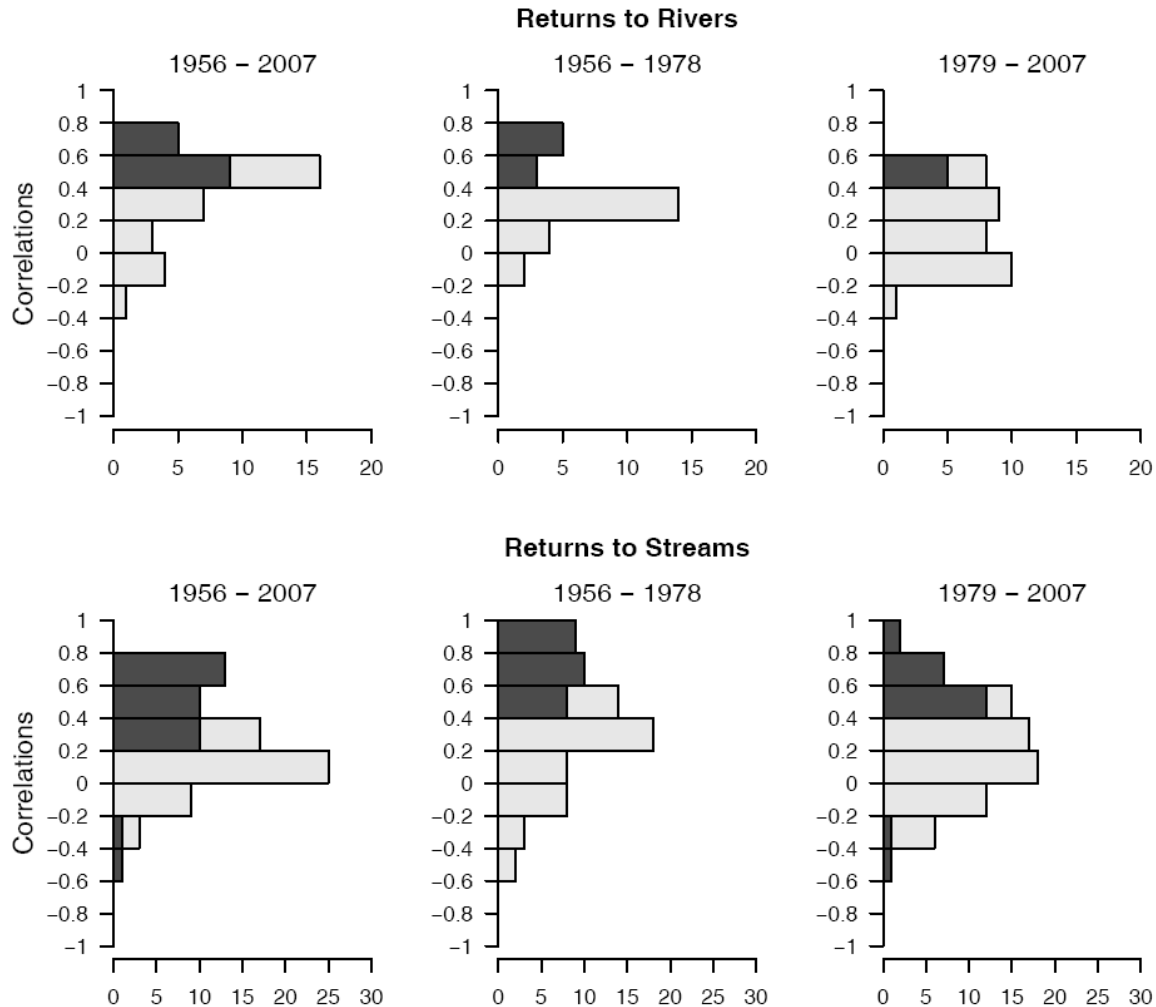
Variance scaling in data

Tilman et al. (1998)³⁴ showed that the relationship between the variance of an asset (σ_i^2) and its mean abundance (m_i) can be described by the relationship $\sigma_i^2 = cm_i^z$, where c is a constant and z is a parameter describing how the variance scales with the mean. Statistical averaging is an important component of portfolio effects when the value of z is greater than 1. We fit this scaling relationship to the data considered at the three levels of spatial aggregation described in the main paper (i.e., among rivers, among total returns to stream populations in the Wood River watershed, and spawning population sizes in streams of the

