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Integrating disparate data sources to investigate spatiotemporal population dynamics in U.S.
West Coast fishes

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Abstract

Integrating disparate data sources to investigate spatiotemporal population dynamics in U.S. West Coast fishes

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Fluctuations in fish populations are driven by many factors, including environmental, community, and anthropogenic variability. In my dissertation, I integrate a variety of data sources to model population dynamics and investigate how different fish species of conservation and management concern respond to this variability. I focus on a different species and study system in each chapter, tailoring the analysis to the key information gaps and available data. In my first chapter, I collate two sources of data, a reconstructed catch history and limited length data, to develop a data-limited population assessment model for threatened Yelloweye Rockfish in Puget Sound. Despite a high degree of uncertainty, I found that demographic information suggests that this population has recovered significantly in recent decades. Second, I construct a multistate model to estimate the combined influences of climate and hydropower on the movement decisions of adult Steelhead returning to the Columbia River Basin. I found that Steelhead movements are strongly thermally influenced, but that allowing individuals to move via dam spillways may increase survival to natal tributaries. Third, I model the proximate trophic drivers of marine survival in interior Columbia River Basin Fall Chinook Salmon, integrating three separate fishery-independent surveys that provide complementary data on the community

in the coastal ocean. Top-down effects were generally more supported than bottom-up effects, with spatiotemporal overlap between salmon and their predators playing a key role in modulating survival. Finally, I investigate the drivers of spatiotemporal recruitment variability in Sablefish on the U.S. West Coast, using output from oceanographic models to describe environmental conditions. I found that while the presence of Sablefish recruits was not associated with the local environmental conditions examined, the abundance of recruits was associated with cooler temperatures and higher productivity. This dissertation reveals new mechanisms of variability in multiple key species on the U.S. West Coast, providing additional context for the management and recovery of these species.

Acknowledgements	8
Introduction	10
Chapter 1. Data-limited fishery assessment methods shed light on the exploitation history and population dynamics of ESA-listed Yelloweye Rockfish in Puget Sound, Washington	19
1.1 Abstract.....	19
1.2 Introduction	19
1.3 Methods	23
1.3.1 Catch reconstruction	23
1.3.2 Commercial catch reconstruction	25
1.3.3 Recreational catch reconstruction.....	26
1.3.4 Length composition data sources	27
1.3.5 Population dynamics model	28
1.4 Results	32
1.4.1 Catch reconstruction	32
1.4.2 Population dynamics	33
1.5 Discussion.....	36
1.6 Acknowledgements	42
1.7 References	42
Chapter 2. Modeling climate and hydropower influences on the movement decisions of an anadromous species	47
2.1 Abstract.....	47
2.2 Introduction	47
2.3 Materials and Methods	51
2.3.1 Overview	51
2.3.2 Movement data processing	53
2.3.3 Covariate data processing.....	54
2.3.4 Model.....	55
2.3.5 Predicting Final Fates	58
2.4 Results	58
2.4.1 Homing probability and overshoot.....	59
2.4.2 Temperature	60
2.4.3 Spill.....	62
2.4.4 Final fates under different scenarios.....	64
2.5 Discussion.....	66
2.5.1 Insights from an integrated model	66

2.5.2 Effects of temperature and spill.....	67
2.5.3 Limitations of the Columbia River Basin PIT-tag network	68
2.5.4 Conclusions	70
2.6 Acknowledgements	70
2.7 References	70
Chapter 3. Trophic drivers of salmon marine survival revealed by spatiotemporal data integration	76
3.1 Abstract.....	76
3.2 Introduction	77
3.3 Methods	80
3.3.1 Overview	80
3.3.2 Salmon marine survival data	81
3.3.3 Fishery-independent surveys	83
3.3.4 Species distribution models for juvenile salmon, prey, and predators	85
3.3.5 SDM-derived marine survival covariates: abundance and spatial overlap.....	86
3.3.6 Marine survival model.....	87
3.4 Results	90
3.5 Discussion.....	93
3.6 Acknowledgements	97
3.7 References	97
Chapter 4. Spatially explicit recruitment modeling in Sablefish (<i>Anoplopoma fimbria</i>) on the U.S. West Coast.....	105
4.1 Abstract.....	105
4.2 Introduction	105
4.3 Methods	107
4.3.1 West Coast Groundfish Bottom Trawl Survey.....	108
4.3.2 Oceanographic covariates.....	108
4.3.3 Modeling the distribution of adult female spawners	109
4.3.4 Hypothesized drivers of age-0 recruit presence and abundance.....	109
4.3.5 Statistical model	121
4.4 Results	124
4.4.1 Overview	124
4.4.2 Encounter probability model	126
4.4.3 Positive catch model.....	127
4.5 Discussion.....	131

4.6 Acknowledgements	134
4.7 References	134
Synthesis.....	140
Chapter 1 Appendix.....	147
Chapter 2 Appendix.....	167
Chapter 3 Appendix.....	269
Chapter 4 Appendix.....	349

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Introduction

Fish populations fluctuate dramatically through time, driven by changes in the environment, fishing pressure, and the combined effects of human and natural stressors (Shelton and Mangel 2011, Essington et al. 2015). Shifts in fish population productivity are common (Vert-Pre et al. 2013), and variability in recruitment (the productivity of a stock, or the number of new fish entering a population) is typically poorly predicted by only the abundance of the spawning population (Szuwalski et al. 2015). Hundred-fold variability in annual recruitment is relatively common, driven by extremely variable survival in the early life history stages. (Houde 2008). In addition to variability in recruitment, which is the primary driver of population fluctuations on longer temporal scales (Shelton and Mangel 2011), variability in demographic processes like growth (Lorenzen 2016) and mortality (Thorson et al. 2015, Jacobsen and Essington 2018) are major sources of these fluctuations on the shorter timescales on which management typically operates. As a result of these dynamics, fishery production can vary by orders of magnitude (Thompson et al. 2022b). Furthermore, with anthropogenic forcing leading to an increased prevalence of novel ecosystem conditions, it is imperative to understand and account for the mechanisms driving population variability (Jacox et al. 2018, Morgan et al. 2019, Thompson et al. 2022a).

Recognizing these dynamics, there has been a growing emphasis on capturing some of this variability and ecological complexity in frameworks for both endangered species conservation and fisheries management. In the U.S., these frameworks were established by the Endangered Species Act (ESA), passed in 1973 and designed to conserve species and protect them from extinction, and the Magnuson-Stevens Fishery Conservation and Management Act (MSA), passed in 1976 to guide management of fisheries in U.S. marine waters (3-200 nmi offshore). The conservation science spurred by the ESA has tackled issues such as habitat associations (Schwartz 2008), invasive species (Dueñas et al. 2018), environmental forcing (Isaak and Young 2023), and predator-prey interactions (Hanson et al. 2021). Fisheries management under the MSA has begun to move towards ecosystem-based fisheries management (EBFM), championed as a holistic approach to managing fisheries whereby the various ecological, physical, and socioeconomic aspects of marine ecosystems are taken into account when managing living marine resources (Leslie and McLeod 2007, Patrick and Link 2015). In the United States, NOAA Fisheries has formally adopted an EBFM Policy and Road Map to articulate the agency's goals and practical steps towards EBFM implementation (NMFS 2016). Among the benefits of EBFM specifically mentioned in NOAA Fisheries policy are increased fishery and ecosystem sustainability, improved accuracy and comprehensiveness of management advice, and improved forecasting ability (NMFS 2016).

However, while agencies are moving towards management frameworks that seek to account for environmental and ecological interactions, most of the world's fisheries are severely data limited, meaning that abundance, demographic, or other data are insufficient to conduct robust population assessments (Costello et al. 2012). The same is true for species that are not harvested, but of conservation concern (Cooke et al. 2012), with population understanding hampered by the lack of available data, often owing to limited agency resources and the rarity of the listed species (Schwartz 2008). Nevertheless, mandates to scientifically assess population status exist under the ESA and MSA. Indeed, the 2006 amendments to the MSA established legal mandates to identify annual catch limits for all stocks (Newman et al. 2015). This requires the application of a suite of methods known as data-limited fisheries assessment methods (Dowling et al. 2016). While there is a great diversity of these methods, they all require a number of assumptions, with increasing numbers of assumptions with less data (Carruthers et al. 2014, Dowling et al. 2015). However, data-limited methods can be appropriately applied when tailored to the particular management need and data context while acknowledging uncertainty (Dowling et al. 2019).

My first chapter focused on applying these methods to one population: the ESA-listed distinct population segment of Yelloweye Rockfish (*Sebastes ruberrimus*) in the Puget Sound/Georgia Basin. Due to their late age at maturity and low productivity, Yelloweye Rockfish are highly vulnerable to fisheries exploitation (Parker et al. 2000, Williams et al. 2010). Yelloweye Rockfish in this region are distinct from populations on the outer coast of the United States and Canada, and historical exploitation of this genetically isolated population led to large declines in this population and its eventual listing as threatened under the ESA. With its listing under the ESA and the implementation of its recovery plan (NMFS 2017), it is legally required for this population to be periodically re-assessed – despite having little data to inform its population status. In this chapter, I reconstructed the catch history of this species in Puget Sound, collated length data from research surveys, and fit a data-limited stock assessment model to estimate its population status.

When considerable data is available on population abundances for multiple species and environmental conditions, drivers of ecological dynamics can begin to be disentangled. Many approaches exist for studying these dynamics, including ecosystem models (Christensen and Walters 2004), bioenergetics models (Rose et al. 2024), and individual-based models (Shin and Cury 2001). While useful for testing theory and generating plausible dynamics, these methods can be sensitive to small changes in manually calibrated parameter values and their realism is difficult to evaluate (Bracis et al. 2020). An alternative suite of approaches utilizes correlative statistical models fit to long time series to identify potential ecological mechanisms (Hampton et al. 2013a). Long observational time series are key sources of information on ecological dynamics, as they capture temporal variability, can reveal responses to perturbations, and can estimate connections between different state variables (Hampton et al. 2019).

A primary concern, however, with drawing inference from ecological time series is the potential issues of multicollinearity and spurious relationships (Dormann et al. 2013). When the degree of collinearity between two variables changes through time, this relationship is considered nonstationary (Litzow et al. 2019), and the resulting change causes the value of one variable to no longer be informative about the other. For example, while climate indices like the Pacific Decadal Oscillation and the North Pacific Gyre Oscillation were previously correlated with ecological processes like salmon productivity and planktonic ecosystem dynamics (Mantua et al. 1997, Di Lorenzo et al. 2008), these correlation structures have broken down over time (Litzow et al. 2020). These recent developments underscore a key caveat to using correlations in time series data to understand ecological responses: when underlying mechanistic drivers are not adequately captured or understood, attempts to project ecological responses using statistical correlations have the potential to collapse. This suggests that modeling proximate mechanisms, like physiological responses to stress, predation, and growth, may yield more stable inference.

Capturing these proximate mechanisms requires integrating multiple long-term ecological datasets, which individually often only capture one part of a larger story. Although many of these data collection efforts concurrently collect ancillary information on environmental properties or co-occurring taxa, they are typically focused on a single species or process. For example, over 57 million individual fish have been tagged in a massive passive integrated transponder (PIT) tagging program designed to monitor the movement and survival of juvenile and adult salmonids at hydroelectric projects in the Columbia River Basin (Tenney et al. 2023). In the marine environment, surveys were designed to monitor larval and juvenile stages of rockfishes for indices of recruitment (Field et al. 2021), or designed to collect abundance and demographic data for use in stock assessments (Keller et al. 2017).

Integrating these disparate datasets allows ecologists to answer bigger questions than they can with individual datasets (Hampton et al. 2013b). The opportunity to do this exists in the Pacific Northwest and on the U.S. West Coast, where many fisheries research surveys exist, capturing multiple species and life stages (Gallo et al. 2022). The need to address these ecological questions in this region is also great given the numerous conservation challenges. Washington State is home to 22 distinct population segments (DPSs) or evolutionarily significant units (ESUs) of fish species that are federally listed as threatened or endangered. Most of these are Pacific Salmon and Steelhead, which face a number of threats throughout their anadromous life cycle, including impacts from hydropower, invasive species, climate change, and habitat loss (Nehlsen et al. 1991, Crozier and Siegel 2023). Additionally, low and variable marine survival has been noted as a limiting factor in recovery of these populations (Petrosky et al. 2020). In the marine waters of the U.S. West Coast, groundfish populations are rebounding after a history of overexploitation, with many stocks having been declared rebuilt after previously having been assessed to be overfished (Warlick et al. 2018). However, these stocks exhibit episodic

recruitment, with healthy populations often the result of only a handful of strong year classes. This process is also poorly understood and potentially vulnerable to climate impacts (McClure et al. 2023). For example, in Sablefish (*Anoplopoma fimbria*), concerns over declining recruitment (Tolimieri et al. 2018) have been replaced by concerns over the ecological implications of massive recent recruitment events (Daly et al. 2024).

In this dissertation, I used a diversity of quantitative approaches to integrate disparate data sources and investigate both population dynamics and ecological drivers of key processes, including movement, survival, and recruitment. My first chapter, which differs from my other chapters in that it focuses on the population dynamics of a single species without modeling ecological or environmental influences, estimated the status of ESA-listed Yelloweye Rockfish in Puget Sound. By combining a reconstructed catch history with length data from recent and historical surveys, this chapter formed the basis for the five-year-review for ESA-listed Yelloweye Rockfish in the Puget Sound/Georgia Basin (Lowry et al. 2024). In my second chapter, I fit a Bayesian multistate movement model to estimate the combined influences of hydropower and climate on the movement decisions of Steelhead in the Columbia River Basin. In this large river basin, millions of Steelhead have been tagged and subsequently detected by a complex array of hundreds of antennas, necessitating a modeling approach that captures this complexity to understand movement drivers. By integrating tagging data with mainstem river temperatures, hydropower operations, and conditions in tributaries, I estimated the movement and survival of Steelhead to natal tributaries under different climate and hydropower scenarios. In my third chapter, I modeled the proximate trophic drivers of marine survival in interior Columbia River Basin fall Chinook salmon by integrating data from three different fishery-independent surveys. I investigated the relative influence of top-down versus bottom-up effects on survival, as well as the role of spatiotemporal overlap between juvenile salmon and their predators and prey on survival. In my fourth chapter, I modeled the recruitment of age-0 Sablefish as a spatially explicit process, integrating trawl survey data with oceanographic modeling outputs to investigate the influences of spawning stock biomass and the environment on the abundance and distribution of recruits. Overall, this dissertation provides key context for how fish on the U.S. West Coast respond to environmental variability, hydropower management decisions, and changing trophic landscapes.

References

Bracis, C., S. Lehuta, M. Savina-Rolland, M. Travers-Trolet, and R. Girardin. 2020. Improving confidence in complex ecosystem models: The sensitivity analysis of an Atlantis ecosystem model. *Ecological Modelling* 431:109133.

- Carruthers, T. R., A. E. Punt, C. J. Walters, A. MacCall, M. K. McAllister, E. J. Dick, and J. Cope. 2014. Evaluating methods for setting catch limits in data-limited fisheries. *Fisheries Research* 153:48–68.
- Christensen, V., and C. J. Walters. 2004. Ecopath with Ecosim: Methods, capabilities and limitations. *Ecological Modelling* 172:109–139.
- Cooke, S., C. Paukert, and Z. Hogan. 2012. Endangered river fish: factors hindering conservation and restoration. *Endangered Species Research* 17:179–191.
- Costello, C., D. Ovando, R. Hilborn, S. D. Gaines, O. Deschenes, and S. E. Lester. 2012. Status and solutions for the world's unassessed fisheries. *Science* 338:517–520.
- Crozier, L. G., and J. E. Siegel. 2023. A Comprehensive Review of the Impacts of Climate Change on Salmon: Strengths and Weaknesses of the Literature by Life Stage. *Fishes* 8:1–50.
- Daly, E. A., B. E. Chasco, C. A. Morgan, B. J. Burke, K. E. Osborne, and D. L. Draper. 2024. Implications of increased spatial and trophic overlap between juvenile Pacific salmon and Sablefish in the northern California Current. *Marine and Coastal Fisheries* 16.
- Di Lorenzo, E., N. Schneider, K. M. Cobb, P. J. S. Franks, K. Chhak, A. J. Miller, J. C. McWilliams, S. J. Bograd, H. Arango, E. Curchitser, T. M. Powell, and P. Rivière. 2008. North Pacific Gyre Oscillation links ocean climate and ecosystem change. *Geophysical Research Letters* 35:2–7.
- Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B. Gruber, B. Lafourcade, P. J. Leitão, T. Münkemüller, C. McClean, P. E. Osborne, B. Reineking, B. Schröder, A. K. Skidmore, D. Zurell, and S. Lautenbach. 2013. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36:27–46.
- Dowling, N. A., A. D. M. Smith, D. C. Smith, A. M. Parma, C. M. Dichmont, K. Sainsbury, J. R. Wilson, D. T. Dougherty, and J. M. Cope. 2019. Generic solutions for data-limited fishery assessments are not so simple. *Fish and Fisheries* 20:174–188.
- Dowling, N. A., J. R. Wilson, M. B. Rudd, E. A. Babcock, M. Caillaux, J. Cope, D. Dougherty, R. Fujita, T. Gedamke, and M. Gleason. 2016. FishPath: a decision support system for assessing and managing data-and capacity-limited fisheries. *Assessing and Managing Data-Limited Fish Stocks*. Alaska Sea Grant, University of Alaska Fairbanks.
- Dowling, N., C. Dichmont, M. Haddon, D. Smith, A. Smith, and K. Sainsbury. 2015. Empirical harvest strategies for data-poor fisheries: a review of the literature. *Fisheries Research* 171:141–153.
- Dueñas, M.-A., H. J. Ruffhead, N. H. Wakefield, P. D. Roberts, D. J. Hemming, and H. Diaz-Soltero. 2018. The role played by invasive species in interactions with endangered and threatened species in the United States: a systematic review. *Biodiversity and Conservation* 27:3171–3183.
- Essington, T. E., P. E. Moriarty, H. E. Froehlich, E. E. Hodgson, L. E. Koehn, K. L. Oken, M. C. Siple, and C. C. Stawitz. 2015. Fishing amplifies forage fish population collapses.

- Proceedings of the National Academy of Sciences of the United States of America 112:6648–6652.
- Field, J. C., R. R. Miller, J. A. Santora, N. Tolimieri, M. A. Haltuch, R. D. Brodeur, T. D. Auth, E. J. Dick, M. H. Monk, K. M. Sakuma, and B. K. Wells. 2021. Spatiotemporal patterns of variability in the abundance and distribution of winter-spawned pelagic juvenile rockfish in the California Current. *PLoS ONE* 16:1–25.
- Gallo, N. D., N. M. Bowlin, A. R. Thompson, E. V. Satterthwaite, B. Brady, and B. X. Semmens. 2022. Fisheries Surveys Are Essential Ocean Observing Programs in a Time of Global Change: A Synthesis of Oceanographic and Ecological Data From U.S. West Coast Fisheries Surveys. *Frontiers in Marine Science* 9:1–18.
- Hampton, S. E., E. E. Holmes, L. P. Scheef, M. D. Scheuerell, S. L. Katz, D. E. Pendleton, and E. J. Ward. 2013a. Quantifying effects of abiotic and biotic drivers on community dynamics with multivariate autoregressive (MAR) models. *Ecology* 94:2663–2669.
- Hampton, S. E., M. D. Scheuerell, M. J. Church, and J. M. Melack. 2019. Long-term perspectives in aquatic research. *Limnology and Oceanography* 64:S2–S10.
- Hampton, S. E., C. A. Strasser, J. J. Tewksbury, W. K. Gram, A. E. Budden, A. L. Batcheller, C. S. Duke, and J. H. Porter. 2013b. Big data and the future of ecology. *Frontiers in Ecology and the Environment* 11:156–162.
- Hanson, M. B., C. K. Emmons, M. J. Ford, M. Everett, K. Parsons, L. K. Park, J. Hempelmann, D. M. Van Doornik, G. S. Schorr, and J. K. Jacobsen. 2021. Endangered predators and endangered prey: Seasonal diet of Southern Resident killer whales. *PloS one* 16:e0247031.
- Houde, E. D. 2008. Emerging from Hjort’s shadow. *Journal of Northwest Atlantic Fishery Science* 41:53–70.
- Isaak, D. J., and M. K. Young. 2023. Cold-water habitats, climate refugia, and their utility for conserving salmonid fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 80:1187–1206.
- Jacobsen, N. S., and T. E. Essington. 2018. Natural mortality augments population fluctuations of forage fish. *Fish and Fisheries* 19:791–797.
- Jacox, M. G., M. A. Alexander, N. J. Mantua, J. D. Scott, G. Hervieux, R. S. Webb, and F. E. Werner. 2018. Forcing of multi-year extreme ocean temperatures that impacted California Current living marine resources in 2016. *Bull. Amer. Meteor. Soc* 99.
- Keller, A. A., J. R. Wallace, and R. D. Methot. 2017. The Northwest Fisheries Science Center’s West Coast Groundfish Bottom Trawl Survey: History, Design, and Description. NOAA Technical Memorandum:47.
- Leslie, H. M., and K. L. McLeod. 2007. Confronting the challenges of implementing marine ecosystem-based management. *Frontiers in Ecology and the Environment* 5:540–548.
- Litzow, M. A., L. Ciannelli, P. Puerta, J. J. Wettstein, R. R. Rykaczewski, and M. Opiekun. 2019. Nonstationary environmental and community relationships in the North Pacific Ocean. *Ecology* 100:1–8.

- Litzow, M. A., M. E. Hunsicker, N. A. Bond, B. J. Burke, C. J. Cunningham, J. L. Gosselin, E. L. Norton, E. J. Ward, and S. G. Zador. 2020. The changing physical and ecological meanings of North Pacific Ocean climate indices. *Proceedings of the National Academy of Sciences of the United States of America* 117:7665–7671.
- Lorenzen, K. 2016. Toward a new paradigm for growth modeling in fisheries stock assessments: Embracing plasticity and its consequences. *Fisheries Research* 180:4–22.
- Lowry, D., J. Selleck, K. Andrews, and J. Cope. 2024. Yelloweye Rockfish (*Sebastes ruberrimus*) and Bocaccio (*Sebastes paucispinis*) of the Puget Sound/Georgia Basin 5-Year Review: Summary and Evaluation.
- Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society* 78:1069–1080.
- McClure, M. M., M. A. Haltuch, E. Willis-Norton, D. D. Huff, E. L. Hazen, L. G. Crozier, M. G. Jacox, M. W. Nelson, K. S. Andrews, L. A. K. Barnett, A. M. Berger, S. Beyer, J. Bizzarro, D. Boughton, J. M. Cope, M. Carr, H. Dewar, E. Dick, E. Dorval, J. Dunham, V. Gertseva, C. M. Greene, R. G. Gustafson, O. S. Hamel, C. J. Harvey, M. J. Henderson, C. E. Jordan, I. C. Kaplan, S. T. Lindley, N. J. Mantua, S. E. Matson, M. H. Monk, P. Moyle, C. Nicol, J. Pohl, R. R. Rykaczewski, J. F. Samhuri, S. Sogard, N. Tolimieri, J. Wallace, C. Wetzel, and S. J. Bograd. 2023. Vulnerability to climate change of managed stocks in the California Current large marine ecosystem. *Frontiers in Marine Science* 10:1–21.
- Morgan, C. A., B. R. Beckman, L. A. Weitkamp, and K. L. Fresh. 2019. Recent Ecosystem Disturbance in the Northern California Current. *Fisheries* 44:465–474.
- Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries* 16:4–21.
- Newman, D., J. Berkson, and L. Suatoni. 2015. Current methods for setting catch limits for data-limited fish stocks in the United States. *Fisheries Research* 164:86–93.
- NMFS. 2016. Ecosystem-Based Fisheries Management Policy of the National Marine Fisheries Service:1–9.
- NMFS. 2017. Rockfish Recovery Plan: Puget Sound / Georgia Basin Yelloweye Rockfish (*Sebastes ruberrimus*) and Bocaccio (*Sebastes paucispinis*).
- Parker, S. J., S. A. Berkeley, J. T. Golden, D. R. Gunderson, J. Heifetz, M. A. Hixon, R. Larson, B. M. Leaman, M. S. Love, and J. A. Musick. 2000. Management of Pacific rockfish. *Fisheries* 25:22–30.
- Patrick, W. S., and J. S. Link. 2015. Myths that continue to impede progress in ecosystem-based fisheries management. *Fisheries* 40:155–160.
- Petrosky, C. E., H. A. Schaller, E. S. Tinus, T. Copeland, and A. J. Storch. 2020. Achieving Productivity to Recover and Restore Columbia River Stream-Type Chinook Salmon Relies on Increasing Smolt-To-Adult Survival. *North American Journal of Fisheries Management* 40:789–803.

- Rose, K., K. Holsman, J. Nye, E. Markowitz, T. Banha, N. Bednaršek, J. Bueno-Pardo, D. Deslauriers, E. Fulton, K. Huebert, M. Huret, S. Ito, S. Koenigstein, L. Li, H. Moustahfid, B. Muhling, P. Neubauer, J. Paula, E. Siddon, M. Skogen, P. Spencer, P. Van Denderen, G. Van Der Meeren, and M. Peck. 2024. Advancing bioenergetics-based modeling to improve climate change projections of marine ecosystems. *Marine Ecology Progress Series* 732:193–221.
- Schwartz, M. W. 2008. The performance of the endangered species act. *Annual Review of Ecology, Evolution, and Systematics* 39:279–299.
- Shelton, A. O., and M. Mangel. 2011. Fluctuations of fish populations and the magnifying effects of fishing. *Proceedings of the National Academy of Sciences of the United States of America* 108:7075–7080.
- Shin, Y.-J., and P. Cury. 2001. Exploring fish community dynamics through size-dependent trophic interactions using a spatialized individual-based model. *Aquatic Living Resources* 14:65–80.
- Szuwalski, C. S., K. A. Vert-pre, A. E. Punt, T. A. Branch, and R. Hilborn. 2015. Examining common assumptions about recruitment : a meta-analysis of recruitment dynamics for worldwide marine fisheries:633–648.
- Tenney, J., N. Tancreto, G. Axel, and S. Livingston. 2023. Columbia Basin PIT Tag Information System, 1/1/2023 - 12/31/2023 Annual Report, 1990-080-00.
- Thompson, A. R., N. J. Ben-Aderet, N. M. Bowlin, D. Kacev, R. Swalethorp, and W. Watson. 2022a. Putting the Pacific marine heatwave into perspective: The response of larval fish off southern California to unprecedented warming in 2014–2016 relative to the previous 65 years. *Global Change Biology* 28:1766–1785.
- Thompson, A. R., E. P. Bjorkstedt, S. J. Bograd, J. L. Fisher, E. L. Hazen, A. Leising, J. A. Santora, E. V. Satterthwaite, W. J. Sydeman, M. Alksne, T. D. Auth, S. Baumann-Pickering, N. M. Bowlin, B. J. Burke, E. A. Daly, H. Dewar, J. C. Field, N. T. Garfield, A. Giddings, R. Goericke, J. Hildebrand, C. A. Horton, K. C. Jacobson, M. G. Jacox, J. Jahncke, M. Johns, J. Jones, R. M. Kudela, S. R. Melin, C. A. Morgan, C. F. Nickels, R. A. Orben, J. M. Porquez, E. J. Portner, A. Preti, R. R. Robertson, D. L. Rudnick, K. M. Sakuma, I. D. Schroeder, O. E. Snodgrass, S. A. Thompson, J. S. Trickey, P. Warzybok, W. Watson, and E. D. Weber. 2022b. State of the California Current Ecosystem in 2021: Winter is coming? *Frontiers in Marine Science* 9:1–23.
- Thorson, J. T., C. C. Monnahan, and J. M. Cope. 2015. The potential impact of time-variation in vital rates on fisheries management targets for marine fishes. *Fisheries Research* 169:8–17.
- Tolimieri, N., M. A. Haltuch, Q. Lee, M. G. Jacox, and S. J. Bograd. 2018. Oceanographic drivers of sablefish recruitment in the California Current. *Fisheries Oceanography* 27:458–474.

- Vert-Pre, K. A., R. O. Amoroso, O. P. Jensen, and R. Hilborn. 2013. Frequency and intensity of productivity regime shifts in marine fish stocks. *Proceedings of the National Academy of Sciences of the United States of America* 110:1779–1784.
- Warlick, A., E. Steiner, and M. Guldin. 2018. History of the West Coast groundfish trawl fishery: Tracking socioeconomic characteristics across different management policies in a multispecies fishery. *Marine Policy* 93:9–21.
- Williams, G. D., P. S. Levin, and W. A. Palsson. 2010. Rockfish in Puget Sound: An ecological history of exploitation. *Marine Policy* 34:1010–1020.

