

LETTER

Watershed complexity increases the capacity for salmon–wildlife interactions in coastal ecosystems

Jonathan B. Armstrong¹ | Daniel E. Schindler² | Curry J. Cunningham³ |
 William Deacy^{1,4} | Patrick Walsh⁵

¹Department of Fisheries and Wildlife,
 Oregon State University, Corvallis, Oregon

²School of Aquatic and Fishery Sciences,
 University of Washington, Seattle,
 Washington

³College of Fisheries and Ocean Sciences,
 University of Alaska Fairbanks, Juneau,
 Alaska

⁴Arctic Network, U.S. National Park Service,
 4175 Geist Road, Fairbanks, Alaska 99709
 USA

⁵U.S. Fish and Wildlife Service, Togiak
 National Wildlife Refuge, Togiak, Alaska

Correspondence

Jonathan B. Armstrong, Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, 2820 SW Campus Way, Corvallis, OR 97331.

Email: jonathan.armstrong@oregonstate.edu

Funding information

Gordon and Betty Moore Foundation; Alaska salmon processing industry (funds portion of Alaska Salmon Program); Cedar Tree Foundation David H. Smith Conservation Research Fellowship; National Science Foundation; U.S. Fish and Wildlife Service

Abstract

Habitat alteration and species exploitation are fundamental issues in conservation, yet their interacting effects on food webs are rarely considered. We used a foraging model based on the Wood River basin (Alaska, USA) to explore how watershed development and commercial fisheries affect energy flow from sockeye salmon to brown bears. We found that, where salmon are abundant, fisheries can harvest large fractions of runs without substantially reducing bear consumption of salmon, but that watershed development could strongly reduce bear consumption if it shortens the duration of foraging opportunities by reducing population-level variation in salmon spawn timing. Habitats with the lowest resource abundance (small streams) were particularly profitable for bear foraging because they offer salmon at unique times of the season. This result challenges environmental impact assessments that assume ecological effects respond solely to changes in resource abundance.

KEYWORDS

ecosystem-based management, fisheries, phenology, predation, trade-off, watershed development

1 | INTRODUCTION

A primary challenge of conservation science is to quantify how the effects of human development propagate through biological communities to modify or degrade ecosystem functions and services (Hebblewhite et al., 2005; Koh et al., 2004; Sinclair & Byrom, 2006). A difficulty in anticipating such effects is that species interactions are governed not

only by their abundances (Holling, 1959) but also the habitat context in which species interact (Werner, Gilliam, Hall, & Mittelbach, 1983), both of which are affected by human activities. For example, humans can reduce energy flows to predators by reducing prey abundance through harvest (Cury et al., 2011) or by homogenizing and fragmenting habitat features that mediate predator–prey interactions (Andruskiw, Fryxell, Thompson, & Baker, 2008). However, it is often not clear how

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2019 The Authors. Conservation Letters published by Wiley Periodicals, Inc.

harvest and habitat modification interact to affect ecosystem processes that support important services or species at risk. Here, we explore a case study involving marine commercial fisheries for Pacific salmon (*Oncorhynchus* spp.), flows of these marine-derived resources to brown bears (*Ursus arctos*) in coastal watersheds, and how watershed development may erode the capacities of ecosystems to support inland food webs dependent on salmon subsidies.

Anadromous Pacific salmon support a variety of ecosystem functions in coastal watersheds (Gende, Edwards, Willson, & Wipfli, 2002; Schindler et al., 2003). After accumulating most of their body mass in the ocean, salmon return to their natal rivers to spawn and then die, generating a high-quality resource pulse that supports a wide variety of aquatic and terrestrial consumers in coastal watersheds (Willson & Halupka, 1995). Consumers ranging from insects to bears scavenge or prey on salmon and their eggs. At higher latitudes where growing seasons are shorter (and winters longer), salmon provide a critical energy source for a wide variety of taxa (Armstrong & Bond, 2013; Bentley et al., 2012). Marine fisheries often harvest a large proportion of salmon returning to watersheds, leading to concerns that harvest reduces the resource base supporting terrestrial and freshwater food webs in salmon watersheds and that an ecosystem-based approach to salmon management would more explicitly consider the roles of salmon as a resource subsidy to watershed predators (Darimont et al., 2010; Levi et al., 2012).

A growing body of work demonstrates that intraspecific diversity in salmon attributes mediates energy flows to both fisheries and predators (Deacy, Leacock, Armstrong, & Stanford, 2016; Ruff et al., 2011; Schindler et al., 2013). This diversity is associated with local adaptation of salmon to specific habitat conditions such as water temperature, water depth, stream gradient, and gravel size (Fraser, Weir, Bernatchez, Hansen, & Taylor, 2011; Hilborn, Quinn, Schindler, & Rogers, 2003; Taylor, 1991). For example, geomorphic conditions affect stream hydrology and thermal regimes that cause local selection pressures on optimal spawn timing (Larson, Lisi, Seeb, Seeb, & Schindler, 2016), which can differ by weeks or even months among populations occupying a single river basin (Lisi, Schindler, Bentley, & Pess, 2013; Schindler et al., 2010). Because salmon are primarily available to terrestrial and aquatic predators only when they are actively spawning in shallow waters, seasonal variation in spawn timing among populations generates resource waves that prolong the duration of salmon foraging opportunities for inland consumers (Deacy et al., 2016; Schindler et al., 2013). Thus, consumers that can move to exploit the seasonal spatial progression of spawning salmon benefit more from salmon resources than those in systems with shorter resource waves or in ecosystems where there are impediments to movement (Armstrong, Takimoto, Schindler, Hayes, & Kauffman, 2016; Deacy et al., 2018).

Across the Northern Pacific Rim, there is increasing risk of development in watersheds that support salmon and their predators such as bears (Darimont et al., 2010). For example, the Bristol Bay region of western Alaska is famous for its prolific commercial salmon fisheries (Hilborn et al., 2003; Schindler et al., 2010), tourism focused on bear viewing (Richardson, Huber, & Loomis, 2017), and recreational fisheries for species that rely heavily on salmon resource subsidies (Bentley et al., 2012; Dye & Borden, 2018). However, the watersheds that provide spawning and nursery habitat for anadromous salmon are experiencing increasing pressure from resource extraction (Hébert & Brock, 2017), hydroelectric development (Cherry et al., 2017), and climate warming (Winfree et al., 2018). Development pressures have the potential to degrade watershed features that modify a range of evolutionary and ecological characteristics of salmon populations throughout the region.