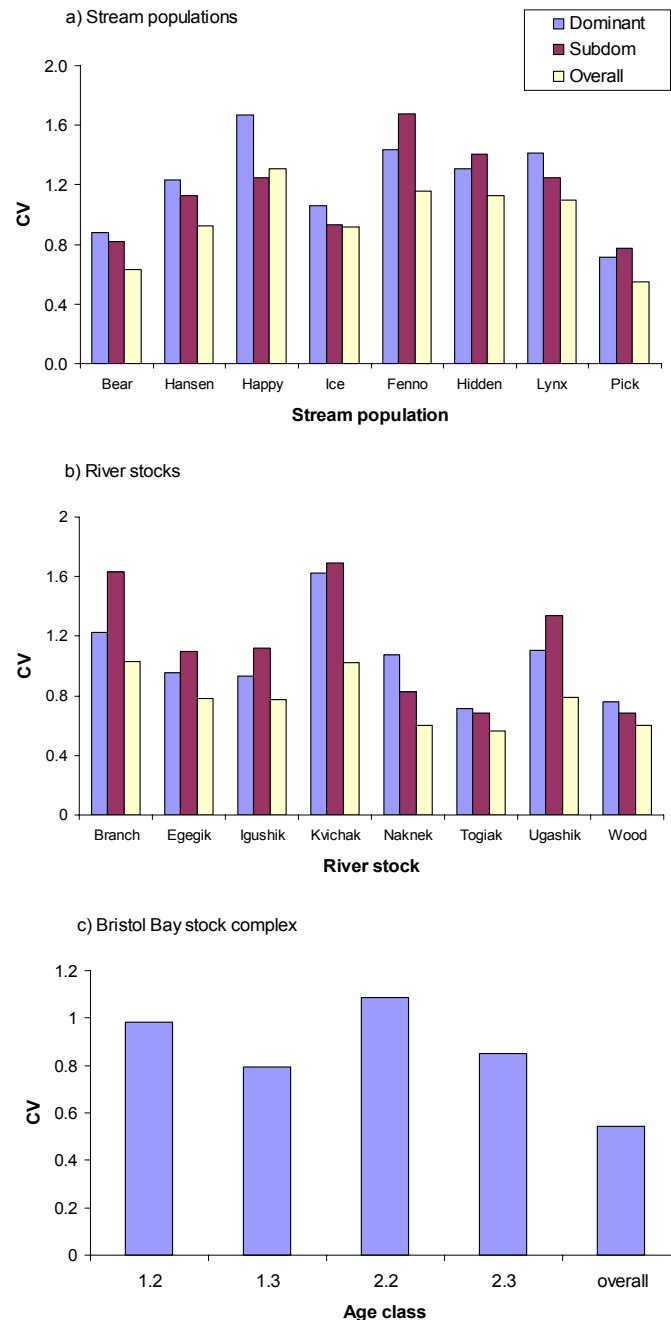
Wood River watershed). For each of these data sets, a strong power relationship existed between the variance and the mean (r^2 values: 0.97, 0.70, 0.94, respectively), and the parameter z was substantially greater than 1 (2.2, 1.7, and 1.9 respectively). Thus, a large component of the portfolio effects observed in the sockeye stock complex in Bristol Bay derives from statistical averaging of the inter-annual returns to various components of the stock complex.



Supplementary Fig. 1. Map of the Wood River system in Bristol Bay, Alaska. Dots show the outlets of streams and rivers that support distinct populations of sockeye salmon. Labeled sites are those for which long-term data on spawner abundance was used for estimating the co-variation among returns.



Supplementary Fig. 2. Histograms of pairwise correlations in annual sockeye returns to major rivers of Bristol Bay (top panels) and streams of the Wood River system (bottom panels). Annual sockeye returns to Bristol Bay rivers between 1956 and 2008 had an average correlation of 0.41 (range: -0.32 to 0.75), and only 39% of the pair-wise comparisons were statistically significant ($p \leq 0.05$, shown in dark shading). At the scale of individual populations in streams of the Wood River system ($n = 8$), the average correlation between populations was 0.25 (range: -0.47 to 0.76), with only 45% of the comparisons being statistically significant (shown in dark shading), of which 6% were negative. A phase shift of the Pacific Decadal Oscillation in the late-1970s was associated with increased abundances of most components of the Bristol Bay sockeye stock complex, thereby strengthening co-variation among stock components when considering the entire time frame from 1956-2008. When the co-variation structure was examined before and after the 1977 regime shift, correlations among components of the stock complex shifted closer to zero. The frequency distribution of pair-wise correlations for the entire time series is shown in the first column, and before (middle column), and after (right column) the PDO shift in the late 1970s. Average correlation coefficients are: rivers: 1956-1978, mean $r = 0.34$, 1979-2007, mean $r = 0.15$; streams 1956-1978, mean $r = 0.37$, 1979-2007, mean $r = 0.21$.



Supplementary Fig. 3. Coefficient of variation (CV) observed for the dominant age classes of sockeye compared to the CV for the entire population, stock or stock complex. Data are shown for a) stream populations, b) river stocks, and c) the entire Bristol Bay stock complex. For rivers and streams we considered only the two dominant age classes in each system. Because there are four dominant age classes that comprise the run at the Bristol Bay scale, we evaluated the variability in all four age classes at this coarsest spatial scale.

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