Chapter 1. Data-limited fishery assessment methods shed light on the exploitation history and population dynamics of ESA-listed Yelloweye Rockfish in Puget Sound, Washington

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1.1 Abstract

The Distinct Population Segment (DPS) of Yelloweye Rockfish (*Sebastes ruberrimus*) inhabiting the Puget Sound/Georgia Basin was listed under the Endangered Species Act (ESA) in 2010, and a formal recovery plan for the DPS was published by NOAA Fisheries in 2017. In this recovery plan, the biological criteria for delisting or downlisting were specified as certain levels of spawning potential ratio (SPR), a commonly used metric of equilibrium stock status for commercially exploited fishes. Although this metric can be estimated from length compositions, the combination of length data with a catch history (which was not previously available for this DPS) improves our understanding of population dynamics over time and allows us to estimate a different measure of stock status, relative (to unfished) spawning stock biomass (SSB), rather than only SPR. To estimate relative SSB and reconstruct the historical dynamics of this DPS, we reconstructed the catch history from fisheries records, collated length data from historical and contemporary hook-and-line surveys, and fit a data-limited version of a statistical catch-at-age model. Despite a high level of uncertainty, we estimate that Yelloweye Rockfish in Puget Sound are above 25% of unfished biomass (a reference point detailed in the recovery criteria) under the assumption of deterministic recruitment, presenting the first direct estimates of Yelloweye Rockfish population status in Puget Sound. However, as informed by recent genetic studies, the DPS boundaries of ESA-listed Yelloweye Rockfish extend from South Puget Sound to Queen Charlotte Strait in British Columbia. The Canadian portion of this population is managed separately and is currently estimated to be at 32% of unfished biomass (95% quantiles: 15 to 68%). Thus, the disjunction between the biological boundaries of the population and the jurisdictional boundaries between Canada and the U.S. present an additional source of uncertainty in assessing recovery that must be addressed to achieve DPS-wide recovery goals.

1.2 Introduction

For species of conservation concern, the data available for population viability analysis or status assessments can be severely lacking, often owing to limited agency resources and the rarity of

listed species (Schwartz 2008). Nevertheless, Section 4(c)(2) of the United States Endangered Species Act (ESA) requires regulatory agencies to conduct a status review once every five years for any listed species, including demographically discrete and significant distinct population segments (DPSs). Therefore, because consequential changes in listing status (i.e., downlisting, delisting, or uplisting) and additional regulatory decisions are highly influenced by these five-year reviews, quantitative analytical methods to assess population status and viability, despite limited data, are crucial for federal agencies to fulfill their mandates.

In the Pacific Northwest, two species of rockfishes have DPSs that are listed under the ESA: Puget Sound/Georgia Basin (PSGB) Yelloweye Rockfish (*Sebastes ruberrimus*) is listed as Threatened, while PSGB Bocaccio (*Sebastes paucispinis*) is listed as Endangered (75 FR 22276, NMFS 2010). Due to their extreme rarity within the DPS boundaries, data on Bocaccio since the time of listing have been very limited, precluding any quantitative analysis. In contrast, Yelloweye Rockfish have been sampled with comparative regularity, and recent genetic evidence confirmed that Yelloweye Rockfish collected from Puget Sound, WA, to Queen Charlotte Strait, B.C. (Fig. 1), are distinct from populations found on the outer coast (Andrews et al. 2018). Yelloweye Rockfish is a deepwater rockfish with low productivity and episodic recruitment (Love et al. 2002), but given their longevity, these episodic recruitment events do not greatly affect population persistence. Yelloweye Rockfish have a maximum reported age of 147 years (Love 2011). Many species of rockfish, due to their late age at maturity and low productivity, are highly vulnerable to fisheries exploitation (Parker et al. 2000; Williams et al. 2010). Yelloweye Rockfish have been heavily exploited throughout their range, which extends from California through the Gulf of Alaska (Gertseva and Cope 2017; Yamanaka et al. 2018; Wood et al. 2021). In each of the areas in which Yelloweye Rockfish are currently fished commercially, the corresponding management agency (Fisheries and Oceans Canada [DFO], NOAA Fisheries, or the Alaska Department of Fish and Game) conducts regular stock assessments, which integrate available fishery-independent and fishery-dependent data into a population model. The most recent status assessment for the West Coast stock estimated that it was at 28% of unfished biomass (Gertseva and Cope 2017), while the coastal British Columbia stock was estimated to be at 18% of unfished biomass (Yamanaka et al. 2018).

Prior to the 1960s, rockfishes in Puget Sound were not a primary target of commercial and recreational fisheries, and monitoring of individual rockfish species within catches was consequently not a priority for the Washington Department of Fisheries (DiDonato 1969; Pálsson et al. 2009). However, new Puget Sound groundfish fisheries were developed in the 1970s and these opportunities were promoted to commercial and recreational fishers displaced by the closure of Canadian waters to foreign fishing fleets and the 1974 U.S. v. Washington federal court ruling that reaffirmed treaty fishing rights and reduced salmon quota for non-tribal fishers (Pálsson et al. 2009). The first Puget Sound groundfish management plan was later published in 1982, though the rapid development of these fisheries in the intervening years resulted in catch

reporting and monitoring that was not comprehensive (Pedersen and DiDonato 1982; Palsson et al. 2009). As a result, abundance information on specific rockfish species in Puget Sound is severely lacking into the 1970s: at the time when the original decision was made to list PSGB Yelloweye Rockfish under the ESA, trends in abundance were based on trends in total rockfishes, with proxy data such as frequency of occurrence in recreational or commercial fishery surveys used to provide species-specific information (Drake et al. 2010).

The lack of estimates for abundance or biological data (e.g., lengths or ages) have limited the ability to assess the status of ESA-listed rockfishes with respect to their species-specific recovery criteria based on spawning potential ratio (SPR) (Tonnes et al. 2016; NMFS 2017). SPR, which is defined as the proportion of the unfished reproductive potential remaining at a given level of fishing pressure (Hordyk et al. 2015), was chosen by the recovery team based on the ability to estimate it using limited data (NMFS 2017). However, data-limited methods capable of estimating SPR or other metrics of stock status from the sparse data available for rockfish species in Puget Sound were not yet well-articulated at the time the listing decision was made in 2010, or during the first five-year review after listing (Tonnes et al. 2016). This is due to the fact that many data-limited assessment methods were developed in response to the 2006 amendments to the Magnuson-Stevens Fishery Conservation and Management Act (MSA), which established legal mandates to identify annual catch limits (ACL) for all stocks (Newman et al. 2015). While the MSA dictates how commercially exploited fish stocks are managed, the ESA concerns species threatened with extinction within a distinct population segment(s). Thus, these recently developed methods to assess fish stocks managed under the MSA present an opportunity to provide new, species-specific insights into the dynamics of an ESA-listed species.

Earlier studies of rockfishes in Puget Sound strongly support a significant decline in overall populations over the past 40 years (Palsson et al. 2009; Williams et al. 2010; Beaudreau and Levin 2014). A previous study of population trajectories of rockfishes in Puget Sound indicated an annual average decrease of 3.9% per year, translating to a 77% decline from 1977 to 2014 (Tolimieri et al. 2017). That study, which represented the best available science at the time of the last five-year review in 2016, was based on two data sources: 1) CPUE from recreational anglers as determined via catch-record cards, phone interviews, and creel surveys (e.g., Kraig and Scalici 2019); and 2) CPUE from a long-term, systematic trawl survey conducted by the Washington Department of Fish and Wildlife (WDFW) (Quinnell and Schmitt 1991; Palsson et al. 2002; Blaine et al. 2020). However, the applicability of these data for informing the status of ESA-listed Yelloweye Rockfish was limited by the infrequency with which this species was detected using these methods (Tolimieri et al. 2017). In the case of the recreational fishery data, regulatory changes, which included reductions in bag limits starting in 1994 (Palsson et al. 2009), a prohibition on Yelloweye Rockfish retention in 2002, and a 120-ft depth limit when targeting bottomfish in 2010, meant that this deep-water species was not well represented by the overall trends in rockfish abundance. In addition, the WDFW trawl survey, which mainly

samples soft bottom habitat, does not effectively sample Yelloweye Rockfish, as this species is typically associated with rocky habitat (O’Connell and Carlile 1993; Love et al. 2002; Pacunski et al. 2013, 2020). Therefore, to inform the status of these species with respect to recovery criteria, methods that disaggregate ESA-listed Yelloweye Rockfish from encounters with other rockfishes are necessary.

We present, here, a case study of how methods typically applied to commercially exploited species can shed light on the status of ESA-listed Yelloweye Rockfish in the PSGB when presented with only a catch history and limited length composition data. By using a modified version of Stock Synthesis, a statistical age-structured population modeling framework (Methot and Wetzel 2013) used to assess other groundfish species in U.S. fisheries, with catch and length data only (Rudd et al. 2021), we generated quantitative estimates of population status that can be used to inform future conservation and management actions under the ESA framework.

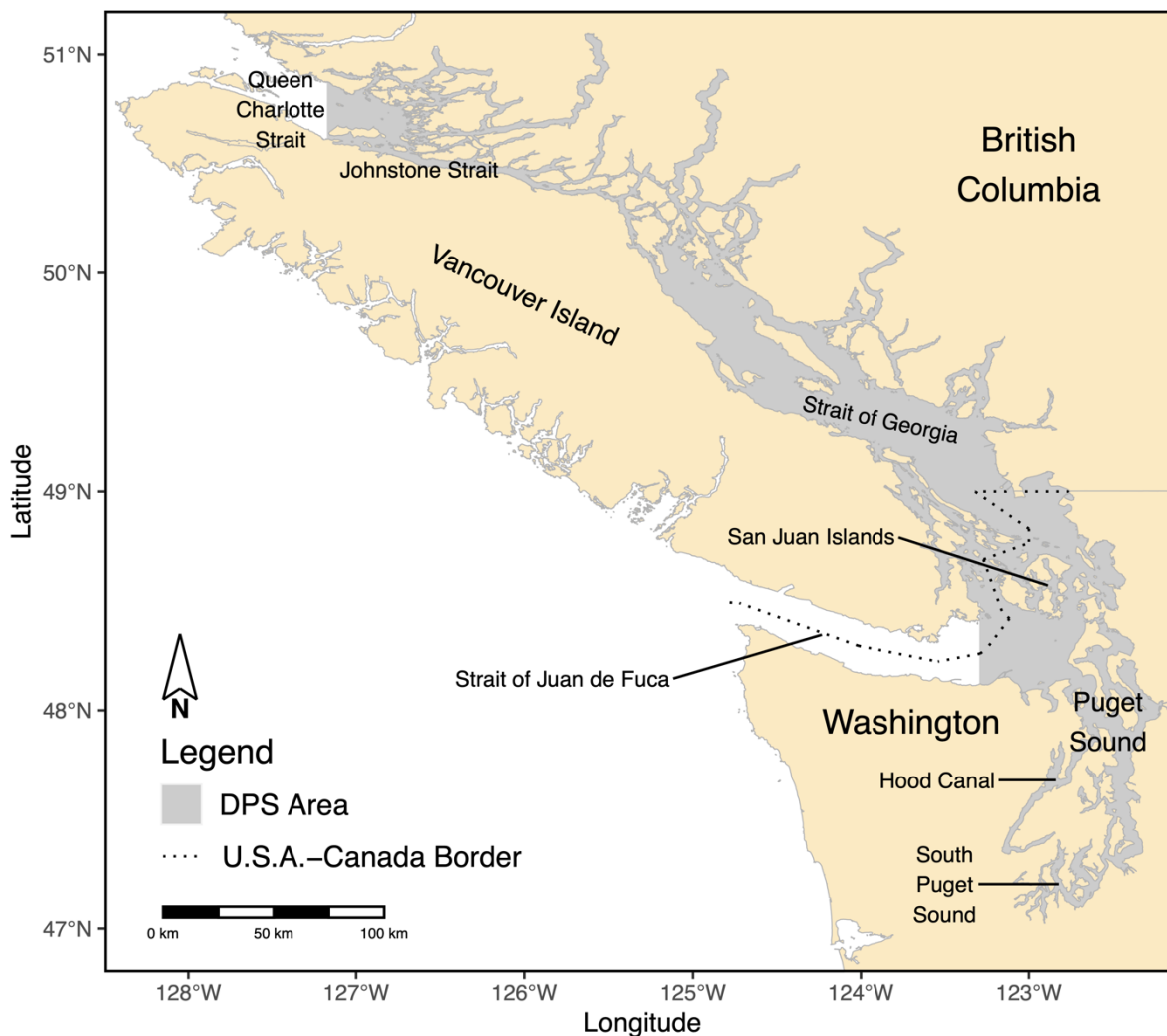


Figure 1. Boundaries of the Puget Sound/Georgia Basin Distinct Population Segment (DPS) of Yelloweye Rockfish.

1.3 Methods

1.3.1 Catch reconstruction

Removal histories provide both magnitude and trend in fishing mortality rates that can help determine the conditions under which fishing mortality affects fish populations (Ralston et al. 2010). A catch reconstruction for Puget Sound Yelloweye Rockfish was completed for the first time in this study in order to develop hypotheses on what removal histories could lead to historically low abundance. This required a reconstruction of the two main fisheries for Yelloweye Rockfish in Puget Sound, the commercial and recreational fisheries.

Rockfish catches from commercial and recreational fisheries in Puget Sound have previously been reported in Palsson et al. (2009); the recreational catches were reported from 1970-2007, and the commercial catches were reported from 1921-2007. Because of limited species composition data and often low confidence in species assignments, these catches were only reported at the genus (*Sebastes*) level (Palsson et al. 2009). In this study, we expanded the taxonomic and temporal resolution of this catch history, estimating commercial catch of Yelloweye Rockfish from 1921-2020 and recreational catch from 1938-2020.

To partition Yelloweye Rockfish catches from estimates of total rockfish catch, we applied the available species composition data (1970-present for commercial landings, 1965-1967 and 1980-present for recreational landings) to these catches and constructed alternative catch history scenarios using uncertainty in these catches. These catch scenarios incorporated spatially and temporally varying sources of uncertainty corresponding to the data sources and the primary associated uncertainty for each time period, an overview of which is presented in the following sections. While there are still remaining sources of uncertainty that could not be addressed through our catch scenario approach, the bounding of uncertainty presented here gives a reasonable estimate of plausible removal histories sufficient for our modeling approach. Detailed information on the catch reconstruction and the creation of catch scenarios can be found in Appendix A.

The resulting catch scenarios were as follows: a “medium” catch scenario, which served as the “most likely” estimate, coupled with “high” and “low” catch scenarios, which attempted to capture the upper and lower bounds of uncertainty. In accordance with a recent genetic study (Andrews et al. 2018) that showed differentiation between the Yelloweye Rockfish population in Hood Canal and the rest of the Puget Sound/Georgia Basin, we excluded Hood Canal from the catch history we present for Yelloweye Rockfish in Puget Sound. Ecological conditions within Hood Canal, specifically seasonal bouts of low dissolved oxygen, have also resulted in the application of a distinct fishery management regime to this area.

1.3.2 Commercial catch reconstruction

The reconstruction of commercial catches of Yelloweye Rockfish in Puget Sound was conducted in three general steps: (1) estimating catches of total rockfish from fisheries records; (2) estimating the proportion of total rockfish catch that was Yelloweye Rockfish; and (3) generating catch scenarios based on the sources of uncertainty associated with steps (1) and (2).

We estimated the total catch of rockfishes using different data sources collected by the Washington Department of Fisheries (WDF), and later the WDFW. Quantitative estimates of landings of rockfishes from the commercial fishery in Puget Sound began in 1921 based on receipts from taxes levied on the sale of various fish products (Nye 1982). This system of estimating landings, which had issues associated with the limited information gleaned from tax receipts (e.g., limited spatial resolution, origin of catch sometimes unclear), was improved in 1935 with the advent of the fish ticket system (Nye 1982). This system required fishermen to report catches on standardized tickets that included fields for critical information such as catch area and gear type. With slight improvements over time, such as the introduction of an interview system in the 1950s to gather additional information from fishing vessel captains (Alverson 1957), the fish ticket system remained in place for the majority of the history of the commercial bottomfish fishery in Puget Sound. Significant regulatory changes banned commercial bottomfish trawl, jig, and troll fishing throughout Puget Sound east of Neah Bay by the early 1990s (Palsson et al. 2009), and the remaining fisheries that employed gear with a risk of rockfish impacts were closed in 2010 (WDFW 2010).

Species composition data from the commercial fishery necessary to prorate the catch of rockfishes into species is very limited. Prior to 1970, when the WDF began collecting field samples of commercial catches, no reliable species composition information exists for rockfishes. The only exception to this for Yelloweye Rockfish are reports of “Red Snapper,” which was a reporting category from 1955-1969 and was a common name for Yelloweye Rockfish used at the time (Kincaid 1919; Smith 1937). Therefore, for our catch reconstruction, during the period of 1955-1969 when “Red Snapper” catch was reported, “Red Snapper” landings were interpreted as the total Yelloweye Rockfish landings for the time period. In all other time periods prior to 1970, Yelloweye Rockfish landings were estimated by prorating total rockfish catch to individual species using species composition data from WDFW commercial landings by gear type and region from 1970-1987 (the closest time period from which species composition data was available) from Pedersen and Bargmann (1986). From 1970 onwards, field samples taken by the WDFW of commercial catches were used to prorate the catch of total rockfish into species from the same or similar time periods.

1.3.3 Recreational catch reconstruction

The recreational bottomfish fishery in Puget Sound has been a significant monitoring challenge for the WDF/WDFW, but is also responsible for the majority of the landings of PSGB Yelloweye Rockfish, which are associated with rocky habitats (Palsson et al. 2009). The estimates of recreational rockfish harvest from 1970-2007 published in Palsson et al. (2009) formed the basis for our catch reconstruction. We expanded the temporal extent of this catch history back to 1938 using early reports by the WDF on the sport fishery and prorated all catch to species using species composition data from the Marine Recreational Fisheries Statistical Survey (MRFSS), which collected data from 1980-2002, or from species composition estimates generated in early studies of the recreational bottomfish fishery (Buckley 1967, 1968; Buckley and Satterthwaite 1970).

Monitoring of recreational fisheries in Puget Sound was historically focused on salmon, with only sparse reports on bottomfish harvest until 1965 (DiDonato 1969). During this time, most bottomfish catch was bycatch from salmon anglers, whose effort and catch was much more closely monitored, and thus catch rates of bottomfish by salmon anglers were used to inform our estimates of Yelloweye Rockfish harvest from 1938-1965. From 1938-1941, the WDF attempted to estimate catches from the sport fishery for the first time, with inclusion of “rockfish” and “red snapper” as reporting categories. These reports, with adjustments made for underreporting, are the start of our time series of recreational catches. However, starting in 1942, the WDF abandoned attempts to report catches of all species and focused only on salmon and total angler effort. CPUE from the 1938-1941 reports were thus applied to estimates of total angler days from the period 1942-1965 to estimate catches of rockfish.

Beginning in 1965, the WDF began attempting to monitor the growing recreational bottomfish fishery (Buckley 1967). This initiated a series of reports on the bottomfish sport fishery for 1965-1973 (Buckley 1967, 1968; Buckley and Satterthwaite 1970; Bargmann 1977). In our catch reconstruction, the report from 1965 was omitted due to anomalies in data reporting and catches from 1970 onwards were re-estimated in (Palsson 1987); we therefore only used the reports from 1966-1969.

From 1970-2003, the WDFW estimated catches from the recreational bottomfish fishery through a combination of catch records from salmon anglers and a dockside creel survey of hook-and-line anglers (Palsson et al. 2009). Catch-record cards were required to be returned by salmon anglers, from which the number of salmon trips were estimated. The creel survey was used to determine the catch per trip of bottomfish, which was then multiplied by the number of trips per month and area to estimate the total number of bottomfish caught (Palsson 1987). An assumption inherent in these estimates is that dockside creel surveys, which sampled only a small fraction of angler trips, were representative with regard to bottomfish encounter rate on a spatiotemporal scale fine enough to justify this expansion method. In addition, reliance on the salmon sport

fishery to estimate bottomfish catches proved problematic following large-scale closures of salmon fisheries from 1994 to 2003 (see Appendix A).

From 2003-2020, the WDFW conducted surveys of the recreational fishery through a telephone survey of licensed fishers to estimate fishing effort and the dockside WDFW creel survey that estimates catch rates of specific species (e.g., Kraig and Scalici 2019). This new system removed the reliance on open salmon fisheries for bottomfish catch estimates and was deliberately designed to obtain data for all target species. Importantly, this reporting system also collects information on released rockfish, which was previously not obtained, allowing separation of encounter rate and retention rate. This change was crucial to estimating fishery impacts after rockfish retention was banned across the whole of Puget Sound in 2010. We applied estimates of released rockfish mortality to this information to estimate total mortality. While there are significant sources of uncertainty in catch estimates from the creel survey (e.g., possible under-reporting, species misidentification, and inconsistent data weighting), fishery mortality from this time period was minor compared to preceding time periods, and this uncertainty is addressed in the catch scenarios (see Appendix A).

1.3.4 Length composition data sources

Catch data on its own is typically insufficient to determine stock status (Free et al. 2020; Ovando et al. 2021). Therefore, the second set of information needed to evaluate the status of Yelloweye Rockfish are biological compositions from the population. While age data is preferred as it gives a direct measure of population age structure, it is more difficult to obtain and is usually lethal, limiting its collection for ESA-listed species. As a proxy for age data, we used length composition data from three hook-and-line research surveys (1974-1977, 2014-2015, 2017-2019) that caught Yelloweye Rockfish in Puget Sound. Because of small sample sizes, data from the two recent surveys were combined, resulting in two distinct time periods of data (a historical and a contemporary sample). Each survey used recreational fishing methods to sample areas where anglers currently or historically targeted rockfish; thus, the length composition data were assumed to reflect the selectivity and encounter likelihood of the recreational fishery. While the recreational fishery is now closed, the selectivity of the surveys during the time period following fishery closure is assumed to be the same as that of the recreational fishery, were it to be open. This is an important assumption of the modeling framework (see Section 2.3).

The best historical data available come from a hook-and-line survey of marine fishes (Washington et al. 1978). This survey covered the years 1974-1977 and was intended to gather information to support the growth of a recreational rockfish fishery and inform understanding of the biology and ecology of rockfish in Puget Sound (Browning 2014). The survey used a variety of recreational fishing methods (e.g., angling with bait such as herring, squid, jigs, or spinners) in 0-180 m of water, with effort focused primarily in Puget Sound Proper (the marine waters

extending eastward from the mouth of Admiralty Inlet), but also extended into the Strait of Juan de Fuca. The sampling area was divided into a grid of units of one square nautical mile, with sampling targeting areas of suspected rockfish habitat. Researchers departed from Seattle or Mukilteo, WA and targeted areas that had the characteristics of high-quality rockfish habitat: complex bottom structure, kelp beds, and areas of known rockfish abundance (Browning 2014). For this analysis, we used only the lengths of Yelloweye Rockfish caught within the DPS boundaries, excluding Hood Canal.

More contemporary length distribution data were gathered from two research projects focused specifically on ESA-listed rockfishes. First, we used length data collected by Andrews et al. (2018) in 2014 and 2015 for all individuals caught within the DPS boundaries, excluding Hood Canal (“ESA Genetics” study). This project used similarly common hook-and-line fishing methods as the Washington et al. (1978) study and typically fished at depths from 30-100m. However, sampling effort for this study was not uniformly distributed, but rather targeted sites where ESA-listed rockfish species were most likely to be found. Site selection was informed by consultation with recreational fishing guides, local fishing captains and angler clubs, and scientists and managers, as well as recent and historical observations from recreational anglers, ROV surveys (Lowry et al. 2022; Pacunski et al. 2013, 2020), SCUBA divers, and other research and monitoring surveys (e.g., Blaine et al. 2020). As a second contemporary source, we used length data collected during a research project studying the rates of and effects of various bait types on rockfish bycatch in the lingcod (*Ophiodon elongatus*) fishery in Puget Sound in 2017-2019 (“Lingcod Bycatch” study; Kelly Andrews, NWFSC, unpublished data). This study used three specific types of bait and targeted 12 sites in the main basin of Puget Sound and the San Juan Islands where lingcod were most prevalent during the “ESA Genetics” study.

1.3.5 Population dynamics model

The main objective of the population dynamics model was to gain insight into the relative stock status, calculated as the fraction of unfished population size, of the PSGB Yelloweye Rockfish DPS across significant sources of uncertainty. The lower end of the uncertainty interval is interpreted as the conservative estimate of population status, as well as an indication of the risk of extinction. We also focus on relative stock size rather than absolute stock size, as the measure of absolute abundance is highly uncertain given the limited data. While measures of absolute abundance are only needed if setting catch limits under fisheries management frameworks, which is both outside the scope and capabilities of our analysis, relative stock status offers a direct measure of population recovery within an ESA context.

The portion of the PSGB DPS of Yelloweye Rockfish that is in United States waters is the only portion of the stock considered in this analysis. While genetic research (Andrews et al. 2018) indicates that there is one panmictic Yelloweye Rockfish population (excluding Hood Canal) from South Puget Sound to Queen Charlotte Strait in British Columbia, the Canadian portion of

the Puget Sound/Georgia DPS was excluded from this analysis. We modeled the United States data separately for three reasons: DFO recently completed an assessment of Yelloweye Rockfish in British Columbia inside waters, for which there is more data available (Haggarty et al. 2021); the population size of Yelloweye Rockfish in Canadian waters is much higher than in Puget Sound and would swamp any signal in the U.S. portion of the DPS; and data-driven recovery actions identified within United States waters of the DPS are under the regulatory authority of NOAA Fisheries and the WDFW and, thus, capable of being enacted by the authors and our partners.

The population dynamics model used for this analysis was Stock Synthesis (SS) with catch and length compositions only (SS-CL; Rudd et al. 2021), with different model formulations used to explore uncertainty. For each of the model formulations, length data from the hook-and-line research projects and the catch histories were the main data inputs into SS-CL. Stock Synthesis (Methot and Wetzel 2013) is an integrated stock assessment framework that provides for flexibility in data treatment, allowing it to be highly scalable to the amount of data available. SS-CL uses the Stock Synthesis framework but includes only catch and length data, and usually fixes the values of life history parameters. The SS-CL formulation of SS has been demonstrated, through simulation testing and comparisons to full stock assessment results, to generate low-bias estimates of key population quantities (including stock status) when life history parameter values are reasonably specified and with as little as one year of length data, although performance improves with larger sample sizes and more years of length data (Rudd et al. 2021).

We explored uncertainty in our different model formulations by changing two major inputs: catch histories and the value of natural mortality. Exploration across possible Beverton-Holt steepness values (a measure of stock productivity, values searched ranged from 0.3 to 1, with the reference model at 0.72) was also performed, but produced very limited model sensitivity, and therefore are not included here. Natural mortality (M) is a common life history trait used to explore parameter uncertainty as it is hard to estimate directly and is highly influential for estimates of stock status (Punt et al. 2021). The SS-CL models were run using three catch scenarios (high, medium, and low), each of which was also applied to a series of M values. The series of M values was based around a lognormal distribution with a mean of 0.044 (Gertseva and Cope 2017) and standard deviation 0.31 as suggested by Hamel and Cope (2022), and results in a series of explored M values from 0.024 (~2.5% quantile) to 0.081 (~97.5% quantile) with a step of 0.004.

Length data from the three research projects previously described (Section 2.2) are the primary data sources for the SS-CL model. While other length composition data were available from samples of recreational catch, these were not included in the final version of the SS-CL model because of their likely biased sampling of larger individuals that do not reflect the selectivity of the fishery. When the SS-CL model was run with this length data included, the model was unable

to fit due to the high number of very large individuals in the dataset with lengths considerably higher than the value for L_{∞} (average asymptotic length). The anomalously high prevalence of very large individuals could be explained by known issues in catch reporting, such as high-grading, whereby large individuals are overrepresented in the data (Ainsworth and Pitcher 2005). Therefore, length compositions from the two time periods described in Section 2.2 are the only length data included in the model and are assumed to represent the recreational fishery selectivity. A total of 28 Yelloweye Rockfish lengths were available from the 1970s, which were summarized into a single year (1975) due to small sample sizes, compared to 62 lengths from the surveys in the 2010s, which were similarly summarized into a single year (2015); the year 2015 was chosen because this was the mean catch year, once all length samples from the contemporary surveys were aggregated. Given the long-life and relatively slow dynamics of yelloweye populations, this aggregation of lengths is not unreasonable. The length compositions are shown in Fig. 2, with the length compositions for 1975 shown in Fig. 2a and the length compositions for 2015 shown in Fig. 2b. Life history parameters for Yelloweye Rockfish were fixed at the values from the most recent stock assessment for the U.S. West Coast stock (Gertseva and Cope 2017) and are provided in Table S1.

SS-CL estimates the initial recruitment size ($\ln R_0$) and the two logistic selectivity parameters while fitting the length composition data via maximum likelihood estimation and assuming inputted catches are removed from the population without error. Within model uncertainty is estimated using asymptotic variance. This variance estimation is influenced particularly by the low sample sizes of the length compositions (this allowing for a broader fit to the length data) but may still be insufficient to capture major sources of uncertainty caused by fixing certain model inputs. The Beverton-Holt stock-recruitment was used in our assessment model, with steepness fixed at 0.72, a value derived from a meta-analysis of West Coast rockfishes with similar life histories (Thorson et al. 2019).