Proponents of development projects often argue that direct footprints are relatively small and pose risks to only a small fraction of a watershed. However, empirical studies of bear–salmon interactions suggest that some small salmon populations can contribute disproportionately to the foraging opportunities of bears. Salmon populations that spawn in small tributary streams are far more vulnerable to predation than populations that spawn in rivers or on lake shores (Quinn, Wetzel, Bishop, Overberg, & Rogers, 2001). Populations returning to small streams also spawn the earliest due to colder temperatures (Lisi et al., 2013), and may be the only salmon available for a substantial window of the salmon-foraging season (Schindler et al., 2013). Thus, although not numerically abundant, salmon populations occupying small habitat features with unique local selection pressures may provide a disproportionately large contribution to flows of marine-derived resources to terrestrial food webs in coastal watersheds.

We developed an empirically parameterized simulation model to explore the interactions between watershed development (which could reduce variation in spawn timing by eliminating populations or homogenizing habitat) and commercial fishery harvest in controlling foraging opportunities for terrestrial predators. Our objectives were to (a) characterize the relationship between salmon abundance (primarily determined by fishery exploitation) and salmon population diversity (a product of watershed complexity) in regulating salmon foraging opportunities for brown bears, (b) assess the degree to which erosion of salmon population diversity affects bear foraging opportunities, and (c) quantify how alternative conservation strategies might fare in maintaining bear foraging opportunity in the face of watershed development. Our results demonstrate the need to identify and protect novel habitats that provide unique opportunities for predator–prey interactions but may not necessarily be dominant features of the landscape. We found that streams, which harbor smaller populations of salmon, contribute disproportionately to the

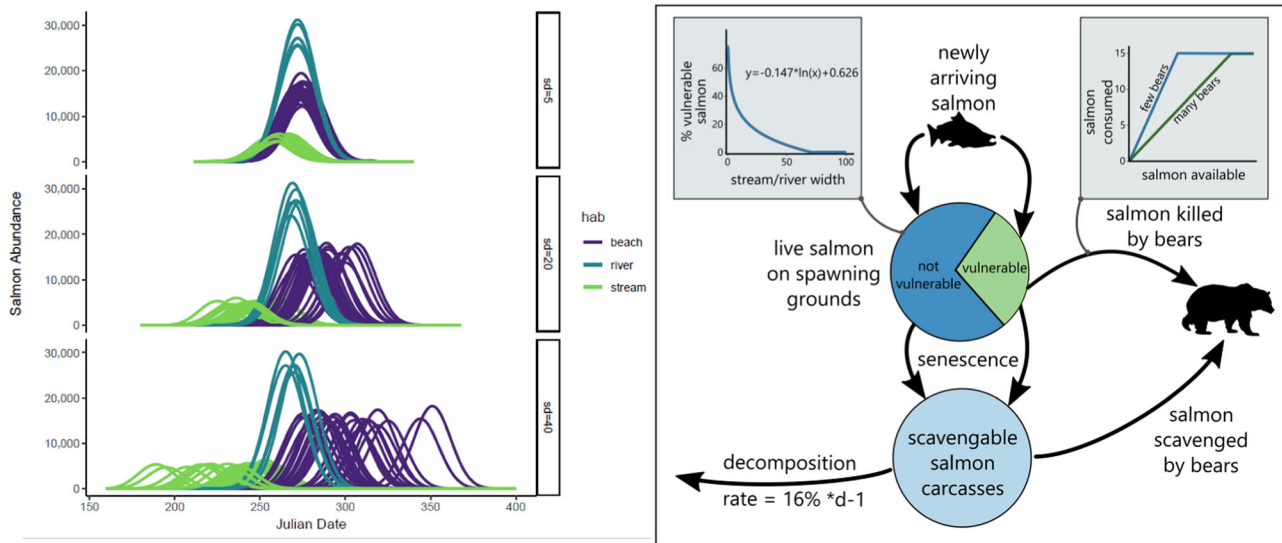


FIGURE 1 Summary of key components in the bear-salmon foraging model. (a) Plot illustrating simulated salmon portfolios in which a total of 1.5 million fish (the escapement after commercial fishing) occur in 60 discrete populations (individual lines) spawning in three habitat types (indicated by line color). Panels show different levels of phenological variation (standard deviation = 5, 20, and 40 top-to-bottom) that prolongs bear foraging opportunity. (b) Flow chart demonstrating key aspects of bear-salmon foraging represented in our simulations

flows of marine-derived resources to important species in coastal food webs, even though these habitats are commonly assumed to have little importance at the ecosystem level.

2 | METHODS

2.1 | Model summary

We simulated individual brown bears foraging across a landscape containing salmon populations that vary in abundance, spawning phenology, and vulnerability to predation (Figure 1, full details in the Supporting Information). The response variable of our simulations was the cumulative number of salmon consumed, averaged across the bear population. Salmon portfolios were based on the Wood River system of southwest Alaska, one of the only large watersheds with comprehensive data on salmon population attributes that mediate bear foraging opportunity (Schindler et al., 2013). This basin is approximately 3,200 km² and contains about 60 sockeye salmon populations that spawn in tributary streams, lake shores, or larger rivers. We only considered sockeye salmon (*O. nerka*) because they comprise >99% of the Pacific salmon returning to the Wood River system (Alaska Salmon Program *unpublished data*). We assume that bear foraging opportunities are regulated by five mechanisms: (a) salmon abundance (Levi et al., 2012; Quinn, Gende, Ruggerone, & Rogers, 2003; Van Daele et al., 2013), (b) habitat-mediated prey vulnerability (Quinn et al., 2001), (c) satiation (Gende, Quinn, & Willson, 2001; Hilderbrand, Jenkins, Schwartz, Hanley, & Robbins, 1999), (d) time constraints alleviated by phenological variation (Deacy et al., 2018; Schindler et al., 2013), and (e)

intraspecific competition (Ben-David, Titus, & Beier, 2004; Egbert, Stokes, & Egbert, 1976; Rode, Farley, & Robbins, 2006).