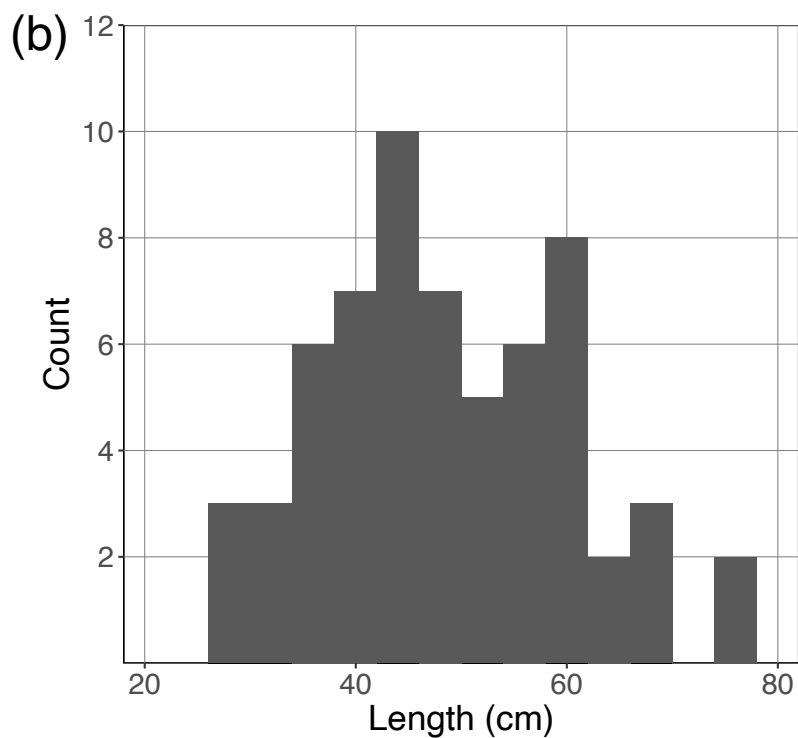
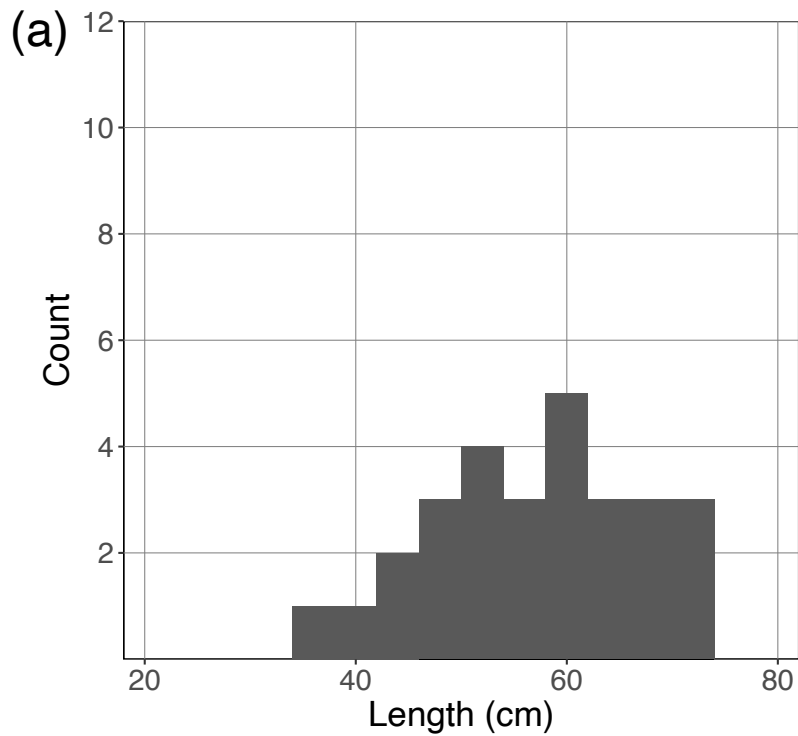


Figure 2. Length composition data included in the stock assessment model. Panel (A) shows data from studies conducted in the 1970s, which were summarized into a single year (1975) for the model. Panel (B) shows data from studies from the 2010s, which were summarized into a single year (2015) for the model.

1.4 Results

1.4.1 Catch reconstruction

Commercial catch of Yelloweye Rockfish began in the early 1920s, was relatively low until an increase in the mid-1940s, after which harvest declined steadily until 1970 (Fig. 3a). Catches were then relatively high until the mid-1990s, when they dropped rapidly. The recreational catch of Yelloweye Rockfish showed a gradual increase in harvest through the first part of the time series, followed by maximum catches from about 1970 to 1990 and another drop over the subsequent two decades (Fig. 3b). These fundamental patterns hold regardless of which catch scenario is considered, though the estimated uncertainty in the extent of the commercial data series is much larger. Overall, the recreational harvest was greater than the commercial harvest; in the base (medium) catch scenario, the total recreational catch represents approximately 60% of total catch.

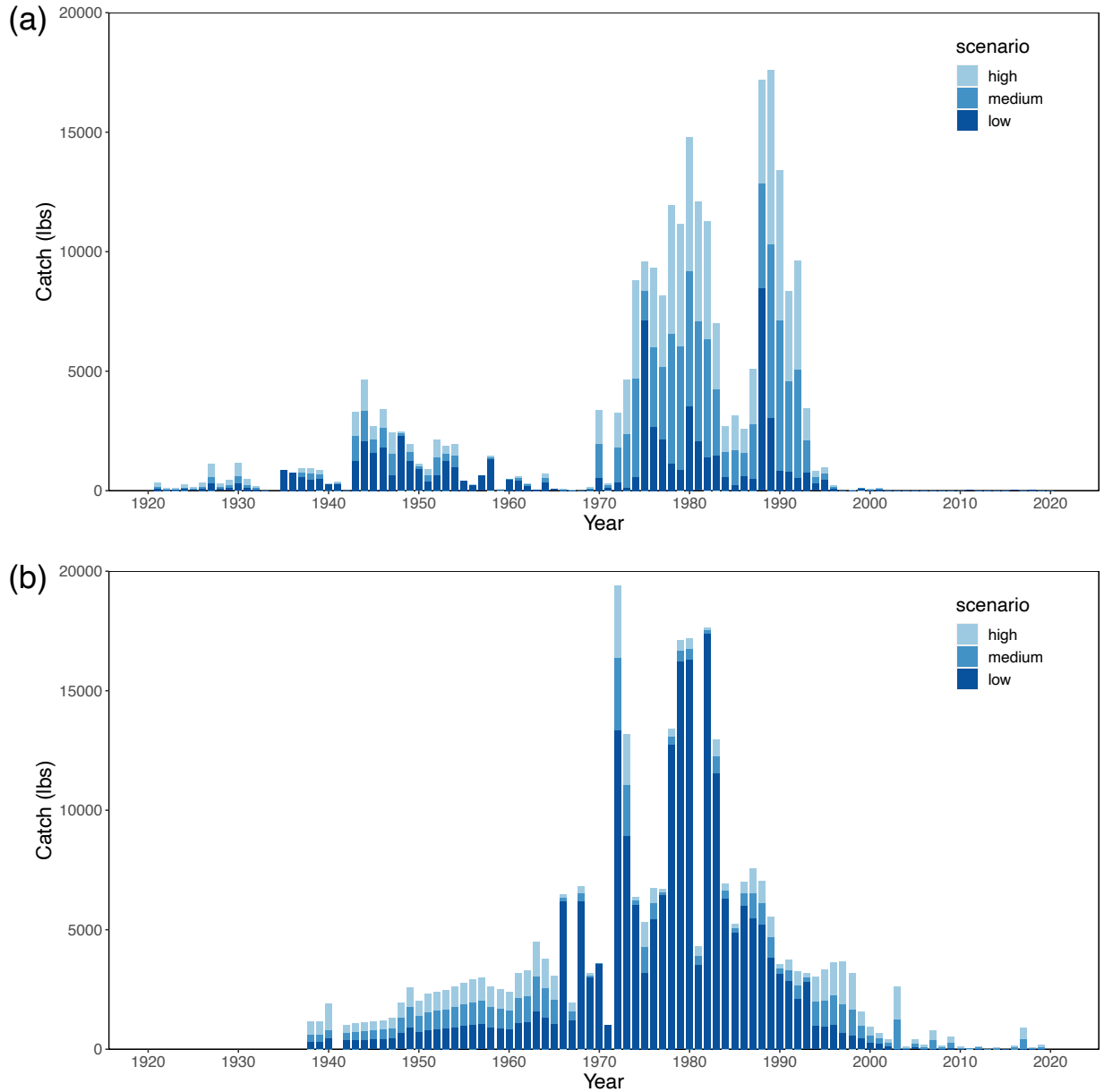


Figure 3. Catch reconstruction for Yelloweye Rockfish in Puget Sound (Hood Canal excluded), showing (A) the commercial catch reconstruction and (B) the recreational catch reconstruction.

1.4.2 Population dynamics

Despite evaluating the sensitivity of model outputs to a wide range of uncertainty across catch histories and M axes, the overall trend of the population was very similar (Fig. 4). Yelloweye Rockfish in Puget Sound declined in abundance starting around 1970, with a minimum abundance in 1994 (for the high and medium catch scenarios) or 1992 (for the low catch scenario), consistent with the perception of possibly critically low stock size (thus the petition to list the DPS under the ESA). The population then increased in abundance over the past two

decades in accordance with essentially no fishing mortality and deterministic recruitment. Relative spawning output shows similar temporal trends in the stock status and very high within model uncertainty, and larger dips in the population in the 1990s with different catch and M values. However, following this decline, significant restrictions in both the commercial and recreational fisheries led to very low fishery impacts for the last 25 years. With the deterministic recruitment assumed by the models (the same assumption used in the coastwide U.S. yelloweye stock assessment), and in the general absence of harvesting, the model suggests that the population has rebounded to >40% of unfished spawning output even at the lowest M values, and >15% if considering the low 95% trajectory of those low M runs. Considering the worst-case scenarios of low M across the catch scenarios, the lower limits of population status do include critically low relative population sizes (Fig. 5). Because the confidence intervals for this model were estimated under the assumption of asymptotic variance, the lowest limits of the population are biologically nonsensical values below zero; these values can be safely ignored as the population did not go extinct. Thus, the model suggests that while it was possible that this Yelloweye Rockfish stock reached very low levels in the 1990s, the low removals for over two decades suggests the population has increased considerably under the assumption of consistent productivity and no removals beyond natural causes.

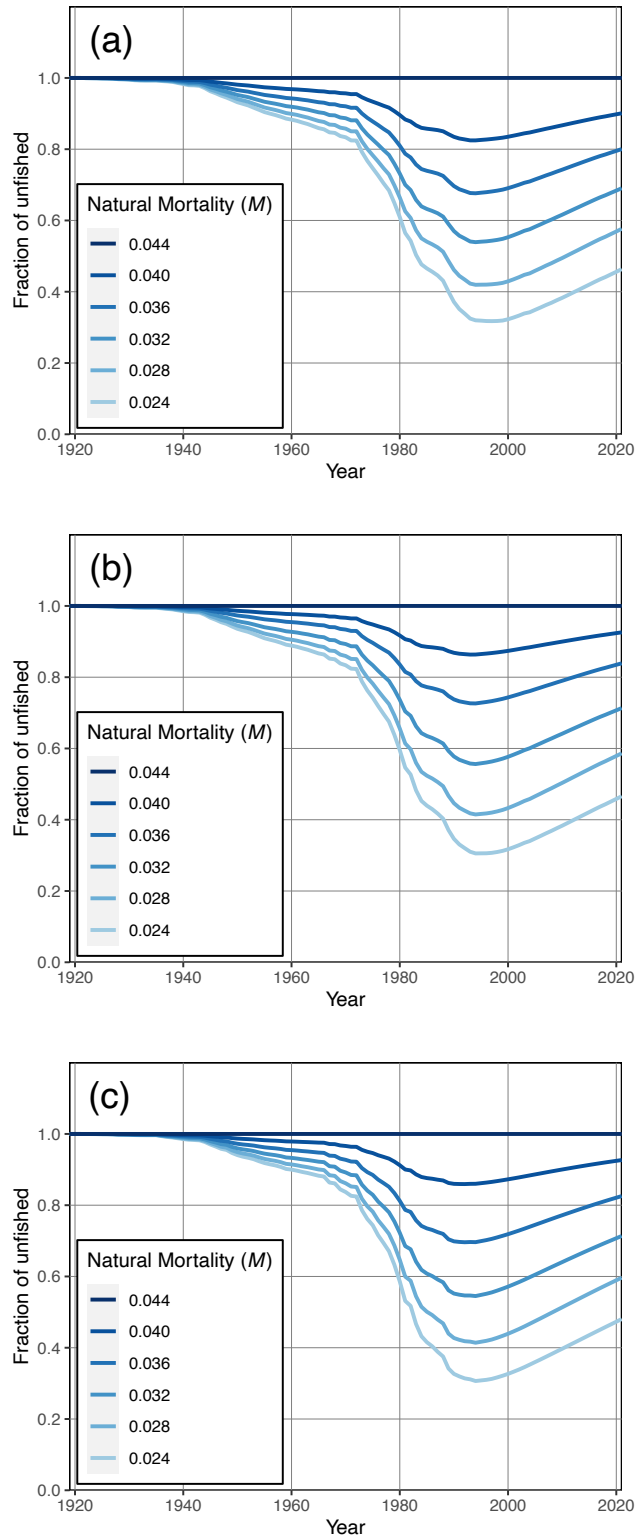


Figure 4. Relative stock size (fraction of unfished spawning output) of the United States portion of the PSGB Yelloweye Rockfish DPS (excluding Hood Canal), profiled over a range of values of natural mortality (M) for the high (A), medium (B), and low (C) catch scenarios.

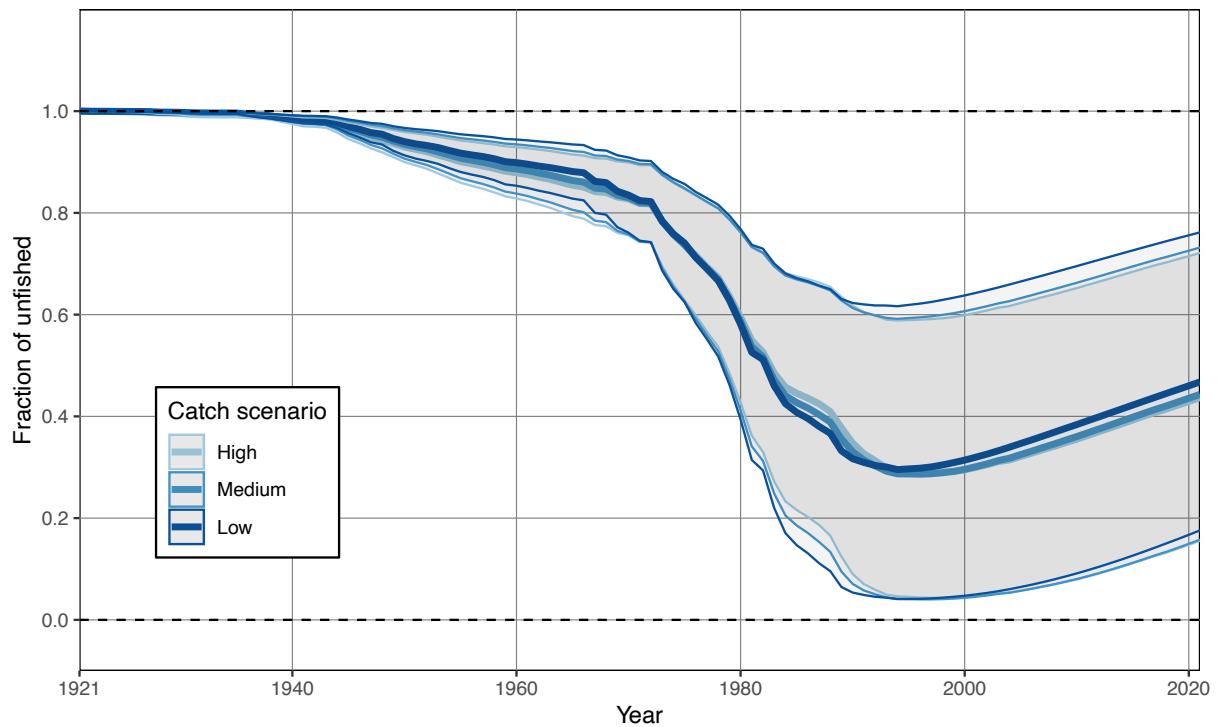


Figure 5. Relative stock size (fraction of unfished spawning output) of the United States portion of the PSGB Yelloweye Rockfish DPS (excluding Hood Canal), based on the lowest M ($=0.024$) scenario across the three catch scenarios. Shaded areas are the 95% confidence intervals.

1.5 Discussion

The management of rare, threatened, and endangered species is often a difficult process plagued by uncertainty due to limited resources and data. The creative application of analytical tools is needed when presented with limited historical and contemporary data on species of conservation concern. In this study, we estimated a plausible range of population dynamics for ESA-listed Yelloweye Rockfish in Puget Sound by collating different sources of information to reconstruct likely removal histories to evaluate population scale, and length composition data from two distinct periods to estimate relative population size using a simple but integrated data-limited stock assessment model. We also explored a major source of possible model misspecification, the natural mortality value, in order to get an expansive understanding of uncertainty in relative stock status. While previous assessments of the status of this population relied on proxy data from congeners and often lacked species-specific insights (Drake et al. 2010; Tonnes et al. 2016), the assessment model applied here provides the first estimates of Yelloweye Rockfish population status in Puget Sound for conservation purposes. The population trajectory, which showed a decline until the 1990s followed by an increase in the population size, is similar to what is seen on the U.S. West Coast, as the coastwide assessment showed low relative stock sizes up through the early 2000s, then an increase to almost 30% of the unfished spawning

output in 2017 (Gertseva and Cope 2017). Notably, the recovery of the population starting in the 1990s suggested by our model is the opposite of the trend found in Tolimieri et al. (2017), which suggested a continuous decline through 2014 (the last year of the study). However, as noted previously, there were various management changes starting in the mid-1990s (prohibition on Yelloweye Rockfish retention, changes in depth limits for recreational fishing to protect ESA-listed Bocaccio and Yelloweye Rockfish) that limited how well the all-rockfish trends presented in Tolimieri et al. (2017) captured trends in Yelloweye Rockfish abundance.

As our analysis focused on evaluating the potential of low stock status, the highly risk averse consideration of the 95% confidence interval under catch uncertainty and very low M values still shows that the Puget Sound Yelloweye Rockfish population reflects a moderate stock status. In the most conservative (not most probable) estimate of stock status explored, using the lowest value for M and the highest catch scenario, the population is still estimated to have a 66% probability of being over 25% of the unfished population size, a key reference point in the recovery criteria (NMFS 2017). We also explored a length-only version of the model (i.e., dropping the catch history and only fitting the length data). These models suggested the current stock status is around 40% with the reference M value, and 15% with the lowest explored M value. One critical difference in the length-only model versus the catch and length model is the length-only model assumes fishing mortality is still occurring, i.e., a constant fishing mortality throughout the time period (Hordyk et al. 2015). Thus, LB-SPR predicts lower relative stock sizes compared to the catch and length model that is able to incorporate the information that removals essentially stopped two decades ago. Despite that major assumption and median result differences, the LB-SPR and SS-CL results still overlap in the message that Yelloweye Rockfish have likely increased since the time of the perceived lowest population size. By applying elements of historical ecology, fisheries science, and conservation biology in a highly collaborative research effort, we collectively offer these results and management-relevant science that will be used to inform recovery efforts for this ESA-listed species.

Marine and anadromous fishes listed under the ESA each have unique recovery criteria tailored to their biology and available data, with a wide variety of monitoring and analytical methods needed to track progress toward meeting recovery goals based on these metrics. As Yelloweye Rockfish and Bocaccio are commercially exploited in other parts of their range, metrics typically used for harvested populations were selected as the biological recovery criteria for the PSGB DPSs (unique amongst ESA-listed species), and thus methods typically used for commercially exploited species were applicable. Many listed fish species tend to have relatively more data for tracking their recovery, which is often correlated with the ease of collecting data for these species based on their life history. Anadromous species, such as the Southern DPS of North American Green Sturgeon (*Acipenser medirostris*), Gulf Sturgeon (*Acipenser oxyrinchus desotoi*), and the Southern DPS of Eulachon (*Thaleichthys pacificus*), each have recovery criteria based on abundance during the freshwater life history stage. Marine fishes, such as PSGB

Yelloweye Rockfish, do not have population estimates that are as easily attainable. As of 2021, there are only seven non-foreign, strictly marine fishes listed under the ESA. Four are elasmobranchs: Giant Manta Ray (*Manta birostris*, throughout its range), Oceanic Whitetip Shark (*Carcharhinus longimanus*, throughout its range), Scalloped Hammerhead (*Sphyrna lewini*, Eastern Pacific DPS, Central & Southwest Atlantic DPS, and Indo-West Pacific DPS), and Smalltooth Sawfish (*Pristis pectinata*, U.S. Population); the other three are teleosts: Nassau Grouper (*Epinephelus striatus*, throughout its range), Yelloweye Rockfish (*Sebastes ruberrimus*, PSGB DPS), and Bocaccio (*Sebastes paucispinis*, PSGB DPS). Of these seven species, only PSGB Yelloweye Rockfish and Bocaccio and the United States DPS of Smalltooth Sawfish have final recovery plans as of 2023. A draft recovery plan was released for the Oceanic Whitetip Shark in January of 2023 and is currently under review (NMFS 2023).

The Smalltooth Sawfish has the most data available of any ESA-listed marine species, and has as an element of its downlisting criteria an annual rate of increase in relative abundance (NMFS 2009). Progress towards meeting this goal is monitored via three fisheries-independent surveys (Brame et al. 2019), which is unique amongst ESA-listed species. The WDFW has used ROV surveys of varying designs and spatial coverages to estimate Yelloweye Rockfish abundance in portions of the PSGB DPS (Lowry et al. 2022; Pacunski et al. 2013, 2020); however, a consistent sampling protocol that can track population abundance through time will be resource intensive, logistically complex, and require long-term, stable funding to implement. Thus, with unique recovery criteria and a paucity of data, the approach outlined in this study is an example of a creative application of quantitative ecological methods tailored to the recovery criteria, available data, and biology of this species. As recovery plans are developed for recently listed marine fishes and more species continue to be listed, creative methods that borrow from similar (or different) fields will be central to efforts to track the status and recovery of these species in their remote habitats.

There are other, ESA-listed species that are even more data-limited than PSGB Yelloweye Rockfish. For example, PSGB Bocaccio is listed as Endangered under the ESA and individuals are rarely encountered in Puget Sound: since 1987, when consistent monitoring surveys in Puget Sound began, research surveys have observed only 14 Bocaccio in Puget Sound within the DPS boundaries (Pacunski et al. 2013; Andrews et al. 2018; WDFW, unpublished data). This is despite trawl surveys conducted since 1987 on an annual or bi-annual schedule (Quinnell and Schmitt 1991; Palsson et al. 1998, 2002, 2003; Blaine et al. 2020), multiple ROV surveys in the San Juan Islands and in Puget Sound proper (Lowry et al. 2022; Pacunski et al. 2013, 2020), and hook-and-line studies that have targeted Bocaccio (Andrews et al. 2018). Its discreteness as a DPS remains unresolved, as at the time of listing this was based on expert opinion (and was not unanimous amongst reviewers) (Drake et al. 2010), and the subsequent genetic study that led to the delisting of Canary Rockfish (and confirmed the discreteness of the PSGB Yelloweye Rockfish DPS) was unable to obtain enough Bocaccio samples to determine whether PSGB

Bocaccio are distinct from Bocaccio on the U.S. West Coast (Andrews et al. 2018). With so few data points, even data-limited fisheries methods such as the ones employed in this study are unable to give any insight into the dynamics of this population. Without the ability to estimate SPR, as is specified in the criteria, it is plausible that this DPS will exist in a sort of “limbo” with no prospect for delisting because of extreme data deficiencies. However, efforts are underway to collect more information on the abundance, genetics, and population trends of Bocaccio in Puget Sound, which may improve the ability to assess their status in the future.

As is the case in population modeling, particularly in data-limited situations, there were considerable sources of uncertainty in our study that can be summarized into two general themes: data uncertainty and model uncertainty. Data uncertainty in this study comes from known sources such as the catch reconstruction and the very low sample sizes and missing years for the length composition, general data representativeness of the underlying population structure, as well as unknown uncertainty sources from data unavailability (e.g., no abundance indices and age compositions). As is the case in catch reconstruction, many different approaches could have been taken to estimate historical removals, and the catch reconstruction presented represents only one approach. In the case of our catch reconstruction, we attempted to summarize uncertainty in the three catch scenarios using time-varying sources of uncertainty, including alternative catch composition data, different treatment of data with poor geographic resolution, and varying estimates of post-release mortality. However, our attempt to avoid using arbitrary, fixed factors to the extent possible when generating these catch scenarios likely underestimated the uncertainty in the data. For example, catch composition data in the commercial landings was only available beginning in the 1970s, but total rockfish landings were available from a half century earlier in the 1920s. Thus, we applied the only available catch composition data to these landings in all catch scenarios despite the temporal gap, thus making the assumption that different rockfish species were at the same relative population level in these two time periods. The recreational bottomfish fishery in Puget Sound has been notoriously difficult to monitor (Palsson et al. 2009), and therefore the estimates of catch that we incorporated into our research have an unknown degree of uncertainty that could not be estimated in our catch reconstruction. Additional sources of mortality in the catch reconstruction for which we could not account were discards in the commercial fishery (as commercial records only recorded landings delivered to processors; Williams et al. 2010) and post-release mortality in the recreational fishery (as the WDFW only began estimating releases beginning in 2003). However, as seen in Fig. 4 and Fig. 5, the different catch scenarios did not have a significant impact on stock status. Lastly, the length composition data were based on small numbers of fish and limited years, which also increased the uncertainty in the estimation of stock status. Rudd et al. (2021) conducted simulation testing of the effect of the availability of length composition data in a species with similar life history characteristics to Yelloweye Rockfish (longer-lived, slow growing). They found that with only one year of length composition data and only fifty samples (the most similar scenario to our study, which has one year of 62 length samples and one year of 28 length

samples), the median absolute relative error of fraction unfished was 0.4, with the 90th quantiles spanning the values -0.6 to 1.3. As such, the small sample sizes available for length compositions for this population suggest considerable uncertainty in the stock status. However, the model outputs do reflect some of this data uncertainty, as seen in the wide uncertainty intervals in relative stock biomass (Fig. 5), and extremely wide uncertainty intervals around absolute stock size. While relative stock biomass (Fig. 5) is more relevant to informing the recovery criteria for this DPS, absolute stock biomass would help inform the resiliency of the DPS to fishing mortality. For example, based on in-season estimates of absolute biomass for the ESA-listed Southern DPS of Eulachon, recreational and commercial fisheries may be opened (National Marine Fisheries Service 2017). While retention of Yelloweye Rockfish is currently prohibited in Puget Sound, some mortality does occur due to barotrauma when these fish are released (Hochhalter and Reed 2011) and a refined estimate of absolute biomass would inform the threat that this fishing mortality poses to the DPS.

Model uncertainty, or uncertainties about the structure of the model itself, can be more insidious than uncertainty in the data, as it can lead to bias and an underrepresentation of the true uncertainty in model predictions (Hill et al. 2007). In our case, we had to assume a deterministic stock-recruit relationship, as evidenced by the monotonic recovery of the population beginning in the 1990s with near-zero fishing pressure (Fig. 5). Unlike data-rich fisheries that have estimates of year-class strengths from recruitment surveys or age data, no estimates of recruitment exist for ESA-listed species, and existing surveys such as ROV surveys are currently limited to detecting rockfish greater than 10 cm in length when they are clearly visible to the primary data-collection camera (Pacunski et al. 2013). Therefore, we cannot verify that the recruitment estimated by the model is occurring. Despite this simplifying assumption, the overall trend in the population, while lagged in time because of a different exploitation history, was not unlike what was seen in the U.S. coastal population (Gertseva and Cope 2017) that also assumed deterministic recruitment, or the DFO assessment of the Inside Yelloweye Rockfish population (Haggarty et al. 2021). The most extreme recruitment case would be no recruitment over the last two decades, a scenario that would lead to a persistently decaying population over time. This seems a very unlikely scenario given smaller individuals were sampled relatively frequently in the population in the most recent time period (Fig. 2). In order to bracket uncertainty in population production, the natural mortality value was explored, with the most emphasis placed on very low M values in order to highlight risk averse model specifications given the recovery goals. While these remaining uncertainties are significant, this coarse resolution is still informative for management given the aim of estimating population status in order to inform recovery criteria under the ESA listing.

A final consideration for the ability of this study to inform the status of PSGB Yelloweye Rockfish is that the model presented in this study only models the U.S. portion of the Puget Sound/Georgia Basin DPS; the Canadian portion, which is subject to commercial exploitation,

was modeled by DFO (Haggarty et al. 2021). The model used for the Canadian portion of the DPS, which has considerably more data available (e.g., abundance indices through ongoing longline surveys) was implemented through the Data Limited Methods toolkit (DLMtool) (Carruthers and Hordyk 2018, 2019) and DLMTool's companion software package, MSEtool (Huynh et al. 2019). Although the uncertainty around the absolute stock size of the Puget Sound portion of the DPS is very wide, the Canadian portion of the DPS is considerably larger than the Puget Sound portion (Fig. S1) and the relative stock status is currently estimated to be 32% of unfished (95% quantiles: 15% to 68%, Fig. S2). Historical removals from the Canadian side of the DPS are also over 20 times larger than removals from the U.S. side, even when the high catch scenario is considered, providing further evidence of the relative size of these two portions of the DPS. The recent COSEWIC report on this population concluded that it was not in imminent danger of extinction, however the status of the designated unit was changed from Special Concern (a status conferred in 2008) to Threatened (COSEWIC 2020). This issue of transboundary fish populations is a common one; however, unlike other species in the region, such as Pacific Halibut (*Hippoglossus stenolepis*) which are managed by the International Halibut Commission (Sumaila et al. 2020), coordinated international management of Yelloweye Rockfish in the Salish Sea does not take place. Thus, these two models, which model different portions of one genetically homogenous stock, present an additional source of uncertainty in assessing the status of the PSGB Yelloweye Rockfish DPS.

In the United States, as in many other countries, separate laws concern the treatment of species conservation versus fisheries management. For instance, the goals of conserving species within an ESA framework is different from a traditional fisheries management (e.g., MSA) framework. Despite different objectives, similar tools can still be used to evaluate metrics reflecting those objectives, with the specific modeling approach dependent on the available data and question of interest. A continuum of methods exists to estimate the status of fish populations with varying degrees of data limitation; these tools can be implemented through the Stock Synthesis Data-Limited tool (<https://github.com/shcaba/SS-DL-tool>). In the present case, SS-CL was selected as it best leveraged the existing data, and was coupled with the evaluation of multiple scenarios to examine uncertainty in relative population status to evaluate highly risk averse (i.e., low probability events regarding smaller relative population sizes) scenarios to ensure DPS conservation rather than trying to pinpoint optimal yield under less risk averse conditions. This work highlights the possibility of linking analytical frameworks to move a species from ESA to a fisheries management framework within a common tool. Conservation biology and natural resource management have traditionally been treated as separate realms and discontinuous in interpretations, yet share common metrics such as stock status. The ESA listing of Puget Sound/Georgia Basin Yelloweye Rockfish offers an example where a more continuous analytical spectrum that evolves as more data becomes available can be applied and more explicitly build a bridge between ESA listings (conservation) and fisheries management (sustainable use).

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1.7 References

- Ainsworth, C. H., and T. J. Pitcher. 2005. Estimating illegal, unreported and unregulated catch in British Columbia's marine fisheries. *Fisheries Research* 75(1–3):40–55.
- Alverson, D. L. 1957. An Appraisal of the Fish Ticket System in Respect to the Washington Otter Trawl Fishery. *WDFW Fisheries Research* 1(4):59–69.
- Andrews, K. S., K. M. Nichols, A. Elz, N. Tolimieri, C. J. Harvey, R. Pacunski, D. Lowry, K. L. Yamanaka, and D. M. Tonnes. 2018. Cooperative research sheds light on population structure and listing status of threatened and endangered rockfish species. *Conservation Genetics* 19(4):865–878.
- Bargmann, G. G. 1977. The Recreational Hook and Line Fishery for Marine Fish in Washington 1968-1973. State of Washington Department of Fisheries (Progress Report No. 33).
- Beaudreau, A. H., and P. S. Levin. 2014. Advancing the use of local ecological knowledge for assessing data-poor species in coastal ecosystems. *Ecological Applications*, 24(2), 244-256.
- Blaine, J., D. Lowry, and R. Pacunski. 2020. 2002-2007 WDFW scientific bottom trawl surveys in the southern Salish Sea: species distributions, abundance, and population trends. Washington Department of Fish and Wildlife, Olympia, WA.
- Brame, A. B., T. R. Wiley, J. K. Carlson, S. V. Fordham, R. D. Grubbs, J. Osborne, R. M. Scharer, D. M. Bethea, and G. R. Poulakis. 2019. Biology, ecology, and status of the smalltooth sawfish *Pristis pectinata* in the USA. *Endangered Species Research* 39:9–23.
- Browning, H. F. 2014. Evidence of habitat associations and distribution patterns of rockfish in Puget Sound from archival data (1974-1977).
- Buckley, R. M. 1967. 1965 bottomfish sport fishery. *Sport Fishery Investigations* 1965 (Supplemental Progress Report):45.
- Buckley, R. M. 1968. 1966 Bottomfish Sport Fishery Occurring in Washington Marine Punch Card Areas 2 through 12. *Sport Fishery Investigations* 1966 (Supplemental Progress Report):45.

- Buckley, R. M., and K. Satterthwaite. 1970. 1967 Bottomfish Sport Fishery. Sport Fishery Investigations (Supplemental Progress Report):56.
- Carruthers, T. R., and A. R. Hordyk. 2018. The Data-Limited Methods Toolkit (DLM tool): An R package for informing management of data-limited populations. *Methods in Ecology and Evolution* 9(12):2388–2395.
- Carruthers, T. R., and A. R. Hordyk. 2019. Using management strategy evaluation to establish indicators of changing fisheries. *Canadian Journal of Fisheries and Aquatic Sciences* 76(9):1653–1668.
- COSEWIC. 2020. COSEWIC assessment and status report on the Yelloweye Rockfish *Sebastes ruberrimus*, Pacific Ocean outside waters population and Pacific Ocean inside waters population in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa:xvi + 72.
- DiDonato, G. 1969. Letter to Mr. Douglas M. Thompson regarding non-salmonid fishery management. State of Washington Department of Fisheries:8.
- Drake, J. S., E. A. Bernston, J. M. Cope, R. G. Gustafson, E. E. Holmes, P. S. Levin, N. Tolimieri, R. S. Waples, S. M. Sogard, and G. D. Williams. 2010. Status Review of Five Rockfish Species in Puget Sound, Washington. Page NOAA Technical Memorandum.
- Free, C. M., O. P. Jensen, S. C. Anderson, N. L. Gutierrez, K. M. Kleisner, C. Longo, C. Minto, G. C. Osio, and J. C. Walsh. 2020. Blood from a stone: Performance of catch-only methods in estimating stock biomass status. *Fisheries Research* 223(September 2019):105452. Elsevier.
- Gertseva, V., and J. M. Cope. 2017. Stock assessment of the yelloweye rockfish (*Sebastes ruberrimus*) in state and Federal waters off California, Oregon and Washington. Portland, OR: Pacific Fishery Management Council.
- Haggarty, D. R., Q. C. Huynh, R. E. Forrest, S. C. Anderson, and M. J. Bresch. 2021. Evaluation of potential rebuilding strategies for Inside Yelloweye Rockfish (*Sebastes ruberrimus*) in British Columbia.
- Hamel, O. S., and J. M. Cope. 2022. Development and considerations for application of a longevity-based prior for the natural mortality rate. *Fisheries Research* 256(August):106477. Elsevier B.V.
- Hill, S. L., G. M. Watters, A. E. Punt, M. K. McAllister, C. Le Quéré, and J. Turner. 2007. Model uncertainty in the ecosystem approach to fisheries. *Fish and Fisheries* 8(4):315–336.
- Hochhalter, S. J., and D. J. Reed. 2011. The effectiveness of deepwater release at improving the survival of discarded yelloweye rockfish. *North American Journal of Fisheries Management* 31(5):852–860.
- Hordyk, A., K. Ono, S. Valencia, N. Loneragan, and J. Prince. 2015. A novel length-based empirical estimation method of spawning potential ratio (SPR), and tests of its performance, for small-scale, data-poor fisheries. *ICES Journal of Marine Science* 72(1):217–231. Oxford University Press.
- Huynh, Q., A. Hordyk, and T. Carruthers. 2019. MSEtool: Management Strategy Evaluation

- Toolkit. R package version 1.4.3.
- Kincaid, T. 1919. An annotated list of Puget Sound fishes. FM Lamborn, Public Printer.
- Kraig, E., and T. Scalici. 2019. Washington State Sport Catch Report 2017. Washington Department of Fish and Wildlife:79.
- Love, M. S. 2011. Certainly more than you want to know about the fishes of the Pacific Coast: a postmodern experience. Really Big Press.
- Love, M. S., M. Yoklavich, and L. K. Thorsteinson. 2002. The rockfishes of the northeast Pacific. Univ of California Press.
- Lowry, D., R. E. Pacunski, J. Blaine, T. Tsou, L. Hillier, J. Beam, E. Wright, and A. Hennings. 2022. Assessing bottomfish and select invertebrate occurrence, abundance, and habitat associations in the southern Salish Sea using a small remotely operated vehicle: results of the 2012-13 systematic survey. Washington Department of Fish and Wildlife, Olympia, WA (Fish Program Technical Report FPT21-XX):44.
- Methot, R. D., and C. R. Wetzel. 2013. Stock synthesis: A biological and statistical framework for fish stock assessment and fishery management. *Fisheries Research* 142:86–99.
- National Marine Fisheries Service. 2009. Recovery Plan for Smalltooth Sawfish (*Pristis pectinata*). Prepared by the Smalltooth Sawfish Recovery Team for the National Marine Fisheries Service, Silver Spring, Maryland.
- National Marine Fisheries Service. 2017. Recovery Plan for the Southern Distinct Population Segment of Eulachon (*Thaleichthys pacificus*).
- National Marine Fisheries Service. 2023. Draft Recovery Plan for the Oceanic Whitetip Shark (*Carcharhinus longimanus*). NMFS, Office of Protected Resources:62.
- Newman, D., J. Berkson, and L. Suatoni. 2015. Current methods for setting catch limits for data-limited fish stocks in the United States. *Fisheries Research* 164:86–93. Elsevier B.V.
- NMFS. 2010. Endangered and Threatened Wildlife and Plants: Threatened Status for the Puget Sound/Georgia Basin Distinct Population Segments of Yelloweye and Canary Rockfish and Endangered Status for the Puget Sound/Georgia Basin Distinct Population Segment of Bocacci. *Federal Register* 75:22276–22290.
- NMFS. 2017. Rockfish Recovery Plan: Puget Sound / Georgia Basin Yelloweye Rockfish (*Sebastes ruberrimus*) and Bocaccio (*Sebastes paucispinis*) (National Marine Fisheries Service. Seattle, WA.).
- Nye, G. 1982. Historical Fisheries and Catch Data Review of the First through Forty-Sixth Annual Reports, State of Washington 1890-1935. Washington Department of Fish and Wildlife.
- O’Connell, V. M., and D. W. Carlile. 1993. Habitat-specific density of adult yelloweye rockfish *Sebastes ruberrimus* in the eastern Gulf of Alaska. *Fish. Bull.* 91:304–309.
- Ovando, D., R. Hilborn, C. Monnahan, M. Rudd, R. Sharma, J. T. Thorson, Y. Rousseau, and Y. Ye. 2021. Improving estimates of the state of global fisheries depends on better data. *Fish and Fisheries* 22(6):1377–1391.
- Pacunski, R. E., W. a Palsson, and H. G. Greene. 2013. Estimating Fish Abundance and

- Community Composition on Rocky Habitats in the San Juan Islands Using a Small Remotely Operated Vehicle (January):57.
- Pacunski, R., D. Lowry, A. Hennings, E. Wright, L. Hillier, W. Palsson, and T. Tsou. 2020. Quantification of bottomfish populations , and species-specific habitat associations , in the San Juan Islands , WA employing a remotely operated vehicle and a systematic survey design (October).
- Palsson, W. A. 1987. Bottomfish catch and effort statistics from boat-based recreational fisheries in Puget Sound, 1970-1985. State of Washington, Department of Fisheries.
- Palsson, W. A., P. Clarke, S. Hoffman, and J. Beam. 2002. Results from the 2000 transboundary trawl survey of the eastern Strait of Juan de Fuca and Discovery Bay. Washington Department of Fish and Wildlife Technical Reports. Washington Department of Fish and Wildlife, Mill Creek, WA:87.
- Palsson, W. A., S. Hoffmann, J. Beam, and P. Clarke. 1998. Results from the 1997 transboundary trawl survey of the southern Strait of Georgia. Washington Department of Fish and Wildlife Technical Reports. Washington Department of Fish and Wildlife, Mill Creek, WA:79.
- Palsson, W. A., S. Hoffmann, P. Clarke, and J. Beam. 2003. Results from the 2001 transboundary trawl survey of the Southern Strait of Georgia, San Juan Archipelago and adjacent waters. Washington Department of Fish and Wildlife Technical Reports. Washington Department of Fish and Wildlife, Mill Creek, WA (May):117.
- Palsson, W. A., T. Tsou, G. G. Bargmann, R. M. Buckley, J. E. West, M. Lou Mills, Y. W. Cheng, and R. E. Pacunski. 2009. The Biology and Assessment of Rockfishes in Puget Sound. Washington Department of Fish and Wildlife (September):208.
- Parker, S. J., S. A. Berkeley, J. T. Golden, D. R. Gunderson, J. Heifetz, M. A. Hixon, R. Larson, B. M. Leaman, M. S. Love, and J. A. Musick. 2000. Management of Pacific rockfish. *Fisheries* 25(3):22–30.
- Pedersen, M., and G. DiDonato. 1982. Groundfish Management Plan for Washington's Inside Waters. Washington Department of Fisheries Progress Report (170):123.
- Pedersen, M. G., and G. G. Bargmann. 1986. 1984 supplement for the groundfish management plan for Washington's inside waters. Washington Department of Fisheries Progress Report No. 247:60.
- Punt, A. E., C. Castillo-Jordán, O. S. Hamel, J. M. Cope, M. N. Maunder, and J. N. Ianelli. 2021. Consequences of error in natural mortality and its estimation in stock assessment models. *Fisheries Research* 233(September 2020).
- Quinnell, S., and C. Schmitt. 1991. Abundance of Puget Sound Demersal Fishes: 1987 Research Trawl Survey Results. State of Washington Department of Fisheries:267.
- Ralston, S., D. E. Pearson, J. C. Field, and M. Key. 2010. Documentation of the California catch reconstruction project.
- Rudd, M. B., J. M. Cope, C. R. Wetzel, and J. Hastie. 2021. Catch and Length Models in the Stock Synthesis Framework: Expanded Application to Data-Moderate Stocks. *Frontiers in*

- Marine Science 8(August):1–18.
- Schwartz, M. W. 2008. The performance of the endangered species act. *Annual Review of Ecology, Evolution, and Systematics* 39:279–299.
- Smith, R. T. 1937. Report on the Puget Sound otter trawl investigations... University of Washington.
- Sumaila, U. R., J. Palacios-Abrantes, and W. W. L. Cheung. 2020. Climate change, shifting threat points, and the management of transboundary fish stocks. *Ecology and Society* 25(4):1–9.
- Thorson, J. T., M. W. Dorn, and O. S. Hamel. 2019. Steepness for West Coast rockfishes: Results from a twelve-year experiment in iterative regional meta-analysis. *Fisheries Research* 217(June 2017):11–20. Elsevier.
- Tolimieri, N., E. E. Holmes, G. D. Williams, R. Pacunski, and D. Lowry. 2017. Population assessment using multivariate time-series analysis: A case study of rockfishes in Puget Sound. *Ecology and Evolution* 7(8):2846–2860.
- Tonnes, D., M. Bhuthimethee, J. Sawchuk, N. Tolimieri, K. Andrews, and K. Nichols. 2016. Yelloweye rockfish (*Sebastes ruberrimus*), canary rockfish (*Sebastes pinniger*), and bocaccio (*Sebastes paucispinis*) of the Puget Sound / Georgia Basin 5-Year Review : Summary and Evaluation Office of Protected Resources (April 2016).
- Washington, P. M., R. Gowan, and D. H. Ito. 1978. A biological report on eight species of rockfish (*Sebastes* spp.) from Puget Sound, Washington. Northwest and Alaska Fisheries Science Center Processed Report (April):50.
- WDFW. 2010. Rule-making order, CR-103e, emergency rule closing several commercial fisheries in Puget Sound. Washington Department of Fish and Wildlife, Olympia, WA.
- Williams, G. D., P. S. Levin, and W. A. Palsson. 2010. Rockfish in Puget Sound: An ecological history of exploitation. *Marine Policy* 34(5):1010–1020.
- Wood, K., R. Ehresmann, and M. Jaenicke. 2021. Assessment of the Demersal Shelf Rockfish Stock in the Southeast Outside District of the Gulf of Alaska. NPFMC Gulf of Alaska Stock Assessment and Fishery Evaluation Document (December).
- Yamanaka, K. L., M. M. McAllister, M. Etienne, A. M. Edwards, and R. Haigh. 2018. Stock Assessment for the outside population of Yelloweye Rockfish (*Sebastes ruberrimus*) In British Columbia, Canada for 2014. DFO Can. Sci. Advis. Sec. Res. Doc. 2018/001:ix + 150.

Chapter 2. Modeling climate and hydropower influences on the movement decisions of an anadromous species

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2.1 Abstract

In large river basins, migratory fish populations are threatened by the combination of hydropower and climate change. With river temperatures rising and hydropower development increasing globally, the longstanding monitoring programs for threatened Pacific salmon populations in the Columbia River Basin present an opportunity to study these impacts over extended time scales. We fit a statistical model to 20 years of PIT-tagging data to jointly model the effects of temperature and dam operations (spill management) on the movement of Steelhead (anadromous *Oncorhynchus mykiss*) during their adult pre-spawn migration. We modeled the relationship between these factors and behaviors that pose mortality risks, including natal tributary overshoot (ascending a dam upstream of a natal tributary) and non-natal tributary use. We then used the posterior distributions of model-estimated parameters to predict the homing success of fish to natal tributaries under different climate and hydropower scenarios. Across the populations in our study, movement decisions were consistently thermally influenced, with temperature having a negative relationship with natal homing and a positive relationship with both natal tributary overshoot and non-natal tributary use. Another consistent finding across the populations in our study was that higher overshoot rates were associated with lower homing rates. Despite data limitations associated with the PIT-tag array network, we found evidence for population-specific benefits of winter spill on natal homing success, which is currently being implemented to assist the downstream migration of overshooting Steelhead. We demonstrate how integrating the effects of climate and hydropower management actions with movement ecology provides powerful insights into how species may respond to future scenarios. In our case study, we found that pre-spawn mortality of Steelhead is likely to increase with future climate change due to temperature-driven interactions with the hydrosystem, but there is potential for hydropower managers to partially offset these impacts.

2.2 Introduction

Rivers are both biodiversity hotspots (Dudgeon et al. 2006) and provide societal benefits, including supplying water for drinking and agriculture, provisioning food, and as sources of recreation and transportation (Postel and Carpenter 1997). However, freshwater systems have been extensively modified; few free-flowing large rivers remain globally, and in some regions of

the world such as North America and Europe, they are essentially absent (Grill et al. 2019). As rivers are dammed, the resulting loss of connectivity and alteration of flows impedes the migration of fish, reduces sediment and nutrient transport, favors taxa adapted to lake and pond habitats (including many exotic species), and shifts temperature regimes (Pringle 2003, Carlisle et al. 2011, Liermann et al. 2012). With ongoing and projected massive increases in hydropower development (Zarfl et al. 2015) undammed large river basins will largely cease to exist, and these multifaceted impacts of dams will proliferate. As rivers are increasingly dammed, they are also warming (Wanders et al. 2019), driven both by climate change and the thermal impacts of altered streamflows (Van Vliet et al. 2011, Scott et al. 2023). Increased temperatures threaten freshwater biodiversity in many ways, such as through changes in phenology, community composition, and pathogen transmission (Reid et al. 2019). Furthermore, the impacts of climate change on species in heavily modified rivers may be especially pronounced, as responses to increasing temperatures may either be constrained by habitat fragmentation or drive greater interactions with dams (Woodward et al. 2010). As such, current and future conservation and management of freshwater systems requires an understanding of how the two major stressors of dams and rising temperatures affect aquatic species. Developing this understanding in the face of the growing complexity and intensity of threats to freshwater biodiversity also necessitates increasingly complex analytical approaches that can model the interacting effects of stressors while accounting for uncertainty.

The Columbia River Basin is emblematic of the challenge of the combined stressors of climate and hydropower. This complex social-ecological system has been dramatically reshaped over the past 150 years. Prior to the arrival of European American settlers in the second half of the 19th century, the basin was a highly productive system that supported runs of millions of Pacific Salmon (Chapman 1986) that sustained the Indigenous peoples of the basin (Butler and O'Connor 2004, Campbell and Butler 2010). However, myriad modifications have been made to the basin over the past two centuries. Following the start of large-scale immigration by colonial settlers in the 1850s, many tributaries of the Columbia River were degraded as streambeds were dredged for mining (Fulton 1970), irrigation diversions blocked fish passage or reduced streamflows (Stober et al. 1979), and logging operations disrupted stream habitats (Craig and Hacker 1940). Since then, numerous dams (including over 370 hydroelectric dams) have been constructed throughout the basin for flood control, navigation, irrigation, and hydroelectricity (Leonard et al. 2015). These impacts to salmon habitats, along with massive harvests in the late 19th and early 20th century (Craig and Hacker 1940), led to a precipitous decline in runs. Today, twelve distinct population segments or evolutionarily significant units of Columbia River salmon are listed under the Endangered Species Act (ESA).

Management efforts to recover Pacific salmon in the Columbia River Basin have evolved significantly over the past century. In 1938, the Mitchell Act was authorized by the U.S.

Congress to offset salmon population declines through the operation of fish hatcheries and improved fish passage (Silver et al. 2024); however, numerous negative impacts of hatcheries on wild salmon have also been documented (Hilborn and Hare 1992). In 1980, the Pacific Northwest Electric Power Planning and Conservation Act was passed, which allocated additional resources to offset the impacts of hydroelectric development in the basin on fish and wildlife (Leonard et al. 2015); these efforts accelerated following the listing of the populations under the ESA in the 1990s (Jaeger and Scheuerell 2023). In recent years, management has begun considering the ongoing and worsening impacts of climate change (USACE 2020). The Columbia River has already experienced significant warming and changes to flow regimes as a consequence of the reservoir system, increasing air temperatures, and changes in the hydrologic cycle (Scott et al. 2023). Snowpack has decreased in the basin (Mote et al. 2018) and while overall precipitation is predicted to increase, less will fall as snow and the timing of snowmelt is predicted to occur earlier (Ficklin et al. 2014). These climatic changes are likely to lead to increased impacts from the hydrosystem, as well as a reduced ability to mitigate these impacts. Changes in precipitation regimes may restrict dam operators' options for managing flow and spill, which are frequently manipulated to assist in migration of salmon.

Steelhead (anadromous *Oncorhynchus mykiss*) present unique recovery challenges in this management context due to their unusual life history. While Steelhead exhibit variation in run timing across their range, the vast majority of interior Columbia stocks are summer-run, returning to fresh water from the marine environment between June and October when the mainstem river is the warmest (Busby et al. 1996). Summer-run steelhead are also known as stream-maturing Steelhead because they are still in a sexually immature state when they enter fresh water, spending up to a year there prior to spawning the following spring (Busby et al. 1996). During their pre-spawn freshwater residence as adults, they exhibit a wide variety of complex pre-spawn behaviors (Keefer et al. 2016). The majority hold in downstream non-natal tributaries (High et al. 2006), behavior that is increasingly common at higher temperatures when these tributaries serve as thermal refugia (Keefer et al. 2008). Some individuals also ascend dams upstream of their natal tributaries in a behavior known as tributary overshoot and hold in upstream habitats in the mainstem or in non-natal tributaries (Keefer et al. 2008, Richins and Skalski 2018). During their pre-spawn adult migration, some Steelhead move downstream over dams in a movement known as fallback (Boggs et al. 2004). Fallback events can occur downstream of a fish's natal origin (en-route fallback), which is typically followed by the reascension of the dam. Fallback can also occur following tributary overshoot (post-overshoot fallback) (Keefer et al. 2015, Richins and Skalski 2018). After spawning, some Steelhead also migrate back downstream as kelts (post-spawn adults that migrate back out to the ocean), as Steelhead are the only iteroparous Pacific salmon (Quinn 2005). These fish must pass up to nine mainstem hydroelectric dams both as outmigrating juveniles/kelts and returning adults, leading to many interactions with the hydrosystem. As a result, actions are taken to aid in Steelhead migration across their different life history stages (USACE 2020).

All distinct population segments (discrete and significant populations) of Steelhead above Bonneville Dam (the first dam on the Columbia River encountered by returning adults) are listed as threatened under the ESA, and counts of returning Steelhead to Bonneville Dam have been lower in the last five years than they were at the time of listing (NMFS 2022a, 2022b, 2022c, 2022d). Mitigating pre-spawn mortality of adult Steelhead is cited specifically as a key recovery action, as low freshwater productivity (number of smolts per returning adult) implicates the freshwater phase as a major limiting factor for Steelhead recovery (Ford 2022). However, the multidirectional, population-specific, and environmentally influenced movement patterns of pre-spawn adult Steelhead make this particularly challenging. Behaviors such as tributary overshoot (Richins and Skalski 2018), non-natal tributary use (Keefer et al. 2009, 2018), and migration timing (Siegel et al. 2021) are thermally influenced. River conditions and hydrosystem operations likely affect fallback, with this effect changing depending on the stage of the pre-spawn migration and the type of fallback. En-route fallback is likely involuntary (i.e., it occurs as a result of river conditions and/or individual condition) and therefore is likely related to variables such as the volume of spill (i.e., water that passes the dam via the spillway), as this would serve to push fish back downstream over a dam via the spillway. Spill volume also is highly correlated with flow conditions in the river (Siegel et al. 2021), which has been related to en-route fallback rates in spring-summer Chinook (Boggs et al. 2004). In contrast, post-overshoot fallback is a desirable outcome for fish, as this movement helps them get closer to their natal tributary and occurs when they make the decision to go back downstream toward their natal tributary. Given the volitional nature of this movement, it is likely that the mere presence of spill allows fish to find a safe route back downstream, and that the volume of spill is less important in driving movement. This hypothesis is supported by past studies that have linked the number of days of spillway operation in March to post-overshoot fallback (Richins and Skalski 2018) and have found that small amounts of surface flow were effective for routing steelhead kelts away from turbines (Wertheimer and Evans 2005). While many studies have described the incidence of individual pre-spawn migratory behaviors, and in some cases have regressed behaviors on a single explanatory variable (Keefer et al. 2009, Richins and Skalski 2018), population-scale recovery will be determined by the cumulative and interactive effects of these various drivers of movement behaviors.

In the present study, we fit a statistical model of the complete pre-spawn migration of adult Steelhead to data from Passive Integrated Transponder (PIT) tag detections. In the Columbia River Basin, a massive PIT-tagging program has been used to monitor the movements of salmonids since 1987 (Tenney et al. 2023). These tags assign unique barcodes to fish, which are passively detected as they move past any of the hundreds of detection sites throughout the basin, allowing us to reconstruct movement histories of individual fish. We modeled the movement of over 60,000 adult Steelhead from 2005-2024 from their detection at Bonneville Dam to their final detections in the basin as a function of natal origin, rearing history, juvenile pathway (i.e., transported around dams or in-river migrants), mainstem temperature, spill operations, and

random year effects. We included rearing history and juvenile pathway in the model because of the documented influence of juvenile experiences on adult movement decisions (Keefer and Caudill 2012). We modeled the effect of temperature and spill on movement to reflect specific hypotheses about these covariates. Specifically, we examined the effect of temperature on dam ascents and movement into tributaries, while we modeled the effect of either spill volume or spillway availability on fallback, based on the type of fallback. We modeled the effect of spill volume at dams on en-route fallback, and the effect of spillway availability on post-overshoot fallback. With these various relationships modeled jointly, we assessed the relative importance of each factor in determining the fates of returning adults, which is key to informing management actions that are cost-effective, aid population recovery, and are responsive to a changing climate.

2.3 Materials and Methods

2.3.1 Overview

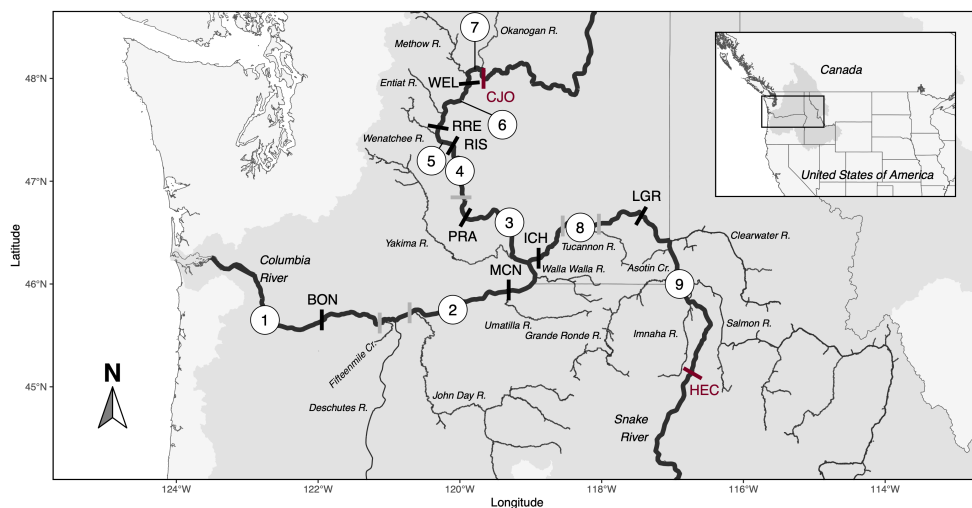
Our study focused on the movement pathways of adult Steelhead returning to natal tributaries in the Columbia River Basin (Fig. 1). Detection data from PIT-tagged natural and hatchery origin Steelhead from the Columbia River Basin, obtained from the Columbia Basin PIT Tag Information System (PTAGIS), represented the movements of returning adult Steelhead. We retained records for only those individuals of known natal origin (i.e., tagged as juveniles in hatcheries, for hatchery origin fish, or tagged and released in natal tributaries, for natural origin fish). Our dataset spanned the years 2005-2024 and included 37 different populations, which we defined as unique combinations of natal origin, rearing type, and juvenile pathway (Appendix C).