2.2 | Scenarios explored

To explore the relationship between salmon fisheries and inland food webs, and how this was modified by watershed complexity, we varied escapement from 0.2 to 6 million fish to reflect observed variation around the Wood River's management target of 0.7–1.8 million (high values reflect large runs that exceed fisheries capacity; Erickson, Brazil, Chang, McKinley, & Clark, 2015). To explore how phenological variation mediated the effect of salmon abundance on bears, we simulated across three levels of variation in sockeye salmon spawn timing across the watershed (σ_{phen}): 5, 20, and 40. The Wood River's salmon populations have a σ_{phen} value of approximately 22 and a total duration of approximately 3 months (Lisi et al., 2013). Areas with high geomorphic diversity and multiple salmon species, such as the Copper River Delta (Campbell, Dunham, Reeves, & Wondzell, 2018), exhibit $\sigma_{phen} > 50$ and have spawning salmon present for >6 months (Gordon Reeves U.S. Forest Service *unpublished data*).

Next, we explored how watershed development that eliminates salmon populations (e.g., mining that degrades, dewater, or contaminates spawning sites; U.S. EPA 2014) could affect seasonal bear consumption of salmon. We considered three alternative rules for ordering the removals: (a) “protect the most abundant salmon populations” (remove in reverse order of population size), (b) “remove populations randomly,”

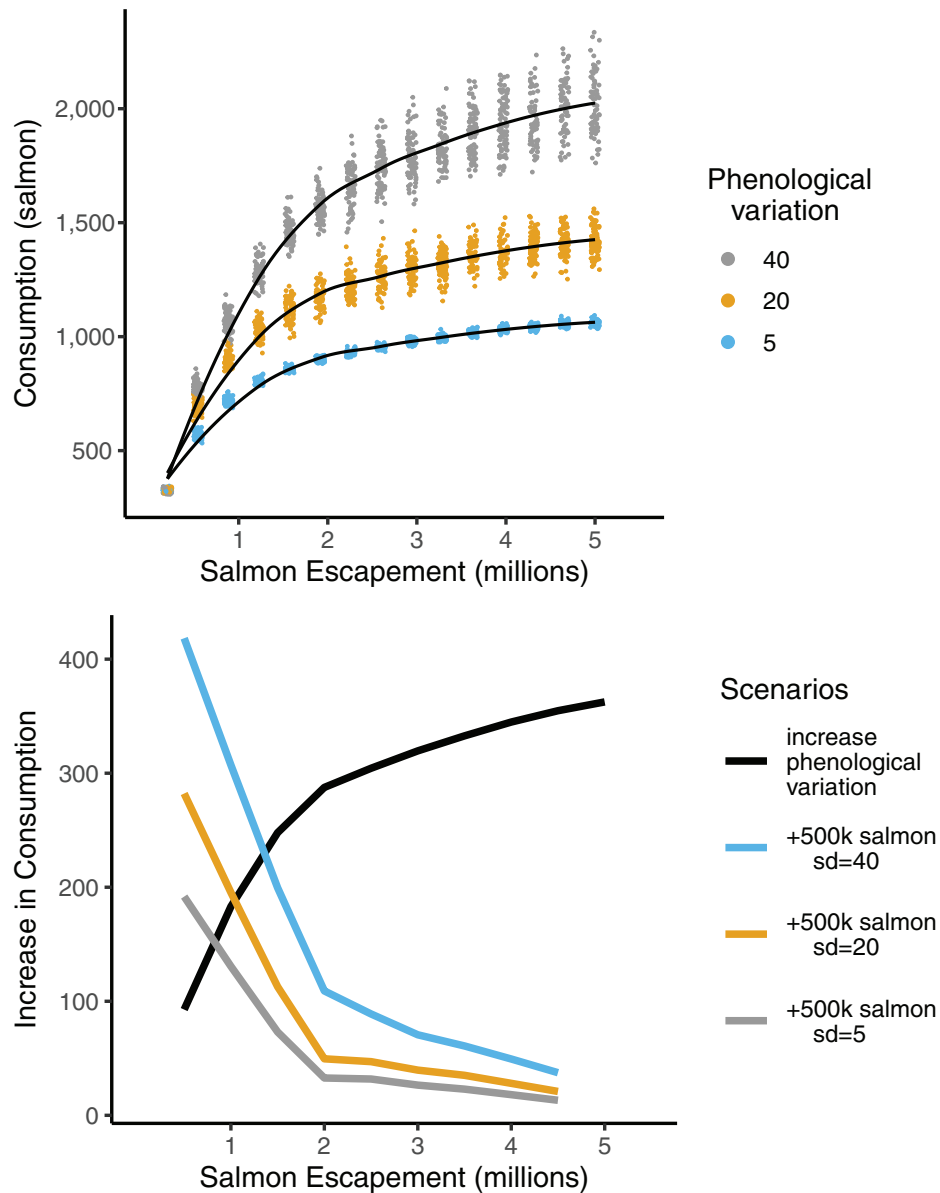


FIGURE 2 (a) Simulation results showing the relationship between salmon escapement (fish remaining after commercial fishing) and bear consumption (mean number of salmon per bear), as a function of phenological diversity among salmon populations (point colors indicate standard deviation). Lines show local polynomial regressions fit to data using weighted least squares. (b) Line plot comparing the effect sizes of salmon escapement and phenological diversity on salmon consumption by bears, across a range of salmon escapements. X-axis indicates initial salmon escapement level; y-axis shows change in salmon consumption that results from increasing the escapement by 500,000 fish (solid lines) or increasing the standard deviation of phenology from 5 to 20. For the effects of escapement, color of solid line indicates different levels of phenological variation as depicted in (a). Both plots show data for the intermediate competition scenario

and (c) “maintain phenological variation” (remove populations with the most common spawn timing).