We paired movement and covariate data in space and time in a multistate movement model to investigate covariates presumed to have an influence on movement. We focused on the effects of two primary covariates (temperature and spill) that have been linked to these key pre-spawn migration movements: non-natal tributary use, natal tributary overshoot, en-route fallback, and post-overshoot fallback. We modeled the effect of temperature on movements into tributaries and upstream movements, the volume of spill on en-route fallback, and the effect of the number of spill days during the winter months (January, February, and March) on post-overshoot fallback.

We modeled the Columbia River and its tributaries as a series of connected states, which we defined as reaches of the mainstem Columbia River or Snake River between dams with PIT-tag detection arrays in the adult ladders, tributaries with PIT-tag arrays, or an absorbing loss category, which fish enter once their detection history ends (Fig. 1). To delineate mainstem states, we used only those dams that had active PIT-tag detection sites in the adult fish ladders for the full study period (i.e., Bonneville, McNary, Priest Rapids, Rock Island, Rocky Reach,

Wells, Ice Harbor, and Lower Granite Dams). We obtained daily average temperature (forebay and tailrace) and daily average spill data from the Columbia River Data Access in Real Time (DART) webpage (www.cbr.washington.edu/dart) for these dams, and provide a visualization of this covariate data in Appendix D.

(A)



(B)

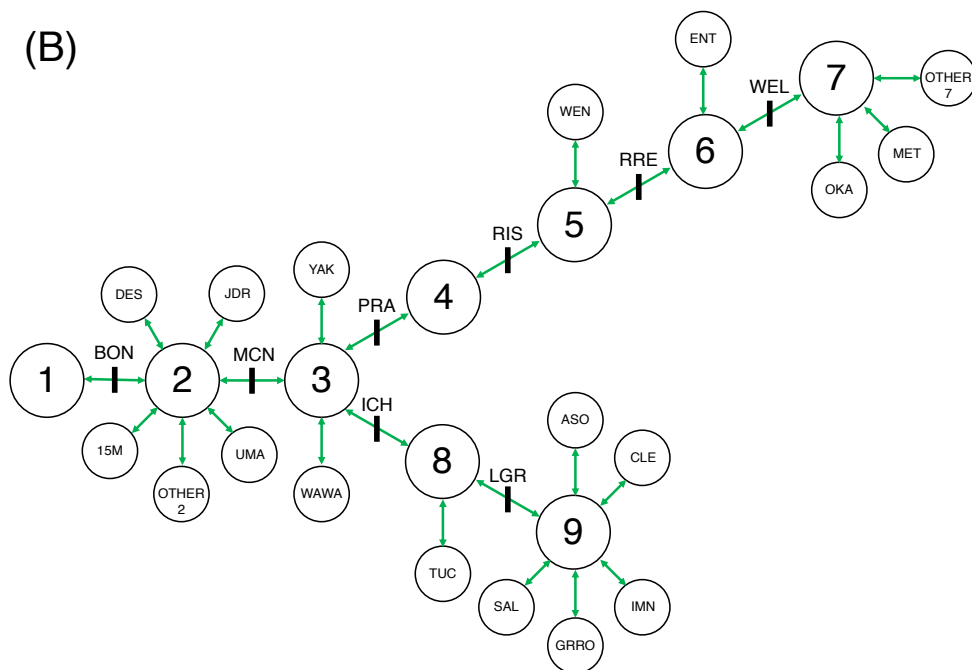


Figure 1. (A) Map of the Columbia River Basin (darker gray shaded area) showing mainstem hydroelectric dams that were modeled as state boundaries (black bars), dams with fish passage

that were excluded from the model (gray bars), and terminal dams with no fish passage (red bars). Tributaries that are model states are also shown. (B) Diagram of the model structure showing mainstem states with numbers corresponding to the river reaches in (A). Allowable transitions are shown as green arrows. An additional allowable transition from any state is the transition to the absorbing loss state. Abbreviations for dams and tributaries in (A) and (B) correspond to the abbreviations in Table 1.

2.3.2 Movement data processing

We converted raw PIT-tag detections into a history of transitions within and between the states of our model based on the location of the specific PIT-tag detection sites and the sequence of detections at different sites (Fig. 1B). For instream tributary sites, we interpreted detections to indicate fish moving into the state (if the previous detection was in a different state) or as remaining in the state (if the previous detection was in the same tributary). Processing detections at dams required interpreting a sequence of detections as a specific passage route. For upstream passage routes at dams (i.e., the adult fishways), the most common passage route consisted of an initial detection at an antenna at the entrance of the fishway and a final detection at the exit of a fishway, which was interpreted as a dam ascent (a transition from the downstream to the upstream mainstem state). However, we also found aborted ascents (detections only at the antennas at the entrance of a fishway) or dam descents via the fishway (initial detection at the exit of the fishway, final detection at the entrance of the fishway), which we interpreted as no transition and a downstream transition, respectively. We treated detections in downstream passage routes (the spillway at Lower Granite Dam, the Bonneville Corner Collector, and the juvenile bypass system at each dam) as transitions from the upstream mainstem state to the downstream mainstem state.

Some of the transition histories contained missing transitions between states, which we interpolated using the connectivity between states (Fig. 1B). This primarily affected downstream movements, which are rarely detected using PIT-tag detection arrays. For example, if we noted two consecutive ascents at Bonneville Dam, or if we observed a fish in the John Day River after ascending McNary Dam (which is upstream of the John Day River), we added a fallback event in between these events. Using a similar strategy of interpolating state transitions based on state connectivity, we also interpolated upstream movements that were missed by the PIT-tag antennas in adult fish ladders, although these missed detections were very infrequent, as detection probabilities in adult ladders are close to 100% (Richins 2017). Detection efficiency in tributaries was modeled explicitly, when possible, given the network of instream PIT-tag antennas (see Appendix A).

2.3.3 Covariate data processing

Temperature data were matched with PIT-tag detections to estimate the temperatures experienced by individual fish. However, because the timing of exit from a state was not always known (e.g., fallback movements or the end of a detection history), we used a standardized approach to estimate the temperature across the likely window of time when fish were in a state. For this approach, we first calculated the median residence time for each state in our model across all fish in the dataset. We chose to summarize the residence time across the full dataset rather than by years because of small sample sizes in some years and little interannual variability in residence time (Appendix B). Then, for each individual fish, we estimated the temperature that they experienced as the temperature over the window of time from their entry date into the state plus the median residence time. We processed spill in two ways to test two different hypotheses: 1) the relationship between spill volume and en-route fallback, and 2) the effect of the presence of an open spillway on post-overshoot fallback. We used the same approach for defining this spill volume covariate as for temperature: estimating residence time windows and taking the mean spill volume during that window. In contrast, we modeled the effect of spill on post-overshoot fallback by quantifying the number of days when spillway passage was available, as the mere presence of spill allows fish to find a safe route back downstream. Because PIT-tag arrays are largely incapable of directly detecting fallback (most dams do not have PIT antennas in the spillway), we were not able to observe post-overshoot fallback directly. Therefore, it was not possible to examine spillway passage availability aligned with the timing of detections, as was done for temperature and spill volume. Instead, we characterized spillway passage availability during the time of potential fallback as informed by subsequent detections. The timing of these subsequent detections (Appendix E) shows a distinctly bimodal pattern, where fish are detected after post-overshoot fallback in either the autumn (primarily August – November) or spring (primarily February – April). However, these two modes of fallback represent different behaviors: while autumn fallback occurs prior to fish finding overwintering habitat, spring fallback occurs after overwintering when fish are attempting to return to natal tributaries (Keefer et al. 2008). Because of its importance for determining successful homing to natal tributaries, we chose to focus on spring post-overshoot fallback following overwintering. In choosing the relevant months in which to characterize spillway availability, an examination of the spill patterns at key overshoot dams like McNary and Ice Harbor Dams shows that very little to no spill occurs in December and spill begins in April in all years for juvenile outmigration, with the months of January, February, and March showing the greatest interannual variability in spillway availability (Appendix D). Given the temporal alignment between this variability in spill and the timing of post-overshoot fallback following overwintering, we chose to focus our analysis on these months. With this processing of the spillway availability covariate, the majority of overshooting fish received this covariate (Appendix E). Further details on how covariate data were processed can be found in Appendix B.

2.3.4 Model

We fit our movement model to each combination of rearing type (hatchery or natural origin), juvenile pathway (in-river or transported), and DPS (Middle Columbia, Upper Columbia, and Snake River). While there were adults that were in-river juvenile migrants from each DPS, the Snake River DPS also included adults that were transported as juveniles; this resulted in a total of eight different datasets that the model was fit to. We therefore estimated every parameter separately across these eight runs, allowing us to differentiate between different DPSs, rearing types, and juvenile pathways. We estimated the probabilities of each possible transition out of a state as a categorical logistic regression. The probability (p) of moving to state m ($m = 1, \dots, n$) from the current state is given as follows:

$$p_m = \frac{\exp(\lambda_m)}{\sum_{k=1}^n \exp(\lambda_k)}$$

The linear predictor for each movement (λ_m), which was estimated independently of the previous movement history of the fish, had some combination of the following variables and parameters:

$$\lambda_m = \beta_{0,m} + \beta_{temp,m}T + \beta_{spill,m}S + \beta_{year,m}$$

where $\beta_{0,m}$, $\beta_{temp,m}$, $\beta_{spill,m}$, and $\beta_{year,m}$ are the intercept term, the effect of temperature (T), the effect of spill (S), and the random effect of year for the movement from the current state to state m , respectively. Not all predictors were included for all movements, and different $\beta_{spill,m}$ and $\beta_{temp,m}$ terms were incorporated based on the seasonality of movements and the nature of specific movements. The intercept term was shared for all movements outside of DPS boundaries, but within DPS boundaries the intercept term was specific to each natal origin. Temperature effects only applied to movements upstream or into tributaries and were estimated separately for movements that occurred during the winter/spring (January 1 – May 31) and the summer/fall (June 1 – December 31). We did this to account for the typical stages of Steelhead pre-spawn migration, where summer/fall movements occur before Steelhead have found overwintering habitat, and winter/spring movements occur as Steelhead move from overwintering habitat to natal tributaries. The effect of temperature was structured the same as the intercept term, with a common effect shared across all DPS individuals while outside of DPS boundaries, but origin- (i.e., natal tributary) specific effects within DPS boundaries. In contrast to temperature effects, spill effects applied only to downstream movements and were modeled in two separate ways depending on the type of fallback (en-route vs post-overshoot, as described above). The effect of year was modeled as an origin-specific random effect for all movements

within DPS boundaries except for post-overshoot fallback movements, to account for the fact that year-to-year variation was captured in the number of winter spill days for that year. This random effect of year was included to capture year-to-year variability in conditions that were not captured by other covariates in the model. Movements into the loss state (which occurred when the detection history ended and could represent either mortality, missed detections at PIT-tag arrays, or movements outside of the network of PIT-tag arrays) were modeled with $\lambda_m = 0$. A graphical depiction of the varying structure of the parameters and covariates is shown in Fig. 2.

To correct for differing detection efficiencies for movements into tributaries, we multiplied the probabilities of movements into states (p_m) by the detection efficiency of that movement, resulting in a new quantity, $p_{obs,m}$ for the probability of observing each movement (estimates of tributary detection efficiencies can be found in Appendix F). As any missed detections would appear as movements into the loss category, $p_{obs,m}$ for the movement $m = \text{loss}$ was adjusted upward by the same amount that $p_{obs,m}$ was adjusted downward using the following equation,

$$p_{obs,loss} = p_{loss} + \sum_{m=1}^n p_m * (1 - p_{det,m})$$

Having generated a vector of observed transition probabilities, the likelihood of observing the next movement (x) of fish z_i was defined as follows:

$$z_{i,x} \sim \text{categorical}(p_{obs,i,1}, p_{obs,i,2}, p_{obs,i,3} \dots p_{obs,i,n}, p_{obs,i,loss})$$

Formally, the likelihood was defined as follows:

$$f(x|\mathbf{p}) = \prod_{m=1}^n p_{obs,m}^{x_m}$$

In this likelihood, $\mathbf{p}_{obs}$ is the vector of observed probabilities and n is the possible movements out of that state.

We estimated all parameters in a Bayesian framework using the Stan programming language (Carpenter et al. 2017), using CmdStan version 2.33.0, cmdstanr version 0.6.1, and R version 4.3.2 (R Core Team, 2020). Each model was run with four chains, each with 2,000 warmup and

2,000 sampling iterations, and was thinned to keep every other sample. Model diagnostic figures can be found in Appendix G.

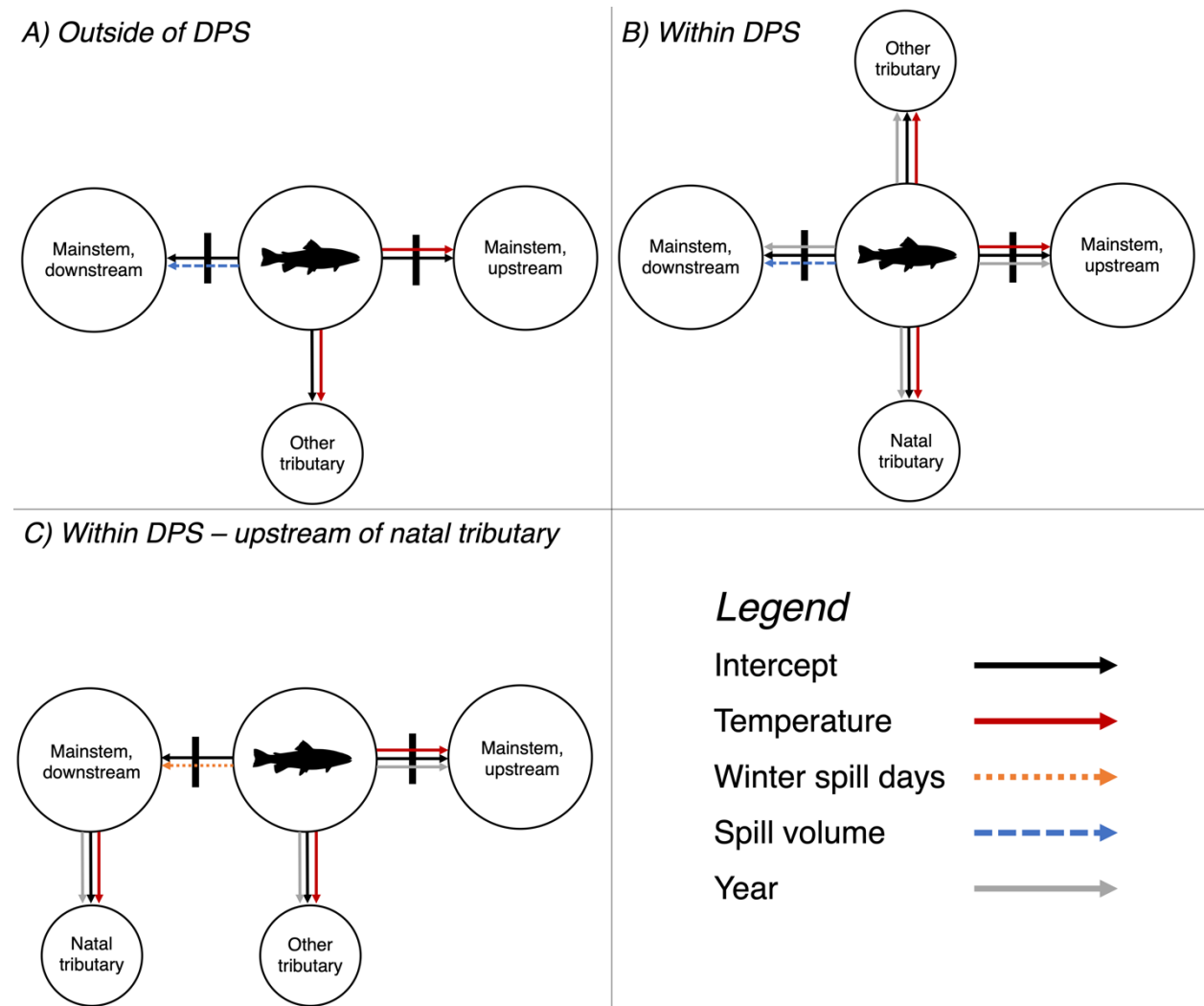


Figure 2. Structure of the multistate model, showing the variable parameterization in three common situations: (A) a fish that is outside of its DPS; (B) a fish that has entered the boundaries of its DPS and is downstream of its natal tributary; (C) a fish that is within its DPS, but has overshot its natal tributary. In all cases, the model intercept and the effect of temperature are origin-specific for movements within DPS boundaries but are shared across origins for movements outside of DPS boundaries. The effects of winter spill days and spill volume are shared across all origins, and the effect of year is origin-specific. The effect of temperature is season-specific, with different parameters estimated for the effect of temperature in the winter/spring vs. summer/fall.

2.3.5 Predicting Final Fates

We used the estimated parameters in a simulation framework to predict the final fates of simulated fish under specific temperature and winter spill scenarios to examine how these two covariates interact to affect the distribution of fish. For these predictions, we simulated the responses of populations from the seven tributaries that had an overshoot dam within 120 river kilometers of the natal tributary, as these were the only populations with overshoot rates greater than 5% and therefore had the greatest potential to show sensitivity to temperature and winter spill conditions. These populations included the John Day, Umatilla, Walla Walla, Yakima, Wenatchee, Entiat, and Tucannon Rivers. For winter spill scenarios, we fixed the number of days of winter spill at the overshoot dam at 0, 30, 60, or 90 days. The temperature scenarios were defined by specific run years from the dataset selected to span the spectrum of conditions experienced by fish. We selected three run years that represented the coldest (2011/2012), median (2019/2020), and hottest (2015/2016) run years in the data set. Both the spill volume and temperature values from these representative run years were used for the subsequent model predictions due to the coupling between river flow/spill conditions and temperature (Appendix H).

To account for the variability in spill and temperature conditions experienced by fish depending on the stage of their migration, we estimated the median values for these covariates separately for fish moving upstream (previous state was a downstream mainstem state) versus moving downstream (previous state was an upstream mainstem state or a tributary), as well as for fish moving during the winter/spring and summer/fall. This resulted in four median temperatures (winter/spring, upstream; winter/spring, downstream; summer/fall, upstream; summer/fall, downstream). These values were then used in simulations to generate predictions of final fate.

Once the conditions for the simulation were set, we predicted the final fates using the following steps: 1) randomly select one iteration from the model (one set of draws for all parameters); 2) simulate 1,000 fish that start at Bonneville Dam and move through the basin, with movements governed by the median covariate values and the values of the parameters from that iteration of the model; and 3) repeat steps one and two 1,000 times, for a total of 1,000,000 simulated fish. We also predicted the spatial distribution of fish from all populations under the median conditions of spill days, spill volume, and temperature during the study period, with these results shown in Appendix I.

2.4 Results

We found that across all populations in our study, temperature increased both natal tributary overshoot and non-natal tributary use. When simulations were run under different climate and

hydropower management scenarios using the model-estimated influence of covariates on movement probabilities, warmer temperatures consistently led to lower homing probabilities. We found population-specific evidence for the influence of winter spill on natal homing success, where two populations (Tucannon River and Walla Walla River) showed an increase in homing with increased winter spill days, but the remaining populations showed little to no evidence for an effect of winter spill days. However, this assessment is likely hampered by the limited ability of the PIT-tag array network to detect fallback. Our results indicate that pre-spawn mortality of Steelhead is likely to increase under future climate scenarios, and that management interventions require further study to determine their efficacy for offsetting these impacts.

2.4.1 Homing probability and overshoot

The probability of overshoot varied considerably across populations. For the furthest upstream populations in our study (the Methow and Okanogan in the Upper Columbia DPS; the Clearwater, Asotin Creek, Salmon, Grande Ronde, and Imnaha in the Snake River DPS), overshoot is not possible because the next mainstem dam is a terminal dam (Fig. 1). For the populations for which we could estimate a probability of overshoot, overshoot ranged from less than 1% in the Deschutes River natural origin population to over 60% in the Walla Walla hatchery origin population (Fig. 3). Furthermore, the probability of overshooting two or more dams was over 10% for the John Day River natural origin, Umatilla River natural origin, Walla Walla River natural origin, Walla Walla River hatchery origin, and Wenatchee River hatchery origin populations (Appendix J). The probability of overshoot was inversely related to the probability of homing across populations (Fig. 3). Additionally, for populations from the same natal tributary, natural origin populations consistently had higher homing probabilities than hatchery origin populations and in-river juvenile migrants had higher homing probabilities than transported juvenile migrants. It is notable that despite having the longest migration pathways, the furthest upstream populations (Asotin Creek and the Imnaha River in the Snake River DPS, and the Methow and Okanogan Rivers in the Upper Columbia DPS) had higher homing probabilities than many origins further downstream that had high overshoot rates. Within each population, the probability of homing decreased with each successive overshoot, although the impact of overshoot on homing success varied considerably across populations (Appendix J).

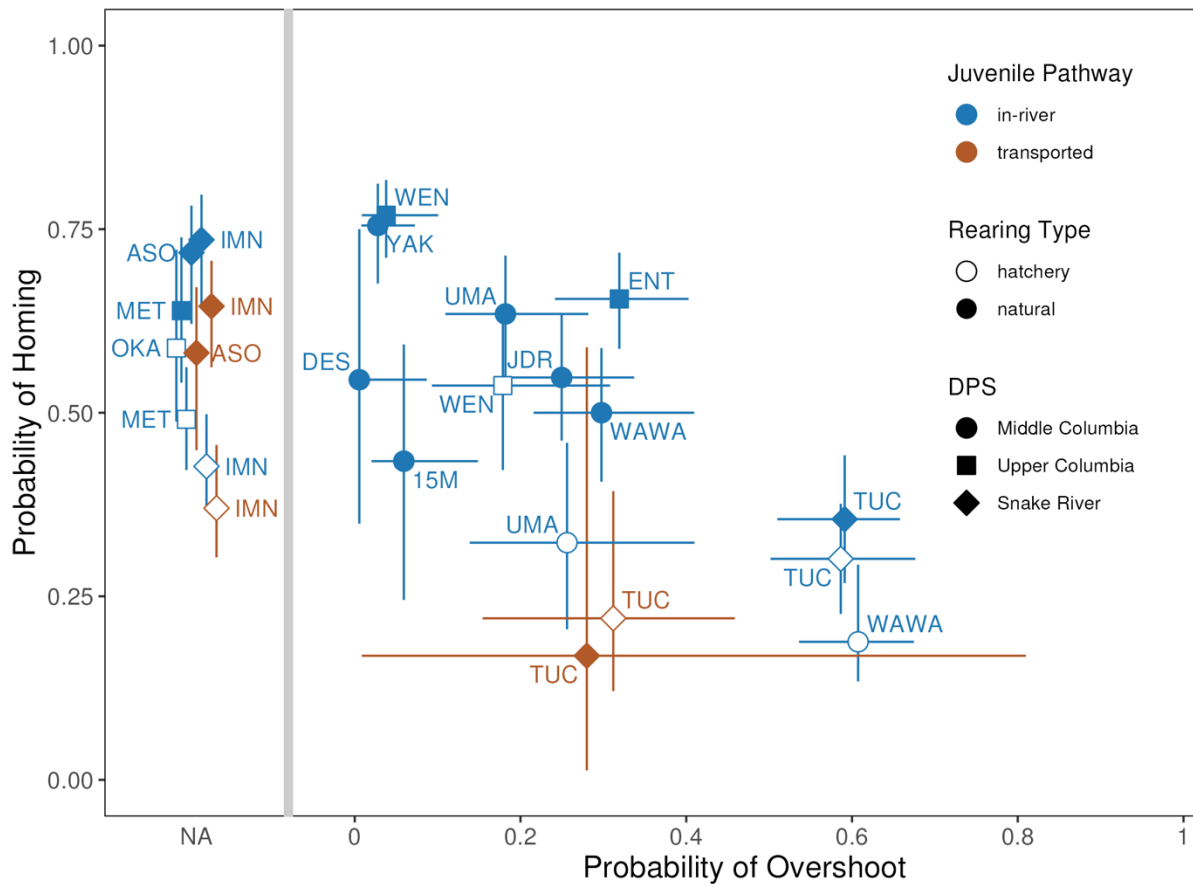


Figure 3. Median probabilities (points) and 95% credible intervals (bars) of homing and overshoot, for each modeled population. Homing is defined here as the probability of the final fate being the natal tributary; overshoot is defined as the probability of ascending the next dam upstream of the natal tributary conditional on being in the mainstem state connecting to the natal tributary. For populations that did not have an overshoot state in the model (because the dam upstream of the natal tributary has no fish passage), the probability of overshoot is noted as “NA.” Populations where homing could not be reliably estimated due to the inability to estimate detection efficiency in the natal tributary (the Salmon River, Clearwater River, and Grande Ronde River) are not shown. Abbreviations for tributaries correspond to those in Table 1.

2.4.2 Temperature

Across all populations, the probability of moving directly to the natal tributary decreased as temperature increased (Fig. 4). As the probability of moving to the natal tributary decreased, other movements increased, but with varying response curves across the different populations. Overshoot increased with increasing mainstem temperature for all populations. For populations from two tributaries (the John Day and Umatilla Rivers), the probability of overshoot began to decline at the highest temperatures as movements into the Deschutes River became increasingly

likely. The Deschutes River is not pictured as a movement probability for the other populations in Fig. 4, as its confluence with the mainstem is upstream of the overshoot dam for those populations. However, for those populations whose natal tributary connects to a mainstem state upstream of the Deschutes River, a similar response curve is seen for the probability of movement into the Deschutes River with increased temperature (Appendix K). Loss from the mainstem state generally increased as temperature increased, although this was not consistent across populations. For example, the Umatilla hatchery population had a considerably higher probability of loss at higher temperatures, whereas for Walla Walla natural and hatchery origin fish, the probability of loss slightly decreases at higher temperatures as overshoot becomes overwhelmingly likely.

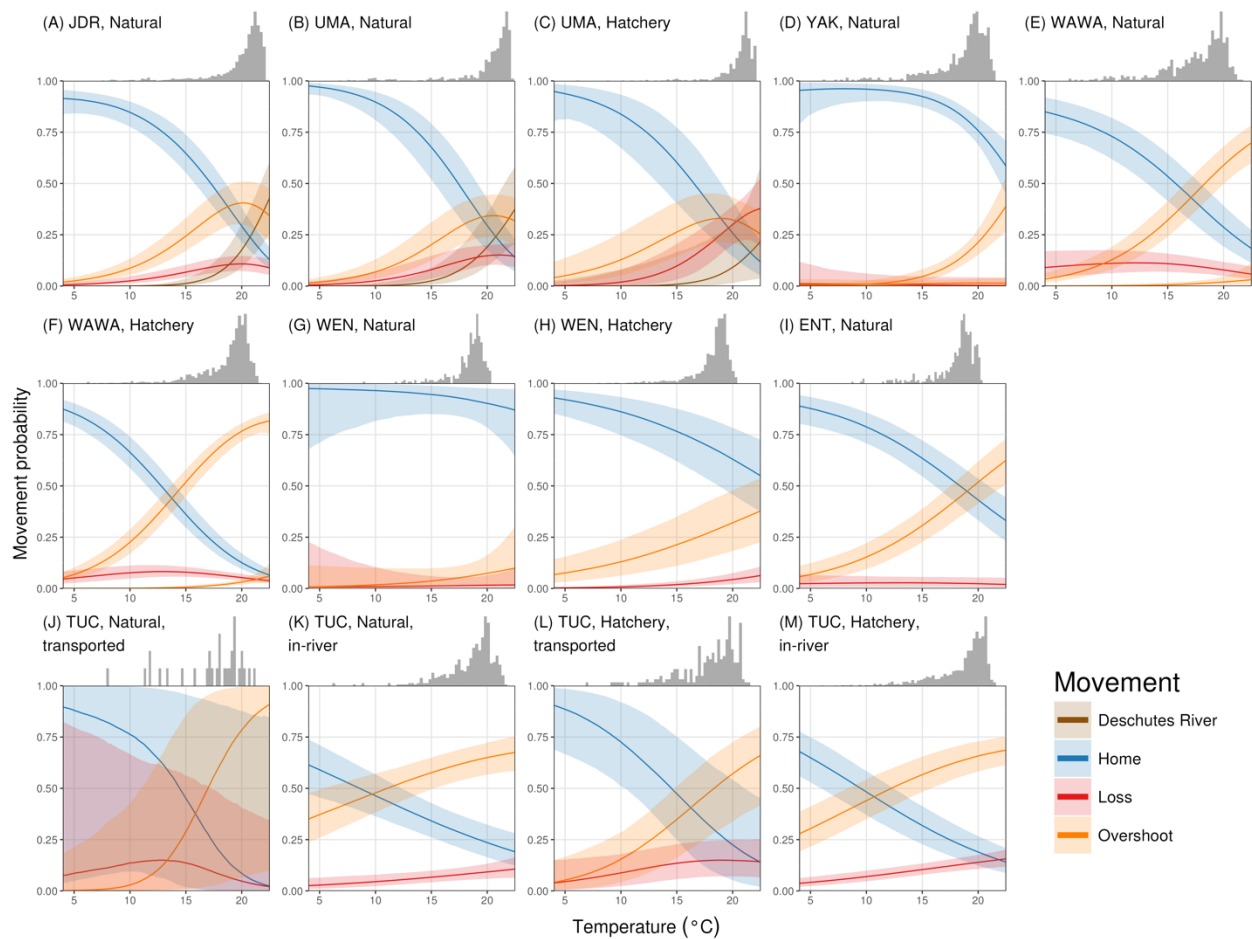


Figure 4. The marginal effect of temperature on movements out of the mainstem state that connects to the natal tributary, with all other covariates fixed at their median values from the study period, for (A) John Day River natural origin Steelhead, (B) Umatilla River natural origin Steelhead, (C) Umatilla River hatchery origin Steelhead, (D) Yakima River natural origin Steelhead, (E) Walla Walla River natural origin Steelhead, (F) Walla Walla River hatchery origin Steelhead, (G) Wenatchee River natural origin Steelhead, (H) Wenatchee River hatchery

origin Steelhead, (I) Entiat River natural origin Steelhead, (J) Tucannon River natural origin transported Steelhead, (K) Tucannon River natural origin in-river Steelhead, (L) Tucannon River hatchery origin transported Steelhead, and (M) Tucannon River hatchery origin in-river Steelhead. The probability of movement into the Deschutes River is shown for John Day River and Umatilla River populations, as these are the only two tributaries shown that connect to the same portion of the mainstem as the Deschutes River. The lines depict the median estimated effect of temperature, with the shaded area representing the 95% credible intervals. Histograms on the plot margins indicate the temperature experiences of individual fish. Abbreviations for tributaries correspond to those in Table 1.

2.4.3 Spill

In contrast to temperature, the effect of winter spill on post-overshoot fallback at the first overshoot dam was highly population-specific (Fig. 5). For many populations, there were insufficient data to estimate the effect of winter spill days with a high degree of confidence. The strongest evidence for a positive relationship between winter spill days and post-overshoot fallback is for the Walla Walla River natural origin population (Fig. 5e). When the relationship between winter spill and post-overshoot fallback was compared across dams, the strongest evidence for positive relationships between winter spill days and post-overshoot fallback was at Ice Harbor Dam on the Snake River (Appendix L).

We also examined the relationship between en-route fallback and spill and found a weak positive relationship between en-route fallback probability and spill volume (Appendix M). However, because the majority of fish do not experience high spill volumes because of the timing of their upstream migration, this relationship is highly uncertain at higher volumes of spill. At the ranges of spill volume fish typically encounter, en-route fallback probabilities at dams typically ranged from 0-5% across populations.

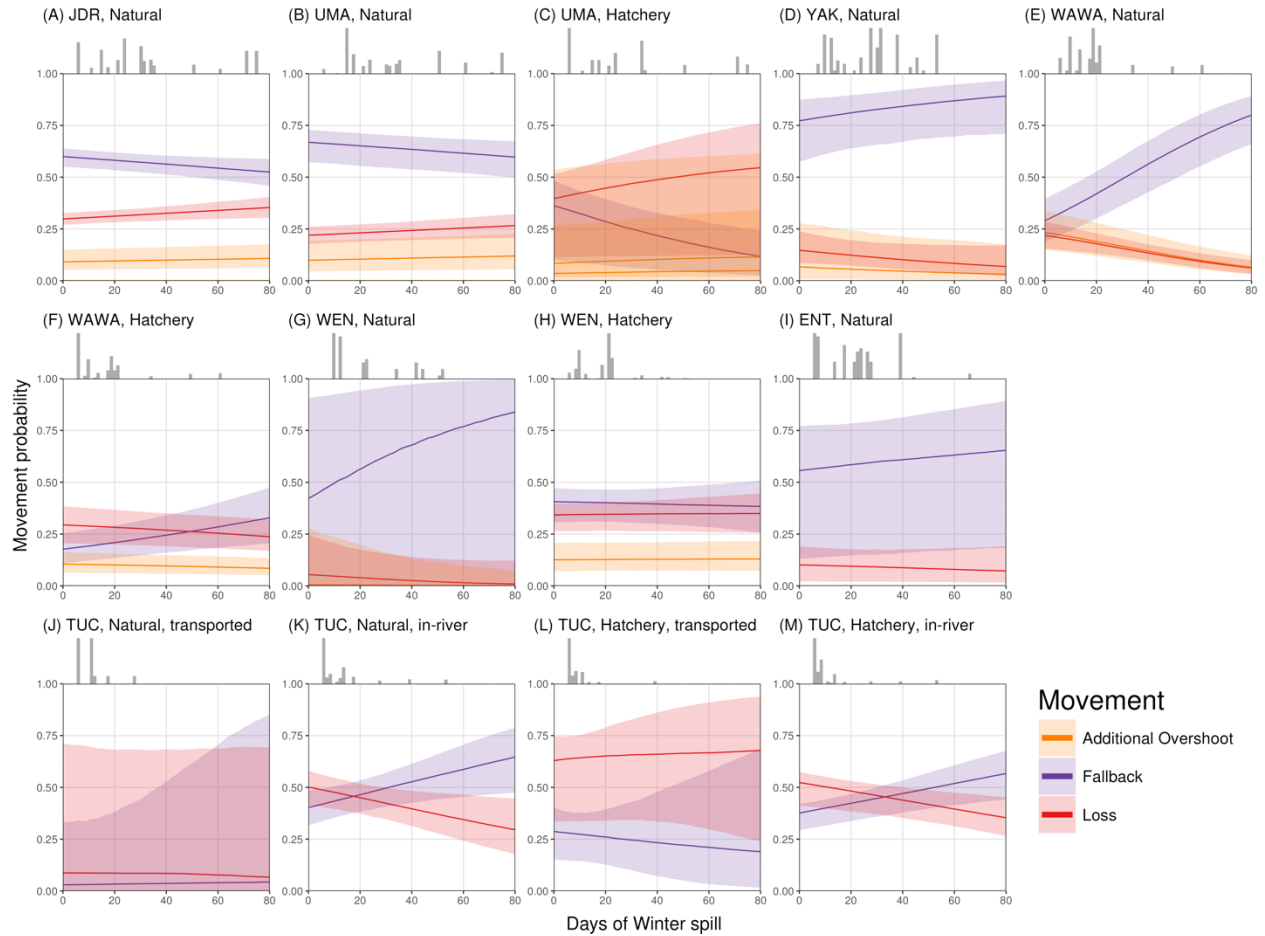


Figure 5. The marginal effect of winter spill days on movement probabilities out of the mainstem state directly upstream of the mainstem state that connects to the natal tributary, with all other covariates fixed at their median values from the study period, for (A) John Day River natural origin Steelhead, (B) Umatilla River natural origin Steelhead, (C) Umatilla River hatchery origin Steelhead, (D) Yakima River natural origin Steelhead, (E) Walla Walla River natural origin Steelhead, (F) Walla Walla River hatchery origin Steelhead, (G) Wenatchee River natural origin Steelhead, (H) Wenatchee River hatchery origin Steelhead, (I) Entiat River natural origin Steelhead, (J) Tucannon River natural origin transported Steelhead, (K) Tucannon River natural origin in-river Steelhead, (L) Tucannon River hatchery origin transported Steelhead, and (M) Tucannon River hatchery origin in-river Steelhead. The lines depict the median estimated effect of winter spill days, with the shaded area representing the 95% credible intervals. Histograms on the plot margins indicate the winter spill experiences of individual fish, although all fish from the same run year experienced the same winter spill days. Abbreviations for tributaries correspond to those in Table 1.

2.4.4 Final fates under different scenarios

Across all populations, the probability of successful homing was strongly affected by temperature, as the probability of homing was consistently higher in the coldest year relative to the hottest year (Fig. 6). However, some populations were more sensitive to temperature than others. For example, the John Day River natural origin population showed a 6-7% decrease in homing from the coldest to the warmest temperature scenario, whereas the Entiat River natural origin population showed only a 2-3% decrease in homing between these temperature scenarios. Additionally, for all tributaries that have both a hatchery and a natural origin population, homing probability was higher for the natural than the hatchery origin population. In contrast, the effect of winter spill days was more variable across populations, with the Walla Walla and Tucannon River populations having strong predicted responses to winter spill days and other populations showing little sensitivity to winter spill.

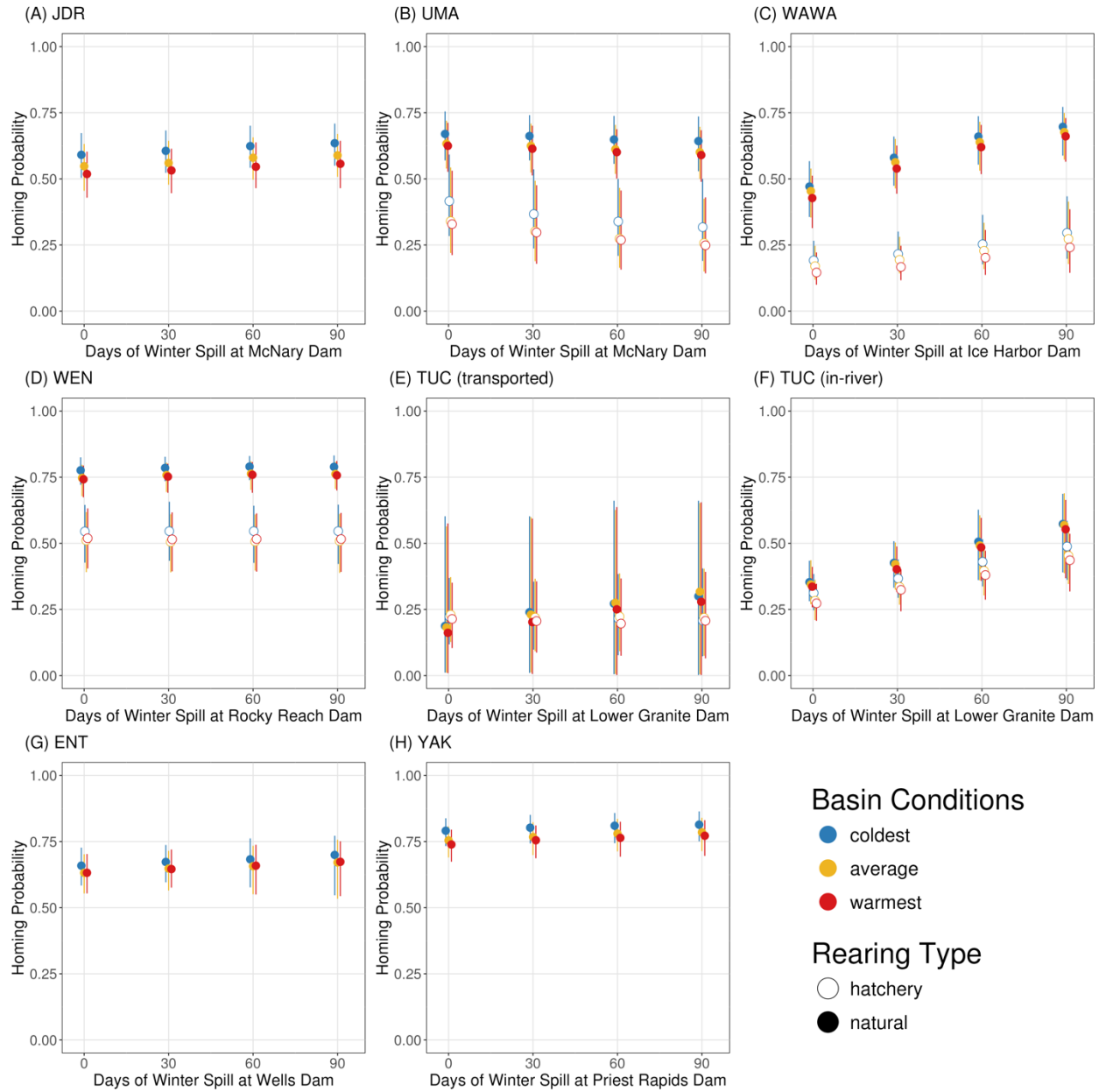


Figure 6. The median and 95% credible intervals for the homing probability for (A) John Day River, (B) Umatilla River, (C) Walla Walla River, (D) Wenatchee River, (E) Tucannon River transported, (F) Tucannon River in-river, (G) Entiat River, and (H) Yakima River Steelhead under different scenarios for basin-wide temperature and winter spill days (0, 30, 60, or 90 days) at the overshoot dam. The temperature scenarios are specific run years from the dataset, with the coldest year being the 2011/2012 run year, the average year being the 2019/2020 run year, and the warmest year being the 2015/2016 run year. Abbreviations for tributaries correspond to those in Table 1.

2.5 Discussion

In an era of intensifying climate change and water conflicts, effective management requires an understanding of how present and future climate scenarios will affect key species and what ability managers have for adapting to these scenarios. In our study of Columbia River Steelhead, we found a consistent negative relationship between temperature in the basin and the probability of fish reaching natal tributaries, and some evidence that increased winter spill increases the probability of fish reaching natal tributaries. By modeling how different factors affect the entire adult migration period, we provide population-scale insights into their relative importance for Steelhead recovery. Furthermore, we demonstrate how incorporating interacting environmental, behavioral, and management factors in a Bayesian framework that propagates uncertainty can be used to inform recovery of species under climate change.

2.5.1 Insights from an integrated model

Our modeling approach has three key characteristics that make it especially useful for informing the management and recovery of species. First, it simultaneously models environmental and management impacts, which informs our understanding of the capacity of management to adapt to the impacts of climate change. Second, it models a key life stage (the pre-spawn migration) in its entirety, allowing us to examine how an outcome of interest (in this case, adult homing to natal tributaries) is affected by conditions at specific portions of the pre-spawn migration. Third, it is implemented in a Bayesian framework, which facilitates the propagation of uncertainty, and enables us to generate posterior predictive estimates of the probability of outcomes of interest through simulation in a complex system where an analytical solution is intractable. These attributes allowed us to conduct a sensitivity analysis, where we estimated the sensitivity of a derived outcome of interest (i.e., natal homing) to changes in covariates (i.e., temperature and winter spill). Movement models developed for fish passage often incorporate environmental covariates, but the focus is typically on small spatial areas to provide tactical advice for improving passage or to estimate survival and movement at specific reaches or junctures (Dodrill et al. 2022, Hance et al. 2022). Our model trades off the fine-scale spatial resolution of these types of models (for comparison see Waterhouse et al. 2020, which models one portion of our study area in much greater detail) for the ability to provide strategic insights at the scale of recovery objectives. Terrestrial applications of similar modeling approaches have yielded actionable insights for managers, such as a spatially explicit individual-based modeling approach that was used to prioritize recovery actions for Greater Sage-grouse in Canada (Heinrichs et al. 2018). In that study, demographic parameters such as survival rates of different life history stages were estimated statistically, and a sensitivity analysis using simulation was similarly conducted to examine population recovery under different scenarios (Heinrichs et al. 2018). Ultimately, our modeling approach may serve as a bridge between multistate movement models, which allow us to estimate movement probabilities (Lebreton et al. 2009), and matrix population

models, where the elasticity of key outcomes of interest (traditionally growth rate) to individual rates can be estimated (Caswell 2019).

The benefit of modeling the full pre-spawn migration of Steelhead as an amalgamation of multiple processes is further demonstrated by the varying scales at which our model provides insight into recovery. At the fine scale, our model estimates the effects of covariates on key movements within specific river reaches for individual populations. For example, we estimate the increase in the probability of fish from different upstream origins moving into the Deschutes River, the site of a major recreational Steelhead fishery, as a function of temperature in the mainstem. At the basin scale, our model reveals the relative importance of these individual processes, and the ways in which these processes interact, on outcomes of interest. Using this framework, this model can be used by managers to estimate the impacts of different climate and management scenarios on populations of interest. This capability is demonstrated through the prediction of final fates under different temperature and spill scenarios presented in Fig. 6. By using the joint posteriors of the parameter estimates to simulate distributions under different basin-scale temperature scenarios, we see an approximately 7% decrease in John Day River natural origin Steelhead homing success from the coldest to the warmest scenario. This same approach could test the impact of temperature changes that could be achieved through management actions such as cold-water releases at dams. For example, the impact of cold-water releases from Dworshak Dam on the Clearwater River (a major tributary of the Snake River), which can lower mainstem temperatures in the upper Snake River by 1-3° Celsius (Peery et al. 2003), could be estimated.

2.5.2 Effects of temperature and spill

Key movements that we modeled included tributary overshoot and non-natal tributary use. These movements each have an associated mortality risk (Keefer et al. 2009, 2016), and we found that both of these behaviors increased significantly with temperature. Richins & Skalski (2018) analyzed relationships between water temperature and overshoot and found significant positive relationships for populations from four out of the seven tributaries that we presented in Fig. 4. With a refined model and additional years of data, we can now draw a stronger conclusion: overshoot increases with temperature for every population. This is particularly concerning given that, similar to other studies of Steelhead overshoot (Murdoch et al. 2022), we found that each successive dam that was overshoot led to a decrease in homing probability (Appendix J). Our findings of a high incidence of fish entering the Deschutes River as well as the relationship between temperature and movement into the Deschutes River is in line with multiple previous studies that found that non-natal tributary use is common and related to temperature (High et al. 2006, Keefer et al. 2009). While beneficial in a pristine system, these responses to thermal cues in the present-day hydrosystem may be maladaptive, serving as an “ecological trap,” defined as a breakdown of the correlation between habitat quality and a formerly reliable cue (Schlaepfer et

al. 2002). In the case of non-natal tributary use, high harvest rates inside these tributaries that serve as thermal refugia have been linked to reduced survival of fish that use these tributaries during their pre-spawn migration (Keefer et al. 2009). Although retention is only allowed for hatchery Steelhead, higher mortality was also recorded for natural origin fish that entered non-natal tributaries, suggesting illegal harvest and mortality following catch and release (Keefer et al. 2009). In the case of overshoot, seeking cooler habitat upstream later requires descending one or more dams to return to a natal tributary, with downstream passage routes often being limited to the powerhouse (Khan et al. 2013), which has high associated mortality (Normandeau Associates 2014). As such, temperature (and therefore climate) driven interactions with the hydrosystem present a major challenge for hydrosystem managers.

We included spill as our hydropower covariate, as it is the primary lever that hydropower managers can use to improve passage at dams. We found a weak positive relationship between en-route fallback and spill, although the probability of en-route fallback at the spill volumes typically experienced by fish were estimated to only be about 0-5% (Appendix M). We found a positive relationship between winter spill days and post-overshoot fallback populations from two tributaries, the Walla Walla River and the Tucannon River, but no relationship for the remaining focal populations (Fig. 5, 6). However, given that mortality associated with passage through hydroelectric turbines is estimated to be about four times that of passage through the spillway (9.3% vs. 2.3% 48-hour mortality, respectively; Normandeau Associates, 2014), spillway operation for aiding downstream migration is likely still providing a benefit that we were unable to detect.

2.5.3 Limitations of the Columbia River Basin PIT-tag network

In our analysis, three key factors limit our ability to estimate the relationship between winter spill and post-overshoot fallback using PIT-tag data. First, with the exception of the spillway detectors installed at Lower Granite Dam in 2020, PIT-tag arrays were not present in dam spillways, meaning that we could only detect fallback via later detections of fish. Therefore, any fallback movements that were not followed by detections in tributaries or in adult fish ladders were missed. Second, the inability to directly detect fallback prevented us from estimating the timing of fallback, but instead only provided a window of time in which fallback could have occurred (between the last detection in an adult fish ladder and the next detection following fallback). This required us to use a coarse temporal scale for spill (days of spill across the months of January, February, and March), which captured general conditions but not the specific conditions that fish encountered (Appendix E). This also precluded us from drawing conclusions about the most effective timing of spill on the fine temporal scale that is most useful to dam managers. The addition of PIT-tag arrays in the spillway, as was installed at Lower Granite Dam on the Snake River in 2020, would be required at more dams to provide this insight. Third, while our long time series includes some variation in winter spill, our time series only includes four

years where surface spill has been intentionally manipulated to aid in adult Steelhead migration, which can be seen in the figures showing spill patterns by year in Appendix D. While dams have provided spill beginning in early April for juvenile salmonid passage since 2005, providing surface spill routes for adult Steelhead has only recently gained traction as a way to provide a safer passage route for fallback. Following the publication of the Environmental Impact Statement for the Federal Columbia River Power System in 2020, dam operators began providing offseason surface spill (October 1 – November 15 and March 1 to March 30) at McNary Dam and the four lower Snake River Dams to reduce mortality of overshooting Steelhead (USACE 2020). In 2024 (the last year of our dataset), the United States Army Corps of Engineers began spilling water every day starting March 1 as part of a litigation stay agreement. To align with this recent development, we present the results of a model where winter spill is modeled as the number of days in March only (rather than January, February, and March) in Appendix N. In this model, we found a qualitatively similar but overall weaker relationship between March spill and post-overshoot fallback compared to the relationship between winter spill and post-overshoot fallback in the base model. As such, additional years of data will likely be required to assess the population-scale effects of spill practices to aid adult passage under this new management regime.

PIT-tag detections also do not allow us to determine what happened to fish after their final detections. The final fate of fish, which we defined as the last state that a fish was detected in, does not definitively tell us where and how the fish died or whether it successfully spawned. Missed detections at the end of a fish's detection history lead to ambiguous final fates; for example, any fallback mortality would not be detected, and the final fate of that fish would appear as the state upstream of the dam. Known gaps in the PIT-tag array network, such as the lack of ability to detect fallback and the lack of PIT-tag arrays at the mouths of key Snake River tributaries, led to inflated mainstem final fates as are seen in Appendix I for some populations. Furthermore, final fates in non-natal tributaries could indicate straying to that tributary and spawning there, or it could represent harvest or natural mortality. We could not explicitly account for harvest, which is a major cause of mortality for hatchery-origin fish (take of natural origin fish is not permitted, although significant unknown mortality of natural origin fish implicates illegal harvest; Keefer et al., 2009). This likely explains the higher final fates of hatchery relative to natural origin Umatilla River fish in the Deschutes River (Appendix I). Harvest is also likely a major contributor to the lower overall probability of eventual homing by hatchery-origin fish (e.g., Fig. 6), as harvest estimates of hatchery-origin individuals are considerable; for example, in 2015 the harvest rate upstream of Priest Rapids was estimated to be 18% (Fuchs et al. 2021).

2.5.4 Conclusions

Dam management on the Columbia and Snake Rivers is dynamic, with yearly developments in monitoring capabilities and hydropower management practices. Our study provides a description of pre-spawn Steelhead movements based on the detection capabilities and basin conditions of the study period, but future monitoring and modeling will continue to refine this story. Recently installed PIT-tag arrays in spillways (Lower Granite Dam) and in adult fish ladders at more dams are an opportunity to better understand patterns of overshoot and fallback throughout the basin. Monitoring Steelhead migration success under new spill practices will permit us to better understand how managers can help Steelhead reach natal tributaries. As the first study to model the full pre-spawn migration of a salmonid in the Columbia River Basin, and by including the effects of climate and hydropower in our model, we reveal ecological insights that are highly applicable to decision making. Scenarios can be tested across the Columbia River Basin to estimate their effects on migration success for different populations of interest. By estimating statistical relationships and using them in a predictive framework, we found that Steelhead are unequivocally threatened by rising mainstem temperatures in the Columbia River. Similar models that integrate movement with environmental and management data could be developed for other aquatic or terrestrial systems and will play a key role in developing our understanding of how to support management and recovery of species.

2.6 Acknowledgements

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2.7 References

- Boggs, C. T., M. L. Keefer, C. A. Peery, T. C. Bjornn, and L. C. Stuehrenberg. 2004. Fallback, Reascension, and Adjusted Fishway Escapement Estimates for Adult Chinook Salmon and Steelhead at Columbia and Snake River Dams. *Transactions of the American Fisheries Society* 133:932–949.
- Busby, P. J., T. C. Wainwright, G. J. Bryant, L. J. Lierheimer, R. S. Waples, F. W. Waknitz, and I. V. Lagomarsino. 1996. Status review of west coast steelhead from Washington, Idaho, Oregon, and California.

- Butler, V. L., and J. E. O'Connor. 2004. 9000 years of salmon fishing on the Columbia River, North America. *Quaternary Research* 62:1–8.
- Campbell, S. K., and V. L. Butler. 2010. Archaeological evidence for resilience of Pacific Northwest salmon populations and the socioecological system over the last ~7,500 years. *Ecology and Society* 15.
- Carlisle, D. M., D. M. Wolock, and M. R. Meador. 2011. Alteration of streamflow magnitudes and potential ecological consequences: A multiregional assessment. *Frontiers in Ecology and the Environment* 9:264–270.
- Carpenter, B., A. Gelman, M. D. Hoffman, D. Lee, B. Goodrich, M. Betancourt, M. Brubaker, J. Guo, P. Li, and A. Riddell. 2017. Stan: A probabilistic programming language. *Journal of statistical software* 76.
- Caswell, H. 2019. *Sensitivity analysis: matrix methods in demography and ecology*. Springer Nature.
- Chapman, D. W. 1986. Salmon and steelhead abundance in the Columbia River in the nineteenth century. *Transactions of the American Fisheries Society* 115:662–670.
- Craig, J. A., and R. L. Hacker. 1940. The history and development of the fisheries of the Columbia River. *Bulletin of the Bureau of Fisheries* XLIX:216.
- Dodrill, M. J., R. W. Perry, A. C. Pope, and X. Wang. 2022. Quantifying the effects of tides, river flow, and barriers on movements of Chinook Salmon smolts at junctions in the Sacramento – San Joaquin River Delta using multistate models. *Environmental Biology of Fishes* 105:2065–2082.
- Dudgeon, D., A. H. Arthington, M. O. Gessner, Z. I. Kawabata, D. J. Knowler, C. Lévêque, R. J. Naiman, A. H. Prieur-Richard, D. Soto, M. L. J. Stiassny, and C. A. Sullivan. 2006. Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews of the Cambridge Philosophical Society* 81:163–182.
- Ficklin, D. L., B. L. Barnhart, J. H. Knouft, I. T. Stewart, E. P. Maurer, S. L. Letsinger, and G. W. Whittaker. 2014. Climate change and stream temperature projections in the Columbia River basin: Habitat implications of spatial variation in hydrologic drivers. *Hydrology and Earth System Sciences* 18:4897–4912.
- Ford, M. J. 2022. Biological viability assessment update for Pacific salmon and steelhead listed under the Endangered Species Act: Pacific Northwest. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-171.
- Fuchs, N. T., C. C. Caudill, A. R. Murdoch, and B. L. Truscott. 2021. Overwintering Distribution and Postspawn Survival of Steelhead in the Upper Columbia River Basin. *North American Journal of Fisheries Management* 41:757–774.
- Fulton, L. A. 1970. Spawning areas and abundance of steelhead trout and coho, sockeye and chum salmon in the Columbia River basin - past and present. National Marine Fisheries Service, Special Scientific Report - Fisheries No. 618.
- Grill, G., B. Lehner, M. Thieme, B. Geenen, D. Tickner, F. Antonelli, S. Babu, P. Borrelli, L. Cheng, H. Crochetiere, H. Ehalt Macedo, R. Filgueiras, M. Goichot, J. Higgins, Z. Hogan,

- B. Lip, M. E. McClain, J. Meng, M. Mulligan, C. Nilsson, J. D. Olden, J. J. Opperman, P. Petry, C. Reidy Liermann, L. Sáenz, S. Salinas-Rodríguez, P. Schelle, R. J. P. Schmitt, J. Snider, F. Tan, K. Tockner, P. H. Valdujo, A. van Soesbergen, and C. Zarfl. 2019. Mapping the world's free-flowing rivers. *Nature* 569:215–221.
- Hance, D. J., R. W. Perry, A. C. Pope, A. J. Ammann, J. L. Hassrick, and G. Hansen. 2022. From drought to deluge: spatiotemporal variation in migration routing, survival, travel time and floodplain use of an endangered migratory fish. *Canadian Journal of Fisheries and Aquatic Sciences* 79:410–428.
- Heinrichs, J. A., C. L. Aldridge, D. L. Gummer, A. P. Monroe, and N. H. Schumaker. 2018. Prioritizing actions for the recovery of endangered species: Emergent insights from Greater Sage-grouse simulation modeling. *Biological Conservation* 218:134–143.
- High, B., C. A. Peery, and D. H. Bennett. 2006. Temporary Staging of Columbia River Summer Steelhead in Coolwater Areas and Its Effect on Migration Rates. *Transactions of the American Fisheries Society* 135:519–528.
- Hilborn, R. W., and Hare, S. R. (1992). Hatchery and wild fish production of anadromous salmon in the Columbia River Basin. Technical Report prepared for Fisheries Research Institute, School of Fisheries, University of Washington.
- Jaeger, W. K., and M. D. Scheuerell. 2023. Return(s) on investment: Restoration spending in the Columbia River Basin and increased abundance of salmon and steelhead. *PLoS ONE* 18:1–21.
- Keefer, M. L., C. T. Boggs, C. A. Peery, and C. C. Caudill. 2008. Overwintering Distribution, Behavior, and Survival of Adult Summer Steelhead: Variability among Columbia River Populations. *North American Journal of Fisheries Management* 28:81–96.
- Keefer, M. L., and Caudill, C. C. (2012). A review of adult salmon and steelhead straying with an emphasis on Columbia River populations. Technical Report 2012-6 prepared for U.S. Army corps of Engineers, Walla Walla District.
- Keefer, M. L., C. Caudill, T. Clabough, K. Collis, A. Evans, C. Fitzgerald, M. Jepson, G. Naughton, R. O'Connor, and Q. Payton. 2016. Final Technical Report: Adult steelhead passage behaviors and survival in the Federal Columbia River Power System. Prepared for U.S. Army Corps of Engineers, Walla Walla District.
- Keefer, M. L., T. S. Clabough, M. A. Jepson, C. C. Caudill, B. J. Burke, and K. E. Frick. 2015. Overwintering Distribution and Fallback Behavior By Adult Radio-Tagged Steelhead in the Federal Columbia River Power System , Migration Years 2013-2014 and 2014-2015. Technical Report 2015-15 prepared for U.S. Army Corps of Engineers, Portland District.
- Keefer, M. L., T. S. Clabough, M. A. Jepson, E. L. Johnson, C. A. Peery, and C. C. Caudill. 2018. Thermal exposure of adult Chinook salmon and steelhead: Diverse behavioral strategies in a large and warming river system. *PLoS ONE* 13:1–29.
- Keefer, M. L., C. A. Peery, and B. High. 2009. Behavioral thermoregulation and associated mortality trade-offs in migrating adult steelhead (*Oncorhynchus mykiss*): Variability among sympatric populations. *Canadian Journal of Fisheries and Aquatic Sciences* 66:1734–1747.