3 | RESULTS

3.1 | Relationship between fishery exploitation and consumption of salmon by bears

Salmon escapement had a positive saturating effect on bear foraging (Figure 2). At salmon escapements less than approx-

imately 0.5 million fish, bears consumed less than approximately 500 salmon and responded strongly to increases in salmon abundance. In contrast, at our maximum escapement levels of 6 million fish, bears consumed nearly 1,200–2,500 salmon and showed little response to further increases in salmon abundance. Phenological variation had strong positive effects on bear foraging that were enhanced by salmon escapement, but dampened by competition (Figures 2 and S1).

Phenological variation mediated trade-offs between salmon fisheries and bears by governing the rate at which

bear foraging saturated with increasing salmon abundance (Figure 2b). Specifically, variation in spawn timing increased (a) the marginal value of salmon at low escapements, (b) the escapement level at which the marginal value of salmon approached zero (the point of saturation), and (c) the foraging opportunity of bears at saturating escapements (Figure 2b). At a threshold of approximately 2 million salmon, adding additional escapement had little effect on bear consumption, whereas phenological variation could still increase bear foraging by nearly 50–100% (compared to a situation with homogeneous run timing). The effect size of phenological variation increased with increasing salmon escapement. In combination with the saturating effect of escapement, this generated two domains in the response of bears. At high salmon abundance, bear consumption was primarily sensitive to phenological variation, whereas at low salmon abundance, bear consumption was primarily sensitive to escapement levels (Figure 2b).

3.2 | Value of small populations

In our simulations, salmon populations in streams were approximately 1/3 and approximately 1/5 as abundant as those in beaches and rivers, respectively. Summed together, stream spawning salmon populations comprised only about 20% of total escapement across the watershed. However, because stream populations exhibit unique phenologies and are more vulnerable to predation, they contributed disproportionately more to bear foraging, providing $48\% \pm 17\%$ (mean ± 1 standard deviation) of the total salmon consumed by bears over the course of a season. In contrast, beach spawning populations contributed 58% of escapement and provided $33\% \pm 9\%$ of salmon consumption, and river populations contributed 23% of escapement and $15\% \pm 4\%$ of consumption. Thus, small populations of salmon contributed roughly half of total bear consumption while representing only one-fifth of total salmon escapement (Figure 3).

3.3 | Effects of eroding salmon portfolios

Eliminating salmon populations always reduced bear foraging levels; however, the magnitude of this effect was highly sensitive to which populations were removed. In simulations that protected the most abundant salmon populations (making streams with smaller populations most vulnerable), low levels of development caused steep declines in bear foraging level (Figure 4). For example, in the low and medium competition scenarios, removing only 20% of total salmon escapement decreased bear consumption by nearly 30% (Figure 4). In contrast, the alternative strategy that maintained phenological diversity by protecting small streams showed lower declines in bear foraging ($\sim 10\%$, Figure 4). Higher levels of competition among bears resulted in greater sensitivity of bear foraging to

development and caused the alternative prioritization strategies to become more similar in their performance (Figure 4).

4 | DISCUSSION

Intact watersheds support a wide range of life history diversity in salmon populations, some of which is expressed as variation in spawn timing that extends the duration of salmon foraging for bears and other wide-ranging consumers (Deacy et al., 2016; Schindler et al., 2013). Although there is increasing interest in managing fisheries to ensure adequate salmon abundance for inland food webs (Darimont et al., 2010; Levi et al., 2012), our results emphasize that managing landscapes and fisheries to maintain phenological diversity is probably at least as important. In our models, increasing salmon escapement within the current range of management goals had positive effects on bear consumption (Figure 2), which corroborates concerns over exploitative competition between fisheries and bears (Hilderbrand, Farley, Schwartz, & Robbins, 2004). However, increasing escapement from the average level observed (1.5 million, $n = 56$ years) to 2-times the average (3 million) only increased consumption by 15–31%. In contrast, at the average observed escapement level, increasing the phenological variation from our minimum to maximum simulated value increased bear consumption by 52–75%. This model prediction is supported by recent empirical work beyond the Wood River Basin; Kodiak brown bears that tracked phenological variation to prolong their salmon foraging exhibited nearly 40–90% higher consumption levels (Deacy et al., 2018). Similarly, salmon species diversity (a proxy for phenological variation) outperformed salmon biomass in predicting the contribution of salmon to black bear diets in coastal British Columbia (Service et al., 2019). Although it is difficult to compare abundance and diversity metrics in a standardized fashion, we believe the variation in phenology we simulated across represents realistic contrasts found in nature that are appropriate to compare to realistic contrasts in abundance.

Phenological diversity within salmon species emerges from local adaptation to different regimes of flow, temperature, and biological productivity (Fraser et al., 2011). Ongoing climate change may reduce the thermal heterogeneity currently expressed across watersheds in Bristol Bay (Armstrong & Schindler, 2013; Lisi et al., 2013) and in other parts of Alaska (Winfrey et al., 2018) by reducing the effect of snowmelt on stream hydrologies (Adelfio, Wondzell, Mantua, & Reeves, 2019). Hatchery salmon production can replace diverse populations of wild fish with homogenous hatchery stocks (Brenner, Moffitt, & Grant, 2012; Hilborn & Eggers, 2000) and exacerbate the challenge of maintaining population diversity in mixed-stock fisheries (Naish et al., 2007). Salmon populations exhibit a wide range of productivities but are