- Khan, F., I. M. Royer, G. E. Johnson, and S. C. Tackley. 2013. Sluiceway Operations for Adult Steelhead Downstream Passage at The Dalles Dam, Columbia River, USA. *North American Journal of Fisheries Management* 33:1013–1023.
- Lebreton, J., J. D. Nichols, R. J. Barker, R. Pradel, and J. A. Spindel. 2009. Modeling individual animal histories with multistate capture–recapture models. *Advances in ecological research* 41:87–173.
- Leonard, N. J., M. A. Fritsch, J. D. Ruff, J. F. Fazio, J. Harrison, and T. Grover. 2015. The challenge of managing the Columbia River Basin for energy and fish. *Fisheries Management and Ecology* 22:88–98.
- Liermann, C. R., C. Nilsson, J. Robertson, and R. Y. Ng. 2012. Implications of dam obstruction for global freshwater fish diversity. *BioScience* 62:539–548.
- Mote, P. W., S. Li, D. P. Lettenmaier, M. Xiao, and R. Engel. 2018. Dramatic declines in snowpack in the western US. *npj Climate and Atmospheric Science* 1.
- Murdoch, A. R., See, K., and Truscott, B. L. (2022). Abundance and Migration Success of Overshoot Steelhead in the Upper Columbia River. *North American Journal of Fisheries Management*, 42(4), 1066-1080.
- National Marine Fisheries Service (NMFS). 2022a. 2022 5-Year Review : Summary & Evaluation of Middle Columbia River Steelhead.
- National Marine Fisheries Service (NMFS). 2022b. 2022 5-Year Review: Summary & Evaluation of Lower Columbia River Chinook Salmon, Columbia River chum Salmon, Lower Columbia River Coho, Lower Columbia River Steelhead.
- National Marine Fisheries Service (NMFS). 2022c. 2022 5-Year Review: Summary & Evaluation of Upper Columbia River Steelhead.
- National Marine Fisheries Service (NMFS). 2022d. 2022 5-Year Review: Summary & Evaluation of Snake River Basin Steelhead.
- Normandeau Associates. 2014. Direct Injury and Survival of Adult Steelhead Trout Passing a Turbine and Spillway Weir at McNary Dam. Prepared for U.S. Army Corps of Engineers, Walla Walla District.
- Peery, C. A., T. C. Bjornn, and L. Stuehrenberg. 2003. Water temperatures and passage of adult salmon and steelhead in the lower Snake River. Idaho Cooperative Fish and Wildlife Research Unit, University of Idaho.
- Postel, S., and S. Carpenter. 1997. Freshwater ecosystem services. *Nature's services: Societal dependence on natural ecosystems* 195.
- Pringle, C. 2003. What is hydrologic connectivity and why is it ecologically important? *Hydrological Processes* 17:2685–2689.
- Quinn, T. P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press.
- Reid, A. J., A. K. Carlson, I. F. Creed, E. J. Eliason, P. A. Gell, P. T. J. Johnson, K. A. Kidd, T. J. MacCormack, J. D. Olden, S. J. Ormerod, J. P. Smol, W. W. Taylor, K. Tockner, J. C. Vermaire, D. Dudgeon, and S. J. Cooke. 2019. Emerging threats and persistent conservation

- challenges for freshwater biodiversity. *Biological Reviews* 94:849–873.
- Richins, S. M. 2017. Influence of juvenile and adult experiences on tributary overshoot and fallback by steelhead in the Columbia River basin. Master's Thesis.
- Richins, S. M., and J. R. Skalski. 2018. Steelhead Overshoot and Fallback Rates in the Columbia–Snake River Basin and the Influence of Hatchery and Hydrosystem Operations. *North American Journal of Fisheries Management* 38:1122–1137.
- Schlaepfer, M. A., M. C. Runge, and P. W. Sherman. 2002. Ecological and evolutionary traps. *Trends in Ecology and Evolution* 17:474–480.
- Scott, M. H., S. A. Talke, D. A. Jay, and H. L. Diefenderfer. 2023. Warming of the lower Columbia River, 1853 to 2018. *River Research and Applications* 39:1828–1845.
- Siegel, J. E., L. G. Crozier, L. E. Wiesebron, and D. L. Widener. 2021. Environmentally triggered shifts in steelhead migration behavior and consequences for survival in the mid-Columbia River. *PLoS ONE* 16:1–28.
- Silver, B. P., T. Gilmore, S. Lazzini, K. Beard, J. Baker, D. Hand, J. Rivera, and J. Voeltz. 2024. Monitoring and Evaluation of Mitchell Act-Funded National Fish Hatcheries in the Columbia River Gorge Complex, 2023 Annual Report. U.S. Fish and Wildlife Service, Columbia River Fish and Wildlife Conservation Office, Vancouver, WA:54.
- Stober, Q. J., M. R. Griben, R. V Walker, A. L. Setter, I. Nelson, J. C. Gislason, R. W. Tyler, and E. O. Salo. 1979. Columbia River irrigation withdrawal environmental review: Columbia River fishery study. Prepared for Department of the Army, Portland District Corps of Engineers, Portland, Oregon.
- Team, R. C. 2020. R: A language and environment for statistical computing. Vienna, Austria.
- Tenney, J., N. Tancroto, G. Axel, and S. Livingston. 2023. Columbia Basin PIT Tag Information System, 1/1/2023 - 12/31/2023 Annual Report, 1990-080-00.
- U.S. Army Corps of Engineers (USACE). 2020. Columbia River System Operations Final Environmental Impact Statement.
- Van Vliet, M. T. H., F. Ludwig, J. J. G. Zwolsman, G. P. Weedon, and P. Kabat. 2011. Global river temperatures and sensitivity to atmospheric warming and changes in river flow. *Water Resources Research* 47.
- Wanders, N., M. T. H. van Vliet, Y. Wada, M. F. P. Bierkens, and L. P. H. (Rens. van Beek. 2019. High-Resolution Global Water Temperature Modeling. *Water Resources Research* 55:2760–2778.
- Waterhouse, L., J. White, K. See, A. Murdoch, and B. X. Semmens. 2020. A Bayesian nested patch occupancy model to estimate steelhead movement and abundance. *Ecological Applications* 30:1–17.
- Wertheimer, R. H., and A. F. Evans. 2005. Downstream Passage of Steelhead Kelts through Hydroelectric Dams on the Lower Snake and Columbia Rivers. *Transactions of the American Fisheries Society* 134:853–865.
- Woodward, G., D. M. Perkins, and L. E. Brown. 2010. Climate change and freshwater ecosystems: Impacts across multiple levels of organization. *Philosophical Transactions of*

the Royal Society B: Biological Sciences 365:2093–2106.

Zarfl, C., A. E. Lumsdon, J. Berlekamp, L. Tydecks, and K. Tockner. 2015. A global boom in hydropower dam construction. *Aquatic Sciences* 77:161–170.

Chapter 3. Trophic drivers of salmon marine survival revealed by spatiotemporal data integration

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3.1 Abstract

A key driver of the population dynamics of Pacific Salmon is variable survival of the marine phase. Indices of ocean productivity have been used as proxies for the conditions that drive marine survival, but non-stationarity in the relationship between these indices and local ecological processes suggests the need for a deeper mechanistic understanding. In this study, we investigate the more proximate trophic drivers of marine survival of interior Columbia fall Chinook Salmon by integrating disparate long-term ecological research datasets. We used spatiotemporal species distribution models to model the ocean distribution of juvenile Chinook Salmon, predatory birds (Common Murres and Sooty Shearwaters) and fish (Pacific Hake), and two prey taxa (zooplankton and young-of-year rockfishes) in the Northern California Current. We then analyzed the relationship between marine survival of tagged fish and the abundance of these predator and prey taxa and their co-occurrence (overlap) with juvenile salmon. We found significant associations of marine survival with indices of predator overlap but not predator abundance, suggesting the importance of spatiotemporal overlap in modulating the effect of predation. Juvenile Chinook Salmon overlap with Common Murres and Pacific Hake was negatively associated with marine survival, while overlap with Sooty Shearwaters was positively associated with marine survival. This unexpected positive association between Sooty Shearwaters and Chinook Salmon marine survival is possibly due to their role as indicators of forage fishes, which may serve to shield juvenile Chinook Salmon from predation. Indices of prey overlap were less associated with marine survival than indices of predator overlap, but indices of zooplankton abundance were positively associated with marine survival, suggesting the importance of overall feeding conditions for survival. Overall, this study suggests that Chinook Salmon marine survival is driven by both top-down and bottom-up processes, and that the spatial overlap between predators and juvenile salmon is likely to be a stronger determinant of top-down control than predator abundance alone.

3.2 Introduction

The difficulty of studying ecological processes is fundamentally linked to the multiple scales within which these processes occur. Ecologists addressing specific questions can rarely account for effects at all scales; instead, they must seek to capture sufficient complexity in conceptual and statistical models to describe observed patterns (Levin 1992). However, data availability significantly constrains the range of model structures that can be tested. Especially in marine ecosystems, indices that summarize environmental conditions at large spatial scales are more readily available than regional or local data and are often used as proxies for the local conditions encountered by organisms (Mantua et al. 1997, Mantua and Hare 2002, Di Lorenzo et al. 2008, Báez et al. 2021). However, the relevance of these indices to local ecological interactions may be limited, as these indices summarize many sources of variability and the resulting relationship between indices and local time series are often non-stationary (Newman et al. 2016, Litzow et al. 2019). Furthermore, these indices are inherently unable to characterize the fine spatial and temporal scales at which organisms experience their environment (Levin 1992), which are ultimately the proximate drivers of processes of interest to ecologists.

Pacific salmon (*Oncorhynchus* spp.), whose life histories span small tributaries to the open ocean (Quinn 2018), are an example of the difficulty of study across scales. In contrast to our understanding of the drivers of population dynamics during the freshwater portion of the life cycle, the oceanic/marine phase of the Pacific salmon life cycle has long been considered a “black box” due to the difficulty of studying salmon in the ocean (Quinn 2018, Langan et al. 2024). However, variability in marine survival can account for the majority of variation in full life cycle survival rates for some populations (Petrosky et al. 2020). The importance of marine survival has led to a long history of correlating Pacific salmon marine survival with available data, primarily large-scale indicators, under the assumption that these indicators are sufficient proxies for local conditions that salmon encounter. For example, synchronous patterns in survival across stocks have been correlated with large-scale oceanographic phenomena such as the Pacific Decadal Oscillation (PDO) and the North Pacific Gyre Oscillation (NPGO) (Mantua et al. 1997, Di Lorenzo et al. 2008, Kilduff et al. 2015, Malick et al. 2017). However, the utility of this approach and the validity of this assumption have come into question due to the observed decoupling of these basin-scale indices with local environmental indices and ecological time series, as well as the swamping of these basin-scale oscillatory signals by global climate change (Litzow et al. 2019, 2020, Cluett et al. 2025). This underscores the importance of investigating more mechanistic drivers of marine survival at finer spatial scales.

Chinook Salmon (*O. tshawytscha*) from the Columbia River Basin have been a major focus of marine survival studies due to their cultural, ecological, and economic importance (Quinn 2018), coupled with precipitous declines that have led to the listing of many populations under the

United States Endangered Species Act (NMFS, 2005). Marine survival studies in this system can generally be classified into two categories: those that model marine survival of large cohorts of tagged fish, and targeted studies that explore potential mechanisms driving marine survival. The former set of studies primarily leverages a longstanding Passive Integrated Transponder (PIT) tagging program that has tagged over 57 million salmonids since 1987 (Tenney et al. 2023). These studies have modeled marine survival using detections at dams of outmigrating juveniles and returning adults as a function of both marine conditions and the carryover effects of freshwater covariates, but have generally relied on coarse indices to characterize ocean conditions (Scheuerell et al. 2009, Miller et al. 2014, Chasco et al. 2021, Gosselin et al. 2021). This approach to measuring marine survival using detections at dams integrates survival across multiple distinct habitats: the lower Columbia River and the Columbia River estuary, the Columbia River plume, and the open ocean. However, survival of the lower Columbia River and estuary of spring/summer Snake River Chinook Salmon estimated using acoustic telemetry (Rechisky et al. 2012) as well as PIT tags (Gosselin et al. 2021) suggest that the proportion of Columbia River Chinook Salmon that survive the estuarine environment is relatively high (0.7-1.0). In contrast, estimates of survival from acoustic telemetry indicate that survival of the Columbia River plume is highly variable (0.13-0.86) (Brosnan et al. 2014) and survival in the coastal ocean is consistently lower (0.04-0.29) than estuarine or plume survival (Rechisky et al. 2012). This low and variable survival during early marine residence has demonstrated the importance of the latter set of studies primarily focused on mechanisms operating in these crucial initial few months following ocean entry.

Mortality during this initial period is hypothesized to be driven primarily by trophic interactions, with predation being a major source of mortality (Beamish and Mahnken 2001, Wells et al. 2025) and early growth being critical to survival (Beamish et al. 2004, Duffy and Beauchamp 2011). However, despite early growth being postulated as a key determinant of marine survival, the evidence for bottom-up effects is mixed. Salmon are opportunistic foragers and consume a variety of taxa including zooplankton (e.g., crab and shrimp larvae, amphipods, and euphausiids) and the larval and juvenile stages of fish, including various forage fishes and young-of-year (YOY) rockfishes (*Sebastes* spp.) (Daly et al. 2009, 2017). Identifying bottom-up pathways that affect salmon marine survival has been difficult, perhaps due to the complexity of this food web and the shifting of prey bases with oceanographic conditions (Daly et al. 2017). A positive relationship between the biomass of potential salmon prey items caught in zooplankton tows and adult returns of Columbia River Basin spring Chinook Salmon was found (Burke et al. 2013). Additionally, salmon returns have been correlated with the abundance of lipid-rich northern copepods (Peterson et al. 2014) and fish larvae (Daly et al. 2013). However, another study on survival of upper Columbia River summer/fall Chinook Salmon found no relationship between indices of ocean productivity and salmon growth or body condition (Miller et al. 2013). Yet another study found that lower stomach fullness and poorer body condition as juveniles was

correlated with high adult returns, suggesting that top-down effects might be more important than bottom-up effects (Dale et al. 2017).

Columbia River Basin Chinook face numerous predators during their juvenile outmigration and early marine residence, including marine mammals (Chasco et al. 2017), piscivorous fishes (Muir et al. 2006), and seabirds (Collis et al. 2002). During the more extended period of residence in the coastal ocean, piscivorous fishes and seabirds are likely the dominant predators (Wells et al. 2025). Pacific Hake (*Merluccius productus*) is the most abundant piscivore in the Northern California Current (NCC), with ecosystem modeling suggesting that this could make them the dominant predator of juvenile Chinook Salmon (Gomes et al. 2024). At the same time, less than 0.1% of Pacific Hake stomachs examined in one study contained juvenile Chinook Salmon (Emmett and Krutzikowsky 2008), suggesting that predation events may be rare and opportunistic. In early summer, when Chinook Salmon are entering the coastal ocean, Common Murres (*Uria aalge*) and Sooty Shearwaters (*Ardenna grisea*) are the numerically dominant seabirds in the NCC, especially in the Columbia River plume (Zamon et al. 2014, Phillips et al. 2017). While diet data for these species in the NCC is limited and suggests that they feed primarily on forage fishes like Northern Anchovy (*Engraulis mordax*), Common Murres have been observed to consume salmon (Wiens and Scott 1975, Varoujean and Matthews 1983, Schrimpf et al. 2012). Juvenile Chinook Salmon are of a similar size as, and occupy similar habitats to, forage fishes like Northern Anchovy (Phillips et al. 2017) which is believed to expose them to predation (Phillips et al. 2021). Indeed, in California, predation of juvenile Chinook Salmon by Common Murres targeting Northern Anchovy led to decreased marine survival (Wells et al. 2017). As the distributions of mammal, fish, and bird predators varies considerably interannually (Ressler et al. 2007, Malick et al. 2020, Zamon et al. 2024), variability in predation pressure driven by variability in the spatiotemporal overlap (Schmitz et al. 2017) of these predators with juvenile Chinook Salmon may be a major driver of interannual variability in marine survival.

In this study, we integrate data from multiple surveys in the NCC with decades of PIT tag data to investigate how trophic interactions in space and time drive marine survival of interior Columbia River Basin Chinook Salmon. We fit spatiotemporal models to data from three surveys that sample different components of the NCC food web to characterize the spatiotemporal distribution, and therefore the potential for trophic interactions, of juvenile Chinook Salmon, their prey, and their predators. Specifically, we explore whether indices of abundance and spatiotemporal overlap between juvenile Chinook Salmon and three key predators (Pacific Hake, Common Murres, and Sooty Shearwaters) and two prey groups (YOY rockfishes and zooplankton) of juvenile Chinook Salmon are associated with differences in marine survival. This study represents a step towards understanding the finer scale mechanisms that drive

differences in marine survival for Columbia River Basin Chinook Salmon and illustrates how spatiotemporal models can facilitate the integration of disparate datasets.

3.3 Methods

3.3.1 Overview

We modeled the marine survival of hatchery Chinook Salmon from the Columbia River Basin as a function of individual-level covariates (outmigration timing, origin, and transport status) and potential predators and prey during their early residence in the NCC. PIT tag data from Chinook Salmon tagged as juveniles in the Columbia River Basin provided data on marine survival. PIT tag data was restricted to two stocks, upper Columbia summer/fall Chinook Salmon and Snake River fall Chinook Salmon, as they reside in the study area longer than other Columbia River Basin stocks (Fisher et al. 2014, Teel et al. 2015). Data from multiple ongoing research surveys in the NCC were used to describe the distribution of juvenile Chinook Salmon during their early marine residence, the abundance and distribution of predators and prey encountered by these fish, and the spatiotemporal overlap between these different distributions. To facilitate the integration of these disparate surveys, we fit species distribution models (SDMs) for each of the predator and prey taxa to model their distribution throughout the study area. While some of the surveys used for this study have a broader geographic extent, we focused on the area of the NCC that stretches from Newport, Oregon (44.7° N) to Cape Flattery, Washington (48.2° N), as this area is sampled annually to capture salmonids from the Columbia River Basin during their early marine residence (Fig. 1).

We modeled marine survival using a two-stage modeling process. In the first stage, we fit SDMs for juvenile salmon, prey taxa, and predator taxa to estimate their density within the study area. These SDMs were used to derive two types of covariates for marine survival: 1) indices of abundance for each taxon within the study area, and 2) indices of overlap between juvenile Chinook Salmon and each of the predator or prey taxa. In the second stage, we modeled the survival of individual PIT-tagged Chinook Salmon as a function of both individual-level covariates and the SDM-derived covariates from the first stage model. An errors-in-variables approach, wherein the estimated error in each covariate value is statistically accounted for (e.g., Thorson et al., 2016), was used to account for the estimated uncertainty in the SDM-derived covariates from the first stage model in the second stage model.

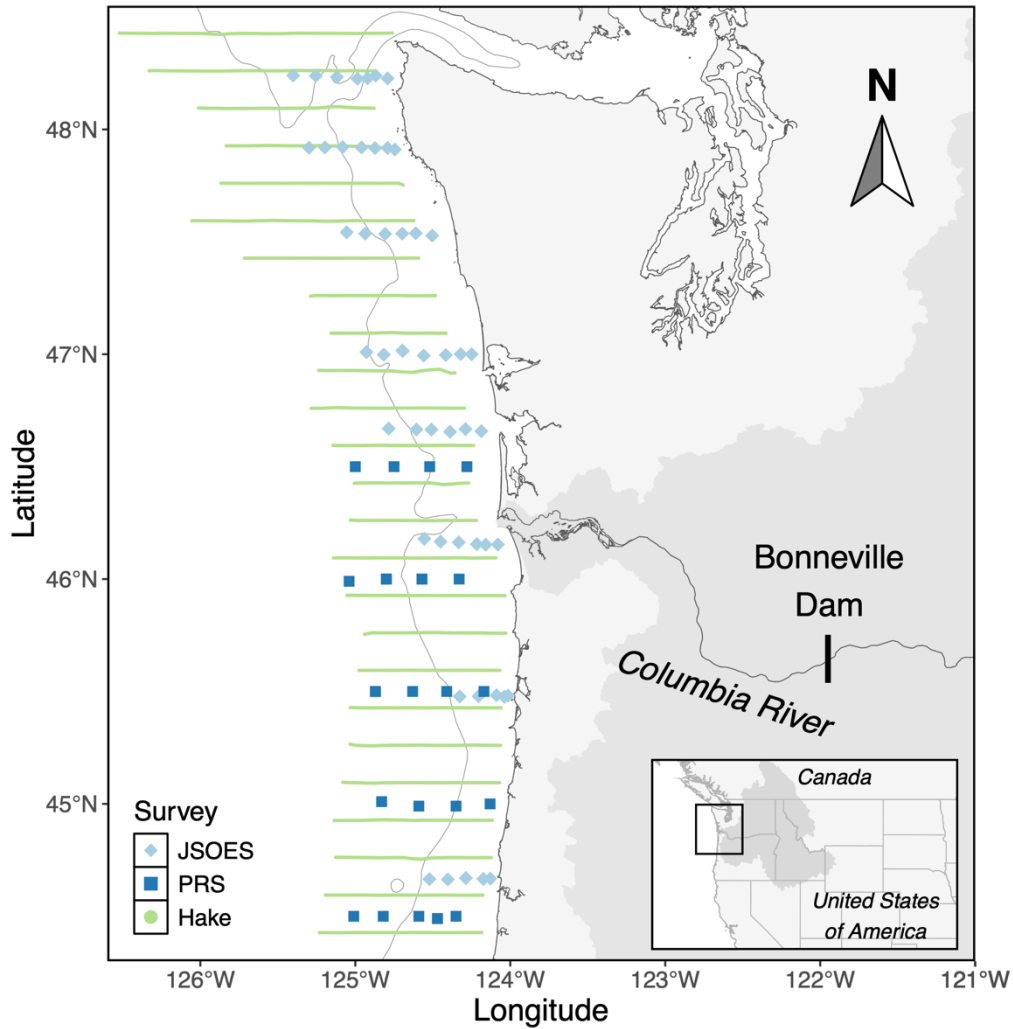


Figure 1. Map showing the Columbia River Basin (dark grey shaded area) and the coastal shelf where juvenile Chinook Salmon are found during their early marine residence. The typical sampling designs of the three fishery-independent surveys in this study are shown, with the exact sampling locations in 2013 visualized here: The Juvenile Salmon and Ocean Ecosystem Survey (JSOES), the Rockfish Pre-Recruit Survey (PRS), and the Pacific Hake Integrated Acoustic and Trawl Survey (Hake). Note that sampling for the PRS and Hake surveys extends beyond this domain, but only the samples that are within the study domain are shown here. The gray line represents the 200-m isobath.

3.3.2 Salmon marine survival data

Detection data from PIT-tagged upper Columbia summer/fall and Snake River fall Chinook Salmon from the Columbia River Basin were obtained from the Columbia Basin PIT Tag

Information System (PTAGIS) and used to assess marine survival. Our analysis included fish that were 1) detected as outmigrating juveniles prior to 15 June at Bonneville Dam (the last dam encountered by juvenile outmigrants, at river kilometer 234) or 2) transported as juveniles prior to 15 June below Bonneville Dam (Appendix E). Fish detected or transported after 15 June would likely still be in the Columbia River or estuary at the time ocean sampling of juveniles took place at the end of June, and therefore we excluded them from the analysis. Subsequent detection as adults at any of the adult fish ladders in the Columbia River Basin was considered evidence of marine survival. Therefore, marine survival as assessed using dam detections includes not only the marine waters of the Pacific Ocean, but also the lower 234 km of the Columbia River and its estuary. Because Chinook Salmon return as primarily 1-, 2-, and 3-year ocean-age fish, the final year of our analysis was juvenile outmigration year 2021, as this was the last year from which all adults were expected to have returned to spawn by 2025. We excluded fish with an ocean age less than 180 days (computed as the time between juvenile detection at or transport below Bonneville Dam and adult detection at Bonneville Dam) to exclude very small, early-maturing male fish (minijacks) that likely never reached our study area on the continental shelf (Johnson et al. 2012). Following these criteria, our sample sizes ranged from 1,119 to 53,257 juveniles per year for Snake River fall run fish and 2 to 14,268 juveniles per year for upper Columbia summer/fall run fish (Table 1).

Table 1. PIT tag sample sizes across the two stock groups. SAR = smolt-to-adult return ratio.

	Snake River Fall			Upper Columbia Summer/Fall		
Juvenile Run Year	Juvenile Outmigrants	Returning Adults	SAR	Juvenile Outmigrants	Returning Adults	SAR
2001	8245	18	0.002	5331	130	0.024
2002	1152	3	0.003	4993	15	0.003
2003	10981	13	0.001	14268	242	0.017
2004	2047	1	0	9360	71	0.008
2005	8424	4	0	2528	22	0.009
2006	40143	297	0.007	8	0	0
2007	1119	8	0.007	2	0	0
2008	31391	1176	0.037	7	0	0
2009	33264	214	0.006	929	34	0.037
2010	53257	1043	0.02	10231	384	0.038
2011	37001	533	0.014	1592	25	0.016
2012	26370	436	0.017	615	18	0.029
2013	3475	79	0.023	1213	45	0.037
2014	2465	24	0.01	2333	21	0.009

2015	10278	144	0.014	3973	58	0.015
2016	11987	121	0.01	4538	129	0.028
2017	18073	48	0.003	3290	59	0.018
2018	20403	243	0.012	3087	86	0.028
2019	15089	183	0.012	3786	105	0.028
2020	5427	241	0.044	7975	239	0.03
2021	3976	116	0.029	4563	84	0.018

3.3.3 Fishery-independent surveys

We integrated data from three ongoing research surveys to characterize the spatiotemporal distribution of juvenile Chinook Salmon, three potential predators, and two prey taxa in the NCC. Appendix F shows the stations sampled in each year and the observations of taxa included in this study. A brief overview of each survey and how the data from each survey was incorporated into the model is provided below. Detailed methods for each of the surveys can be found in Appendix A.

3.3.3.1 Juvenile Salmon and Ocean Ecosystem Survey (JSOES)

The Juvenile Salmon and Ocean Ecosystem Survey (JSOES) samples the coastal ocean from Newport, Oregon (44.7° N) to Cape Flattery, Washington (48.2° N), and typically covers the region of the shelf from 1 to 30 nmi (9 to 56 km) offshore (Fig. 1). All sampling was conducted during daylight hours. This survey has been conducted every year since 1998 between June 16 and July 3, with the majority of years sampled between June 20 and 28. Three data collection methods were used in this survey: surface trawls to collect juvenile salmon and other fishes, oblique zooplankton net tows, and visual seabird observations.