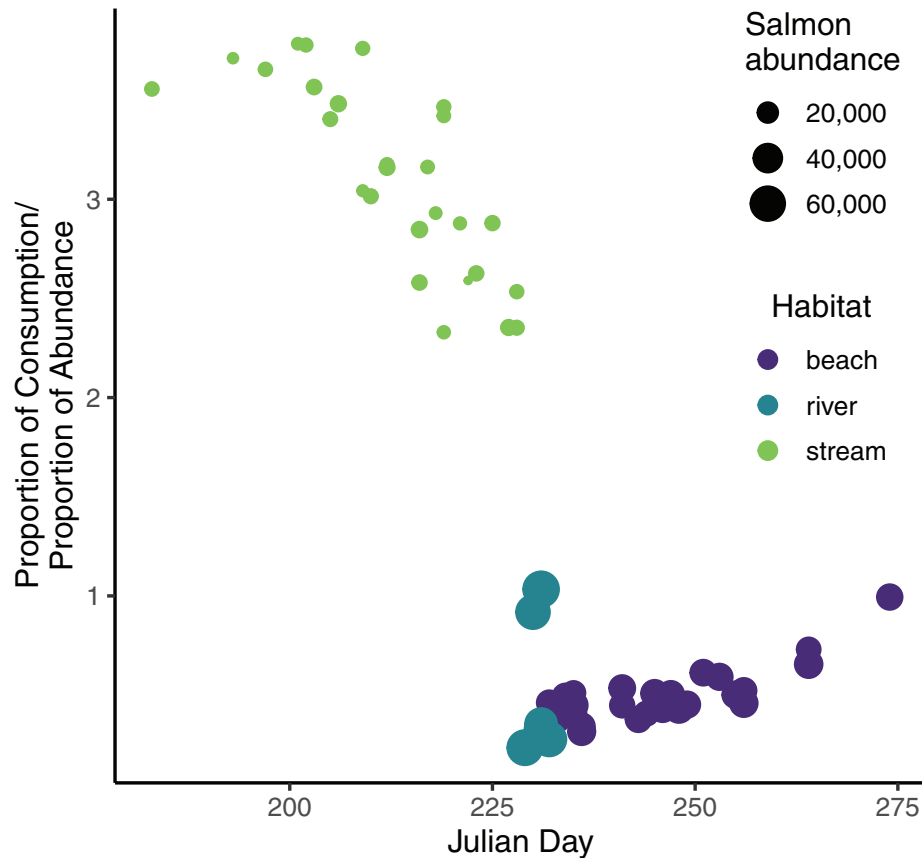


FIGURE 3 Plot depicting how salmon populations (represented as points) differentially contribute to bear consumption as a function of their habitat type and spawning phenology. Y-axis shows each salmon population's contribution to cumulative bear consumption divided by its contribution to total salmon abundance (i.e., watershed-level escapement). X-axis shows date of spawning. Color indicates habitat type and size of dot indicates population abundance

harvested in aggregate. Fishing a stock complex at maximum sustainable yield results in overfishing of less productive populations and has led to intense controversy regarding whether unproductive populations are worth protecting at the expense of fisheries yields (Price, Darimont, Temple, & MacDuffee, 2008; Walters & Martell, 2004; Wright, 1993). Our results show that some of these small populations may be particularly important for maintaining food webs at landscape scales. We found that lack of protection for small populations could severely affect bears, causing $>2\times$ more reduction in salmon consumption compared to alternative conservation strategies (Figure 4). Our results are likely conservative because we assumed habitat mediates predation but not scavenging; in reality, small streams likely offer higher efficiency for scavenging as well as predation. More empirical work is needed to understand the quantitative effect of human actions on phenological diversity and how consumers respond to uneven declines in abundance across salmon stock complexes (Price et al., 2019).

Although our model was based on the Wood River Basin, our results are likely generalizable to other basins that support major salmon fisheries. The key characteristic of the Wood

River system is that its stream spawning salmon populations generate a small fraction of total salmon abundance, but provide earlier spawning salmon in habitats more conducive to bear predation. These phenomena reflect underlying mechanisms that should apply broadly. The area of suitable spawning habitat (i.e., gravel substrate) in tributary streams is typically less than that available in lake shores and large rivers (Burgner et al., 1969), limiting the average production from this habitat type. Tributary streams are generally cooler than lake shores and rivers and cooler temperatures are associated with earlier spawning phenologies in salmon. Last, tributary streams are confining habitats that render salmon more vulnerable to predators than lake shores or rivers. Although more work is needed to robustly quantify these traits across watersheds, they appear to hold across sockeye salmon stock complexes that sustain major fisheries (Deacy et al., 2016; Hilborn et al., 2003).

Our simulations demonstrate that reducing fishing pressure cannot offset losses of phenological diversity because diversity and abundance affect complementary dimensions of bear foraging. Diversity in spawn timing determines how long salmon are present on the landscape, whereas salmon

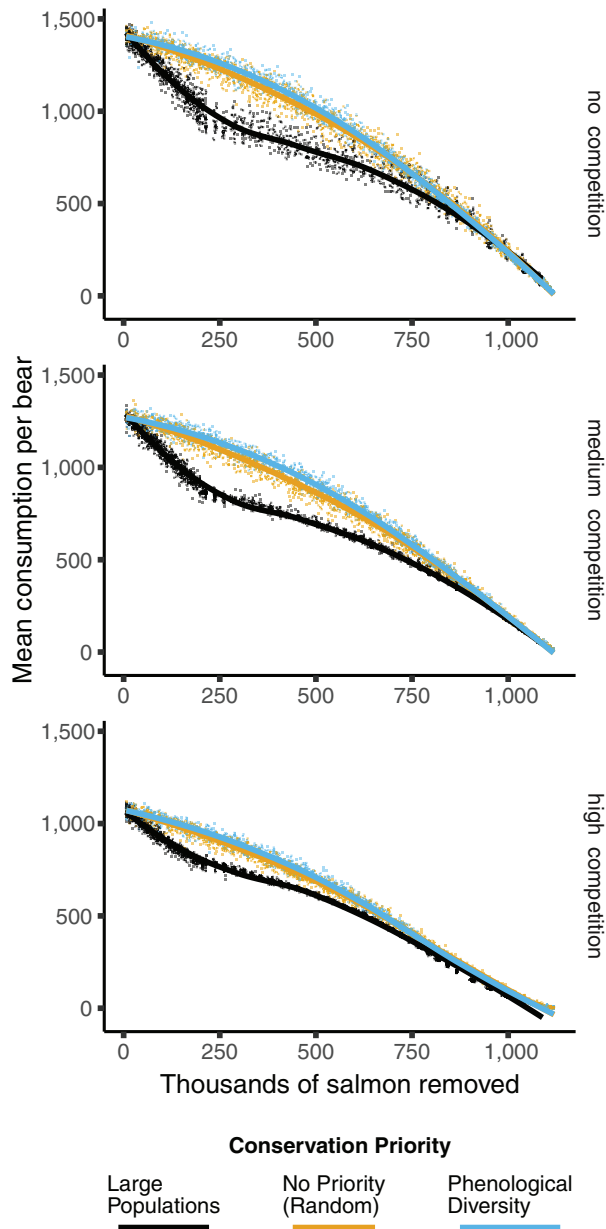


FIGURE 4 The simulated effects of alternative patterns of watershed development on the foraging opportunity of bears. In each simulation, salmon populations were removed sequentially from the watershed, following three alternative conservation prioritization strategies: (a) protect large populations (black), (b) maintain phenological diversity (blue), and (c) random (orange). Panels show results for different levels of interference competition

abundance primarily influences bear energy intake on the days when salmon are present. The positive effect of abundance is capped by physiological capacity (Hilderbrand et al., 1999), creating an asymptotic relationship between salmon density and the number of salmon that bears consume (Figure 2; Quinn et al., 2003). Watershed development that reduces phenological diversity will reduce the capacity for salmon runs to support bears and other wide-ranging salmon consumers.

Our development scenarios eliminated populations entirely (or completely prevented bears from accessing them) rather than reducing their productivity or accessibility. Future work could consider how lesser impacts scale up to affect bears, or how additional ecological complexity, such as selective consumption (Gende et al., 2001) and dominance (Gende & Quinn, 2004), further mediates energy flows from salmon to bears.

A serious challenge in conservation is to understand which aspects of ecological complexity are most important for maintaining ecosystem functions. Ecosystem-based fisheries management accounts for interactions among multiple species, but typically considers simplified food webs with energy flows mediated solely by prey abundance (Christensen & Walters, 2004). We incorporated two empirically documented phenomena, intraspecific diversity in prey attributes and habitat-mediated predation risk, and found that they strongly mediate how the abundance of salmon translates into bear foraging opportunity. By considering the spatial and temporal structure of this ecosystem, we arrive at a very different conclusion about the importance of certain landscape features over others. Even habitat patches that produce small contributions to overall resource production can be disproportionately important to consumers if they provide novel opportunities in space or time. Risk assessments of watershed development activities need to account for the value of such novel features if their intent is to protect key ecosystem integrity.

ACKNOWLEDGMENTS

This research was supported by the David H. Smith Conservation Research Fellowship, the US Fish and Wildlife Service, The National Science Foundation, The Gordon and Betty Moore Foundation, and funds from the Alaska salmon processing industry that support the UW Alaska Salmon Program. Source code for the model is available in appendix B. Taal Levi and Nathan Schumaker provided helpful guidance on the modeling framework. Bill Pyle and others at the Kodiak National Wildlife Refuge helped us refine our model to inform conservation. Two anonymous reviewers provided feedback that improved the paper.

REFERENCES

- Adelfio, L. A., Wondzell, S. M., Mantua, N. J., & Reeves, G. H. (2019). Warm winters reduce landscape-scale variability in the duration of egg incubation for Coho Salmon (*Oncorhynchus kisutch*) on the Copper River Delta, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, 76(8), 1362–1375.
- Andruskiw, M., Fryxell, J. M., Thompson, I. D., & Baker, J. A. (2008). Habitat-mediated variation in predation risk by the American Marten. *Ecology*, 89(8), 2273–2280. <https://doi.org/10.1890/07-1428.1>
- Armstrong, J. B., & Bond, M. H. (2013). Phenotype flexibility in wild fish: Dolly Varden regulate assimilative capacity to capitalize on

- annual pulsed subsidies. *Journal of Animal Ecology*, 82(5), 966–975. <https://doi.org/10.1111/1365-2656.12066>
- Armstrong, J. B., & Schindler, D. E. (2013). Going with the flow: Spatial distributions of juvenile coho salmon track an annually shifting mosaic of water temperature. *Ecosystems*, 16(8), 1429–1441.
- Armstrong, J. B., Takimoto, G., Schindler, D. E., Hayes, M. M., & Kauffman, M. J. (2016). Resource waves: Phenological diversity enhances foraging opportunities for mobile consumers. *Ecology*, 97(5), 1099–1112. <https://doi.org/10.1890/15-0554.1>
- Ben-David, M., Titus, K., & Beier, L. R. (2004). Consumption of salmon by Alaskan brown bears: A trade-off between nutritional requirements and the risk of infanticide? *Oecologia*, 138(3), 465–474. <https://doi.org/10.1007/s00442-003-1442-x>
- Bentley, K. T., Schindler, D. E., Armstrong, J. B., Zhang, R., Ruff, C. P., & Lisi, P. J. (2012). Foraging and growth responses of stream-dwelling fishes to inter-annual variation in a pulsed resource subsidy. *Ecosphere*, 3(12), 1–17. <https://doi.org/10.1890/es12-00231.1>
- Brenner, R. E., Moffitt, S. D., & Grant, W. S. (2012). Straying of hatchery salmon in Prince William Sound, Alaska. *Environmental Biology of Fishes*, 94(1), 179–195. <https://doi.org/10.1007/s10641-012-9975-7>
- Burgner, R. L., DiCostanzo, C. J., Ellis, R. J., Harry, G. Y., Jr., Hartman, W. L., Kerns, O. E., Jr., ... Royce, W. F. (1969). Biological studies and estimates of optimum escapements of sockeye salmon in the major river systems in southwestern Alaska. *Fishery Bulletin*, 67(2), 405–459.
- Campbell, E. Y., Dunham, J. B., Reeves, G. H., & Wondzell, S. M. (2018). Phenology of hatching, emergence, and end-of-season body size in young-of-year Coho Salmon in thermally contrasting streams draining the Copper River Delta, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, 76(2), 185–191.
- Cherry, J. E., Knapp, C., Trainor, S., Ray, A. J., Tedesche, M., & Walker, S. (2017). Planning for climate change impacts on hydropower in the Far North. *Hydrology and Earth System Sciences*, 21(1), 133–151.
- Christensen, V., & Walters, C. J. (2004). Ecopath with Ecosim: Methods, capabilities and limitations. *Ecological Modelling*, 172(2–4), 109–139.
- Cury, P. M., Boyd, I. L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R. J. M., Furness, R. W., ... Sydeman, W. J. (2011). Global seabird response to forage fish depletion—One-third for the birds. *Science*, 334(6063), 1703–1706. <https://doi.org/10.1126/science.1212928>
- Darimont, C. T., Bryan, H. M., Carlson, S. M., Hocking, M. D., MacDuffee, M., Paquet, P. C., ... Wilmers, C. C. (2010). Salmon for terrestrial protected areas. *Conservation Letters*, 3(6), 379–389. <https://doi.org/10.1111/j.1755-263X.2010.00145.x>
- Deacy, W., Erlenbach, J. A., Leacock, W. B., Stanford, J. A., Robbins, C. T., & Armstrong, J. B. (2018). Phenological tracking associated with increased salmon consumption by brown bears. *Scientific Reports*, 8(1), 11008. <https://doi.org/10.1038/s41598-018-29425-3>
- Deacy, W., Leacock, W., Armstrong, J. B., & Stanford, J. A. (2016). Kodiak brown bears surf the salmon red wave: Direct evidence from GPS collared individuals. *Ecology*, 97(5), 1091–1098. <https://doi.org/10.1890/15-1060.1>
- Dye, J. E., & Borden, L. K. (2018). *Sport fisheries in the Bristol Bay Management Area, 2016–2018. Fishery Management Report No. 18-27*. Anchorage, AK: Alaska Department of Fish and Game.
- Egbert, A. L., Stokes, A. W., & Egbert, A. L. (1976). The social behaviour of brown bears on an Alaskan salmon stream. *Bears: Their Biology and Management*, 3, 41–56. <https://doi.org/10.2307/3872753>
- Erickson, J. W., Brazil, C. E., Chang, S. S., McKinley, T. R., & Clark, R. A. (2015). *Review of salmon escapement goals in Bristol Bay, Alaska, 2015. Fishery Manuscript Series No. 15-06*. Anchorage, AK: Alaska Department of Fish and Game.
- Fraser, D. J., Weir, L. K., Bernatchez, L., Hansen, M. M., & Taylor, E. B. (2011). Extent and scale of local adaptation in salmonid fishes: Review and meta-analysis. *Heredity*, 106(3), 404–420.
- Gende, S. M., Edwards, R. T., Willson, M. F., & Wipfli, M. S. (2002). Pacific salmon in aquatic and terrestrial ecosystems. *BioScience*, 52(10), 917–928. [https://doi.org/10.1641/0006-3568\(2002\)052\[0917:pSiaat\]2.0.co;2](https://doi.org/10.1641/0006-3568(2002)052[0917:pSiaat]2.0.co;2)
- Gende, S. M., & Quinn, T. P. (2004). The relative importance of prey density and social dominance in determining energy intake by bears feeding on Pacific salmon. *Canadian Journal of Zoology*, 82(1), 75–85. <https://doi.org/10.1139/z03-226>
- Gende, S. M., Quinn, T. P., & Willson, M. F. (2001). Consumption choice by bears feeding on salmon. *Oecologia*, 127(3), 372–382.
- Hebblewhite, M., White, C. A., Nietvelt, C. G., McKenzie, J. A., Hurd, T. E., Fryxell, J. M., ... Paquet, P. C. (2005). Human activity mediates a trophic cascade caused by wolves. *Ecology*, 86(8), 2135–2144. <https://doi.org/10.1890/04-1269>
- Hébert, K., & Brock, S. (2017). Counting and counter-mapping: Contests over the making of a mining district in Bristol Bay, Alaska. *Science as Culture*, 26(1), 56–87. <https://doi.org/10.1080/09505431.2016.1223112>
- Hilborn, R., & Eggers, D. (2000). A review of the hatchery programs for pink salmon in Prince William Sound and Kodiak Island, Alaska. *Transactions of the American Fisheries Society*, 129(2), 333–350. [https://doi.org/10.1577/1548-8659\(2000\)129<0333:AROTHP>2.0.CO;2](https://doi.org/10.1577/1548-8659(2000)129<0333:AROTHP>2.0.CO;2)
- Hilborn, R., Quinn, T. P., Schindler, D. E., & Rogers, D. E. (2003). Bio-complexity and fisheries sustainability. *Proceedings of the National Academy of Sciences of the United States of America*, 100(11), 6564–6568. <https://doi.org/10.1073/pnas.1037274100>
- Hilderbrand, G. V., Farley, S. D., Schwartz, C. C., & Robbins, C. T. (2004). Importance of salmon to wildlife: Implications for integrated management. *Ursus*, 15(1), 1–10.
- Hilderbrand, G. V., Jenkins, S. G., Schwartz, C. C., Hanley, T. A., & Robbins, C. T. (1999). Effect of seasonal differences in dietary meat intake on changes in body mass and composition in wild and captive brown bears. *Canadian Journal of Zoology*, 77(10), 1623–1630. <https://doi.org/10.1139/z99-133>
- Holling, C. S. (1959). The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Canadian Entomologist*, 91, 293–320.
- Koh, L. P., Dunn, R. R., Sodhi, N. S., Colwell, R. K., Proctor, H. C., & Smith, V. S. (2004). Species coextinctions and the biodiversity crisis. *Science*, 305(5690), 1632–1634.
- Larson, W. A., Lisi, P. J., Seeb, J. E., Seeb, L. W., & Schindler, D. E. (2016). Major histocompatibility complex diversity is positively associated with stream water temperatures in proximate populations of sockeye salmon. *Journal of Evolutionary Biology*, 29(9), 1846–1859. <https://doi.org/10.1111/jeb.12926>
- Levi, T., Darimont, C. T., MacDuffee, M., Mangel, M., Paquet, P., & Wilmers, C. C. (2012). Using grizzly bears to assess harvest-ecosystem tradeoffs in salmon fisheries. *Plos Biology*, 10(4), e1001303. <https://doi.org/10.1371/journal.pbio.1001303>
- Lisi, P. J., Schindler, D. E., Bentley, K. T., & Pess, G. R. (2013). Association between geomorphic attributes of watersheds, water

- temperature, and salmon spawn timing in Alaskan streams. *Geomorphology*, 185, 78–86. <https://doi.org/10.1016/j.geomorph.2012.12.013>
- Naish, K. A., Taylor, J. E., III, Levin, P. S., Quinn, T. P., Winton, J. R., Huppert, D., & Hilborn, R. (2007). An evaluation of the effects of conservation and fishery enhancement hatcheries on wild populations of salmon. *Advances in Marine Biology*, 53, 61–194.
- Price, M., Darimont, C., Temple, N., & MacDuffee, S. (2008). Ghost runs: Management and status assessment of Pacific salmon (*Oncorhynchus* spp.) returning to British Columbia's central and north coasts. *Canadian Journal of Fisheries and Aquatic Sciences*, 65(12), 2712–2718.
- Price, M. H., Connors, B. M., Candy, J. R., McIntosh, B., Beacham, T. D., Moore, J. W., & Reynolds, J. D. (2019). Genetics of century-old fish scales reveal population patterns of decline. *Conservation Letters*. <https://doi.org/10.1111/conl.12669>
- Quinn, T. P., Gende, S. M., Ruggerone, G. T., & Rogers, D. E. (2003). Density-dependent predation by brown bears (*Ursus arctos*) on sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences*, 60(5), 553–562. <https://doi.org/10.1139/f03-045>
- Quinn, T. P., Wetzel, L., Bishop, S., Overberg, K., & Rogers, D. E. (2001). Influence of breeding habitat on bear predation and age at maturity and sexual dimorphism of sockeye salmon populations. *Canadian Journal of Zoology*, 79(10), 1782–1793. <https://doi.org/10.1139/cjz-79-10-1782>
- Richardson, L., Huber, C., & Loomis, J. (2017). Challenges and solutions for applying the travel cost demand model to geographically remote visitor destinations: A case study of bear viewing at Katmai National Park and Preserve. *Human Dimensions of Wildlife*, 22(6), 550–563.
- Rode, K. D., Farley, S. D., & Robbins, C. T. (2006). Sexual dimorphism, Reproductive strategy, and human activities determine resource use by brown bears. *Ecology*, 87(10), 2636–2646. [https://doi.org/10.1890/0012-9658\(2006\)87\[2636:SDRSAH\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[2636:SDRSAH]2.0.CO;2)
- Ruff, C. P., Schindler, D. E., Armstrong, J. B., Bentley, K. T., Brooks, G. T., Holtgrieve, G. W., ... Seeb, J. E. (2011). Temperature-associated population diversity in salmon confers benefits to mobile consumers. *Ecology*, 92(11), 2073–2084.
- Schindler, D. E., Armstrong, J. B., Bentley, K. T., Jankowski, K., Lisi, P. J., & Payne, L. X. (2013). Riding the crimson tide: Mobile terrestrial consumers track phenological variation in spawning of an anadromous fish. *Biology Letters*, 9(3), 20130048. <https://doi.org/10.1098/rsbl.2013.0048>
- Schindler, D. E., Hilborn, R., Chasco, B., Boatright, C. P., Quinn, T. P., Rogers, L. A., & Webster, M. S. (2010). Population diversity and the portfolio effect in an exploited species. *Nature*, 465(7298), 609–612.
- Schindler, D. E., Scheuerell, M. D., Moore, J. W., Gende, S. M., Francis, T. B., & Palen, W. J. (2003). Pacific salmon and the ecology of coastal ecosystems. *Frontiers in Ecology and the Environment*, 1(1), 31–37.
- Service, C. N., Bateman, A. W., Adams, M. S., Artelle, K. A., Reimchen, T. E., Paquet, P. C., & Darimont, C. T. (2019). Salmonid species diversity predicts salmon consumption by terrestrial wildlife. *Journal of Animal Ecology*, 88(3), 392–404.
- Sinclair, A., & Byrom, A. E. (2006). Understanding ecosystem dynamics for conservation of biota. *Journal of Animal Ecology*, 75(1), 64–79.
- Taylor, E. B. (1991). A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. *Aquaculture*, 98(1–3), 185–207.
- United States Environmental Protection Agency. (2014). *Proposed determination of the U.S. Environmental Protection Agency Region 10 Pursuant to Section 404(c) of the Clean Water Act, Pebble Deposit Area, Southwest Alaska*. Seattle, WA: Author.
- Van Daele, M. B., Robbins, C. T., Semmens, B. X., Ward, E. J., Van Daele, L. J., & Leacock, W. B. (2013). Salmon consumption by Kodiak brown bears (*Ursus arctos middendorffi*) with ecosystem management implications. *Canadian Journal of Zoology*, 91(3), 164–174. <https://doi.org/10.1139/cjz-2012-0221>
- Walters, C. J., & Martell, S. J. (2004). *Fisheries ecology and management*. Princeton, NJ: Princeton University Press.
- Werner, E. E., Gilliam, J. F., Hall, D. J., & Mittelbach, G. G. (1983). An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, 64(6), 1540–1548.
- Willson, M. F., & Halupka, K. C. (1995). Anadromous fish as keystone species in vertebrate communities. *Conservation Biology*, 9(3), 489–497. <https://doi.org/10.1046/j.1523-1739.1995.09030489.x>
- Winfrey, M. M., Hood, E., Stuefer, S. L., Schindler, D. E., Cline, T. J., Arp, C. D., & Pyare, S. (2018). Landcover and geomorphology influence streamwater temperature sensitivity in salmon bearing watersheds in Southeast Alaska. *Environmental Research Letters*, 13(6), 064034.
- Wright, S. (1993). Fishery management of wild Pacific salmon stocks to prevent extinctions. *Fisheries*, 15(5), 3–4.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Armstrong JB, Schindler DE, Cunningham CJ, Deacy W, Walsh P. Watershed complexity increases the capacity for salmon-wildlife interactions in coastal ecosystems. *Conservation Letters*. 2019;e12689. <https://doi.org/10.1111/conl.12689>