Juvenile Chinook Salmon caught by surface trawls were divided into two life history types, subyearlings and yearlings, where fish ≤ 140 mm fork length were classified as subyearlings and fish 141-280 mm were classified as yearlings (Percy and Fisher 1990, Fisher 1995, Weitkamp et al. 2012). Juvenile Chinook Salmon were also assigned to specific run and life history groups using genetic methods (Zamon et al. 2024) and catch per unit effort was then calculated for each genetic stock group. Because of the genetic legacy of broodstock transfers between stocks from the Columbia and Snake Rivers, Chinook Salmon populations upstream of Bonneville Dam are not always distinguishable using genetic methods. As such, we combined ocean-caught juveniles into an interior fall stock group, which is composed of upper Columbia River summer/fall and Snake River fall Chinook Salmon. Combined with the size-based life history classifications, the

genetic stock identification methods allowed us to model the density of two juvenile Chinook Salmon groups: interior fall subyearlings and interior fall yearlings.

Oblique zooplankton net tows were conducted using a 0.6 m bongo net with 335 μm mesh. We identified four functional groups (shrimp larvae, non-*Cancer* spp. crab larvae, *Cancer* spp. crab larvae, and hyperiid amphipods) captured using this sampling method as juvenile Chinook prey items based on prior diet studies (Daly et al. 2009, 2017) and modeled the biomass density (as a proxy for energy content) of each of these four functional groups. The assignment of taxa to functional groups is provided in Appendix B. We also extracted the density of the two numerically dominant fish-eating seabirds, Common Murres (*Uria aalge*) and Sooty Shearwaters (*Ardenna grisea*) from the seabird observation data for modeling. These observations were collected using a strip-transect method early in the morning prior to other sampling and assigned to their nearest trawl station (Zamon et al. 2024).

3.3.3.2 Pacific Whiting Conservation Cooperative (PWCC)/Pre-Recruit Survey (PRS)

YOY rockfishes, which dominate juvenile Chinook Salmon diets in some years (Daly et al. 2017) were extracted from two complementary surveys: the Pacific Whiting Conservation Cooperative (PWCC) Survey, conducted from 2001-2009, and the Pre-Recruit Survey (PRS), conducted most years since 2011 (Fig. 1). The spatial coverage of these surveys varied by year and covered varying sections of the coast extending from Cape Mendocino (40.4° N) to Cape Flattery (48.2° N). Although abundance and overlap indices were restricted to the SDM projection for the study area (44.7° N to 48.2° N), the full survey data was used to fit the SDM for YOY rockfishes. Sampling occurred in May and June. Although these two surveys had different sampling designs, both surveys target epipelagic micronekton at nighttime using a modified-Cobb midwater trawl and therefore are treated as one continuous time series in this analysis as in previous analyses (Field et al. 2021). The density of YOY rockfish (any *Sebastes* spp.) per tow was used to fit a species distribution model.

3.3.3.3 Joint U.S. and Canada Pacific Hake Integrated Acoustic and Trawl Survey (Hake Survey)

Data on Pacific Hake, the dominant finfish by biomass in the California Current, was extracted from the Joint U.S. and Canada Pacific Hake Integrated Acoustic and Trawl Survey (hereafter referred to as the “Hake Survey”). This biennial survey conducts transects perpendicular to the coast from Point Conception in California (34.5° N) to Dixon Entrance in British Columbia (54.4° N), with transects extending from approximately the 50-m to the 1500-m isobath (Fig. 1). In this study, we retained all transects from the Washington/Oregon border (42° N) to the

Washington/British Columbia border (48.5° N) to fit the SDM for Pacific Hake, with abundance and overlap indices restricted to the study area (44.7° N to 48.2° N). This survey has been conducted in odd years since 2001 (plus 2012), and in a typical year, our study region (the NCC) was surveyed in August. In this survey, downward-looking Simrad EK60 echosounders operating at multiple frequencies recorded acoustic backscatter continuously during daylight hours, with midwater and bottom trawls used to assign species, size, age, and sex composition to the acoustic backscatter. For this study, acoustic backscatter (measured as nautical-area-backscattering coefficient, or NASC, $\text{m}^2 \text{nmi}^{-2}$) attributed to adult (age 2+) Pacific Hake were binned into 2.5 nmi (4.63 km) bins.

3.3.4 Species distribution models for juvenile salmon, prey, and predators

We fit species distribution models (SDMs) to model the distribution of each taxon in each year using generalized linear mixed effects models, which included fixed effects for covariates and spatial and/or spatiotemporal random effects to model the correlations between observations in space or both space and time. The best-fit SDM for each taxon was selected using the model selection process described below. We included two covariates as potential drivers: sea surface temperature (SST) and distance from shore, as our study taxa are surface and coastally oriented. Daily satellite-derived SST measurements at a 5-km resolution from the NOAA Coral Reef Watch Daily Global 5-km Satellite SST dataset (Skirving et al. 2020) were queried from NOAA's ERDDAP server (<https://coastwatch.noaa.gov/erddap/griddap/noaacrwsstDaily.html>). Distance from shore was calculated using the *sf* package in R (Pebesma 2018). These covariates were modeled as either linear effects or penalized smoothers using the *mgcv* package (Wood 2017). In the SDMs for each taxon, we modeled the observations using a log-linked Tweedie distribution, since in each case the observations contained many zeros (Shono 2008). We used the R package TMB (Kristensen et al. 2016) to fit these models, and implemented the stochastic partial differential equation (SPDE) approach (Lindgren et al. 2011) to efficiently model spatial effects as Gaussian random fields.

For the random effects structure, we evaluated different structures of the spatial and spatiotemporal random effects. Spatiotemporal random fields were modeled as either independent or autoregressive. For both spatial and spatiotemporal random effects, we tested both geometrically isotropic and geometrically anisotropic random fields (Lindgren et al. 2011). Geometric anisotropy removes the constraint that spatial correlation decays equally in all directions, and was implemented by adding a linear transformation matrix **H** that estimates the major axis direction of spatial correlation and the ratio of spatial correlation in the major and minor axes (Thorson et al. 2015).

Different candidate model structures for the SDMs for each taxon were compared using conditional Akaike information criterion, or cAIC (Vaida and Blanchard 2005). We compared models using cAIC because this information criterion compares inference conditional on the random effects structure of the given model, and therefore is more appropriate when comparing model performance for spatial interpolation. To estimate cAIC, we implemented the formula presented in equation 6 of Zheng et al., 2024.

We evaluated different candidate models using the “top-down” strategy for model selection (Zuur et al. 2009) using the following process:

1. Starting with a model with saturated fixed effects, tune the structure of the spatial and spatiotemporal random effects using cAIC as the information criterion.
2. Keeping the random effects structure identified in the previous step, identify the fixed effect structure for our covariates (i.e., year, temperature, and distance from shore) using cAIC as the information criterion. This included exploring two alternative functional forms for temperature and distance from shore: linear and p-splines.

The full model selection process and the model equation for the best-fit SDM for each taxon can be found in Appendix G.

3.3.5 SDM-derived marine survival covariates: abundance and spatial overlap

We used the best-fit SDMs to estimate the relative abundance of each taxon in each year within a common projection grid for our study area. This projection grid had a 5-km resolution, and extended from 0.5 to 65 km offshore and from 10 km south of the most southerly JSOES transect (the Newport Hydrographic Line transect) to 10 km north of the most northerly JSOES transect (the Father and Son transect, just south of Cape Flattery). The projection grid relative to the SPDE mesh can be found in Appendix C, and the estimated densities of each taxon within our projection grid can be found in Appendix H.

Using this projection grid, we then estimated two marine survival covariates for the study region: indices of abundance for each salmon predator or prey taxon, and pairwise indices of overlap between either subyearling or yearling interior fall Chinook Salmon and each of the predator or prey taxa. We calculated an index of abundance by summing the estimated density or biomass for each taxon across all the cells in our projection grid. For our index of overlap, we calculated Pianka’s O (Pianka 1973), a symmetrical index of abundance scaled from 0-1 that captures the co-occurrence of two populations using the proportion of their total abundance that is found at location in a study area (the projection grid in this study) (Carroll et al. 2019). Furthermore, other

studies have found this index to be the most correlated with predation (as measured via gut content analyses) of multiple overlap metrics tested (Goodman et al. 2022). Pianka's O is calculated as follows:

$$O = \frac{\sum_i^n (p_{A_i} * p_{B_i})}{\sqrt{\sum_i^n p_{A_i}^2 * \sum_i^n p_{B_i}^2}}$$

Here, O is the estimated index of collocation, n is the total number of grid cells in the projection area, p_{A_i} is the proportion of species A that is found in cell i , and p_{B_i} is the proportion of species B that is found in cell i . This index is calculated separately for each year.

Prior to estimating these covariates for the zooplankton prey taxa, we created an aggregate prey field across the projection grid by summing the SDM-estimated biomass for each of the prey taxa sampled by the zooplankton net at each cell in the projection grid. This prey field aggregated the estimated biomass of the four prey taxa: shrimp larvae, non-*Cancer* spp. crab larvae, *Cancer* spp. crab larvae, and hyperiid amphipods. We equally weighted each taxon in our aggregate prey field by dividing the biomass of each taxon at each sampling station by the maximum biomass of that taxon at any sampling station across the full time series. This was done because capture efficiency is likely different for each of the taxa in our aggregate prey field.

Uncertainty for our marine survival covariates was estimated differently for the indices of abundance and the overlap metrics. For indices of abundance, we estimated the joint precision matrix $\mathbf{Q}_{joint}$ using the generalized delta method (Kass and Steffey 1989), implemented in TMB using the ADREPORT function (Kristensen et al. 2016). For our overlap metrics, we approximated the predictive standard error using a sample-based approach, as the generalized delta method was prohibitively computationally expensive for these complex derived quantities. Further details on the sample-based approach can be found in Appendix D. The time series of each SDM-derived marine survival covariate can be found in Appendix I.

3.3.6 Marine survival model

Four different marine survival models were fit to examine marine survival of Chinook Salmon from the interior Columbia River Basin. These four models were the result of two binary choices: 1) using either subyearlings or yearlings as our focal salmon life histories for SDM-derived overlap covariates and 2) using either seabirds or Pacific Hake as our focal predators.

Each of the four models included both zooplankton prey and YOY rockfish, in addition to the individual-level covariates.

The two stock groups included in our smolt-to-adult survival data, upper Columbia River summer/fall and Snake River fall Chinook Salmon, are released as both subyearlings and yearlings (Fisher et al. 2014). Therefore, we examine the effect of spatiotemporal overlap of these two life histories with predator and prey taxa on survival. We only included spatiotemporal overlap for one life history at a time as we found that the overlap metrics for the two life histories with each predator or prey taxa were highly correlated. The second choice to use either seabirds or Pacific Hake, and not all predators combined, was necessitated by differences in the survey time series. Because of the varying years of sampling for each survey, combining all data sources together in a single model would have resulted in a short time series with little explanatory power. Therefore, we fit two different survival models to datasets corresponding to the years shared between the zooplankton, YOY rockfish, and either the seabird data (2003-09, 2011, 2015-19) or the Hake survey data (2001-21, odd years only).

The survival model was fit using TMB, where the survival of each individual PIT-tagged fish was modeled as a Bernoulli trial with a logit link function. Specifically, the likelihood of marine survival was defined as follows:

$$z_i \sim \text{Bernoulli}(\phi_i)$$

where z_i is the survival of fish i (0 or 1) and ϕ_i is the linear predictor of marine survival for fish i . ϕ_i is defined as follows:

$$\text{logit}(\phi_i) = \tilde{\mathbf{x}}_i \boldsymbol{\beta}$$

where $\tilde{\mathbf{x}}_i$ is a $1 \times K$ vector of the latent states of covariates whose first entry is 1 and $\boldsymbol{\beta}$ is a $K \times 1$ vector of regression coefficients whose first element is the intercept β_0 and the subsequent terms are regression coefficients for the covariates contained in $\tilde{\mathbf{x}}_i$. Regression coefficients where the 95% confidence interval did not cross zero were interpreted as statistically significant. Latent states for covariates ($\tilde{\mathbf{x}}_i$), estimated using an errors-in-variables approach, were used to facilitate the propagation of uncertainty estimated in the derived quantities from the first stage SDM model. Note that although the subscript i is used to denote individual-level covariates, any SDM-derived covariates were estimated annually and therefore were shared across all fish in a year. As described above, four versions of this model were fit to incorporate either the seabird data or the Pacific Hake data and either the subyearling or yearling ocean salmon data. This meant that the

$\tilde{\alpha}_i$ and β vectors included either the Pacific Hake terms or the Sooty Shearwater and Common Murre terms, and indices of overlap with either subyearlings or yearlings. Prior to fitting the model, all SDM-derived covariates (i.e., indices of abundance and overlap) were z-scored. This allowed the effect sizes of covariates to be directly compared. All covariates are listed in Table 2.

Table 2. Covariates examined in relation to marine survival of PIT-tagged fish. CBR DART = Columbia Basin Research Data Access in Real Time; PTAGIS = Columbia Basin PIT Tag Information System; SDM = Species Distribution Models; YOY = young-of-year.

Covariate	Description	Source
Stock Group	Based on origin and juvenile transport status, resulting in three groups: upper Columbia summer/fall in-river juvenile migrants, Snake River fall in-river juvenile migrants, and Snake River fall transported juvenile migrants	CBR DART
Date	Outmigration date (date of detection at Bonneville Dam or transport below) relative to the mean outmigration date	PTAGIS
Date ²	Square of outmigration date (date of detection at Bonneville Dam or transport below) relative to the mean outmigration date	PTAGIS
Prey Abundance	Index of abundance for biomass of zooplankton net salmon prey items	SDM
Prey overlap	Overlap between the biomass of zooplankton net salmon prey items and either subyearling or yearling interior fall Chinook Salmon	SDM
YOY RF Abundance	Index of abundance for YOY rockfish	SDM
YOY RF Overlap	Overlap between YOY rockfish and either subyearling or yearling interior fall Chinook Salmon	SDM
SOSH Abundance	Index of abundance for Sooty Shearwaters	SDM
SOSH Overlap	Overlap between Sooty Shearwaters and either subyearling or yearling interior fall Chinook Salmon	SDM
COMU Abundance	Index of abundance for Common Murres	SDM
COMU Overlap	Overlap between Common Murres and either subyearling or yearling interior fall Chinook Salmon	SDM

Hake Abundance	Index of abundance for Pacific Hake	SDM
Hake Overlap	Overlap between Pacific Hake and either subyearling or yearling interior fall Chinook Salmon	SDM

The errors-in-variables approach was used to account for the uncertainty in the SDM-derived indices of abundance and overlap when using them as covariates for the second stage survival model (Thorson et al. 2016). We modeled the estimation error in each of our covariates for our survival model using a hierarchical modeling approach:

$$x \sim \text{MVN}(\tilde{x}, \Sigma)$$

In this equation, x is a vector of the estimated values of the SDM-derived covariate, $\tilde{x}$ is a vector of the latent states of the covariate, and Σ is the covariance matrix. For the indices of abundance, $\Sigma = \mathbf{Q}_{joint}^{-1}$ and was estimated using the generalized delta method. For the indices of overlap, the variance was estimated using the sample-based approach (Appendix D) and these variances were input as the diagonal values in the covariance matrix. This allowed the model to account for uncertainty in the predictors by modeling them as distributions rather than points, with the mean of the distribution given by the estimated values and the variance described by the covariance matrix. The fit between the covariates estimated by the SDM (stage 1) and the latent state of these covariates estimated by the SAR model (stage 2) is shown in Appendix J. The results of a sensitivity analysis where the uncertainty in SDM-derived marine survival covariates is not accounted for is shown in Appendix K.

3.4 Results

Each of the taxa in our study exhibited considerable interannual variability in their abundance and distribution within the study area (Appendices H, I). Fig. 2, which for illustrative purposes depicts only two taxa (yearling fall Chinook Salmon and Sooty Shearwaters) and two years (2005 and 2011), shows how these varying distributions also subsequently led to varying degrees of overlap by year (Appendix I).

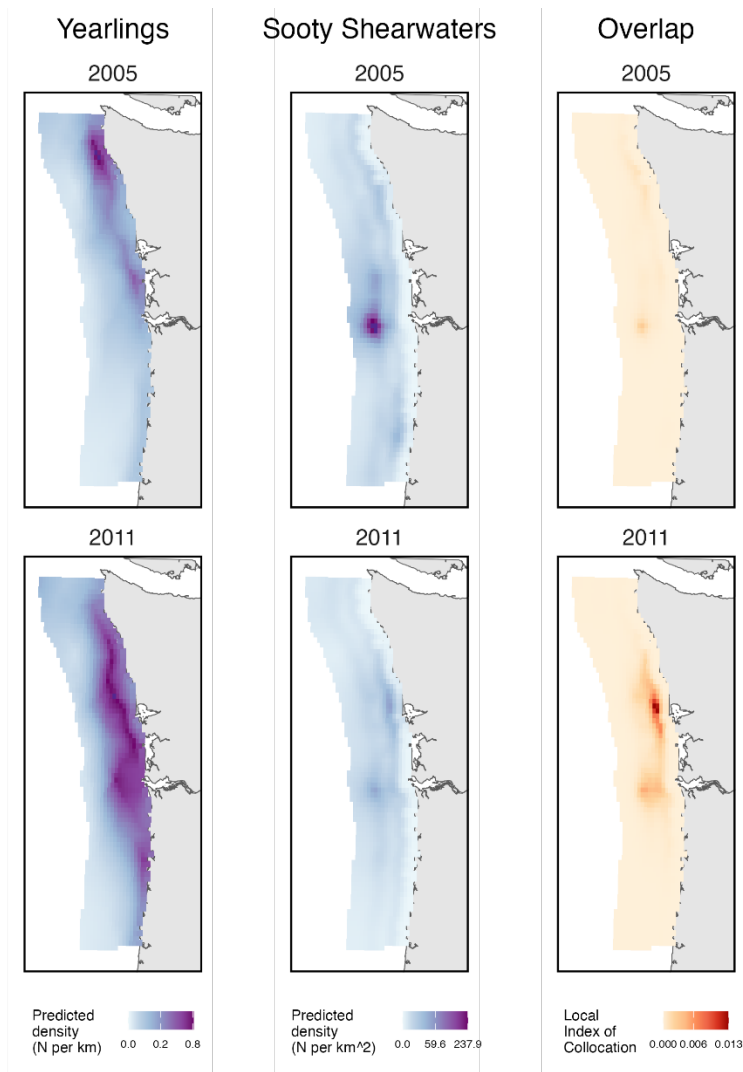


Figure 2. Species distribution models were used to estimate the density of each taxon within the study area. To illustrate the modeling workflow and the interannual variability in overlap, shown here are the estimated density of Yearling interior fall Chinook Salmon and Sooty Shearwaters, and the grid-cell level estimated overlap between the two. The years with the overall lowest (2005) and highest (2011) overlap are shown.

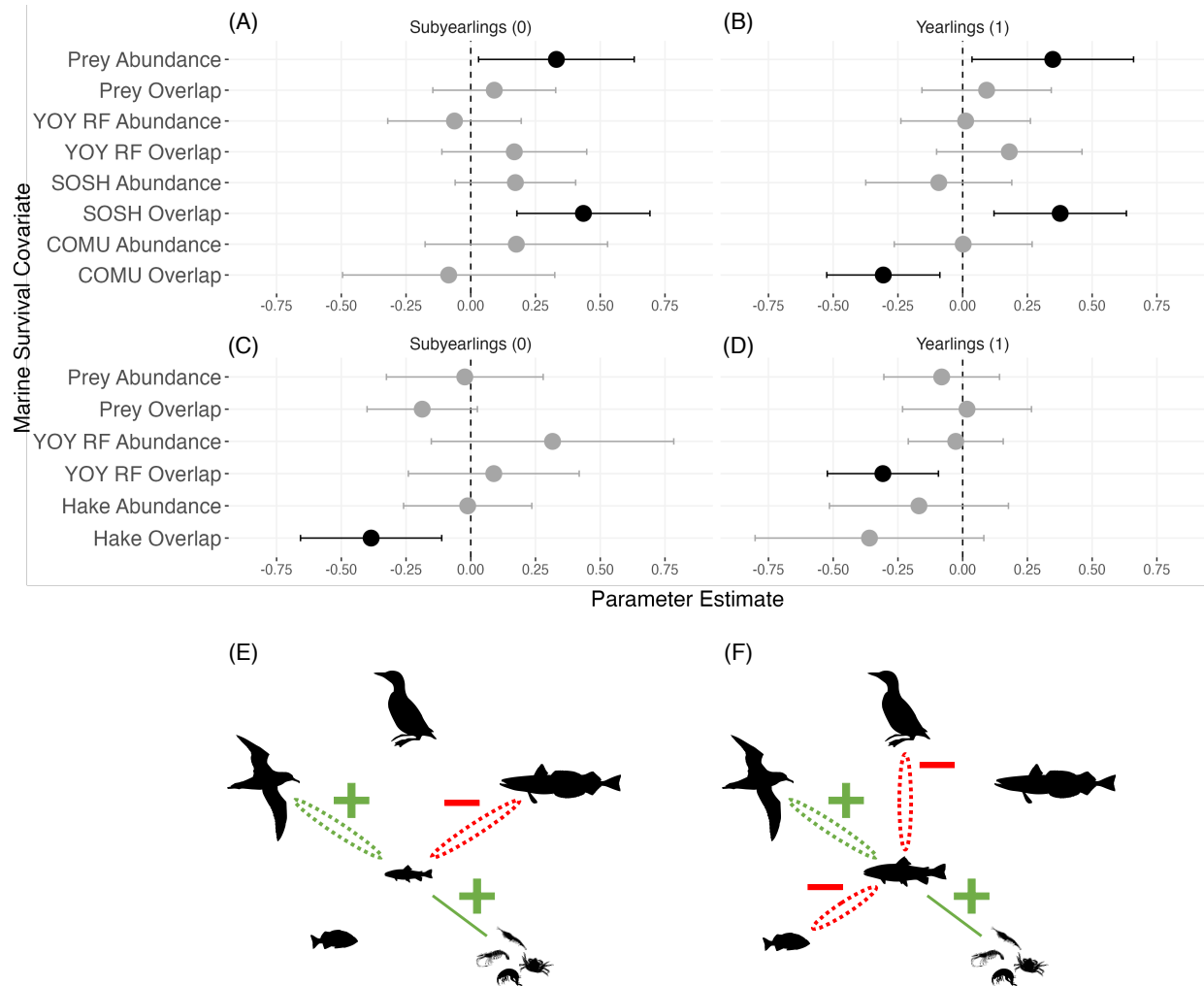


Figure 3. Regression coefficients for the SDM-derived survival covariates in the survival models with seabirds as the focal predators (A, B) and Pacific Hake as the focal predator (C, D). In panels (A) and (C), the parameter estimates are shown for the effect of overlap with subyearling interior Chinook salmon; in panels (B) and (D), the parameter estimates are shown for the effect of overlap with yearling interior Chinook salmon. Points show the maximum likelihood estimates for each parameter, while the bars show the 95% confidence intervals. Covariates with statistically significant values are visualized in black. Statistically significant parameter estimates for subyearlings are visualized in panel (E) and statistically significant parameter estimates for yearlings are visualized in panel (F). Associations between marine survival and overlap are shown with dashed ellipses, while associations between marine survival and abundance are shown with solid lines.

In the models with seabirds as the focal predators (Fig. 3A, B), five significant associations were found between marine survival and abundance and overlap indices derived from SDMs. A positive association between prey abundance and marine survival was observed in both the model with subyearlings (Fig. 3A) and yearlings (Fig. 3B) as the focal salmon life history. A positive association between Sooty Shearwater overlap with both subyearlings and yearlings and marine survival was found (Fig. 3A, B), while a negative association was found only for the overlap between yearlings and Common Murres (Fig. 3B). Prey overlap, YOY rockfish abundance, YOY rockfish overlap, Sooty Shearwater abundance, and Common Murre abundance did not have any significant associations with marine survival in the models with seabirds as the focal predators (Fig. 3A, B).

In the models with Pacific Hake as the focal predator, only two significant associations were found for abundance and overlap indices derived from SDMs. In the model with subyearlings, overlap with Pacific Hake was negatively associated with survival (Fig. 3C), and in the model with yearlings, overlap with YOY rockfishes was negatively associated with survival (Fig. 3D). Prey abundance, prey overlap, YOY rockfish abundance, and Pacific Hake abundance did not have significant associations with survival in these models (Fig. 3C, 3D).

Across all four models, the stock-specific intercept terms estimated that upper Columbia summer/fall fish had the highest marine survival, followed by Snake River fall in-river juvenile migrants, followed by Snake River fall transported juvenile migrants (Appendix L). Fits to data indicated wider confidence intervals in years with higher marine survival, and that the models with Pacific Hake as the focal predator were more had narrower confidence intervals than the models with seabirds as the focal predators (Appendix M).

3.5 Discussion

In this study, we found that interannual variability in the degree of spatiotemporal overlap between juvenile Chinook Salmon and their predators or prey, in addition to differences in the relative abundance of prey, was linked to marine survival (Fig. 3E, F). The strong association between spatiotemporal predator-prey overlap and marine survival underscores the idea that basin-scale indices or other spatially coarse indicators are insufficient to capture the fine-scale trophic interactions that are driving this key process. Furthermore, we demonstrate how integrating multiple long-term monitoring efforts in a creative modeling framework allows for the examination of ecological interactions across trophic levels.

Overlap between the three predator taxa modeled in our study (Common Murres, Sooty Shearwaters, and Pacific Hake) and juvenile Chinook Salmon each had significant associations

with marine survival of Chinook salmon. In contrast, the abundance of each of these predators was never significantly associated with survival across any of the model configurations, supporting the hypothesis that local spatial overlap is a necessary condition for predation and therefore more closely associated with marine survival than overall abundance. However, the ecological interpretation of the associations between marine survival and the overlap of juvenile Chinook Salmon with each of the three predator taxa differs based on their specific life histories and ecology. The negative association between Common Murre overlap with yearling Chinook Salmon and marine survival (Fig. 3A) is consistent with the hypothesis that Common Murre predation on juvenile salmon has a negative effect on survival, and is similar to the link found between Common Murre predation and marine survival for California Central Valley Chinook Salmon based on a low rate of incidental predation (Wells et al. 2017). Common Murres also have been documented to have a preference for larger prey (Buren et al. 2012), which may explain our finding that overlap between Common Murres and yearling Chinook Salmon had a negative association with survival, whereas the overlap between Common Murres and smaller subyearling Chinook Salmon had no association with survival (Fig. 3B).

Similarly, the negative association between Pacific Hake overlap with subyearling Chinook Salmon and marine survival (Fig. 3C) aligns with hypothesized predation. As with Common Murres, prey size preference by Pacific Hake may explain why overlap with subyearling, but not yearling Chinook Salmon was negatively associated with marine survival (Fig. 3D). Pacific Hake rarely consume fish over 150 mm in total length, and the only five juvenile Chinook Salmon found in the 5,320 Pacific Hake stomachs examined in one study were all <135 mm in total length (Emmett and Krutzikowsky 2008), which would be classified as subyearlings according to our 140-mm length cutoff. Furthermore, subyearling fall Chinook Salmon reside in the Northern California Current longer than yearling fall Chinook Salmon (Teel et al. 2015), which may increase their temporal overlap with Pacific Hake in this region. However, there are a number of alternative explanations besides predation for this negative association between overlap and marine survival. Pacific Hake distributions are known to be highly environmentally-driven (Malick et al. 2020, Marshall 2024); as such, the distribution of Pacific Hake may be a proxy for other environmental conditions that affect marine survival. Significant overlap between Pacific Hake and juvenile and sub-adult Chinook Salmon diets indicates shared forage bases (Wells et al. 2024), which suggests that competition may also be an alternative mechanism for the observed effect if prey are limiting.

In contrast to the negative association between marine survival and overlap between juvenile Chinook Salmon and Pacific Hake or Common Murres, overlap between Sooty Shearwaters and juvenile Chinook Salmon had a positive association with marine survival. As the direct trophic effect of piscivorous Sooty Shearwaters on juvenile salmon is necessarily negative, this positive association implies that these seabirds are a proxy for other conditions that are favorable for

marine survival. One potential mechanism is that Sooty Shearwaters, like many seabirds, are indicators of ecosystem conditions (Cairns 1988, Piatt and Sydeman 2007); in the California Current, evidence suggests that Sooty Shearwaters are indicators of forage fish availability. For example, in the Columbia River plume, Sooty Shearwaters have been shown to track non-salmonid fish densities (Phillips et al. 2017), and in the waters off of California, these seabirds have also been found to be indicators of forage fish availability, including Northern Anchovy (*Engraulis mordax*) and Market Squid (*Doryteuthis opalescens*) (Lyday et al. 2015). Co-occurrence between juvenile salmon and forage fish may have a positive effect on marine survival because these fish are prey for juvenile Chinook Salmon (Daly et al. 2009, 2017) and also serve as alternative prey sources for predators that reduce predation pressure on juvenile Chinook Salmon (Emmett and Sampson 2007, Phillips et al. 2021, Vasbinder et al. 2024). Notably, the inverse associations of Common Murres and Sooty Shearwaters with marine survival is likely due to their contrasting foraging ecology in May and June. Early marine residence by juvenile Chinook salmon occurs during Common Murre breeding season, when breeding birds are restricted to foraging within a ~100-km radius around their breeding colonies (Hatch et al. 2000, Davoren et al. 2003, Parrish and Zador 2003, Thomas and Lyons 2017). In contrast, although Sooty Shearwaters occupy the California Current in this same period, they do not breed in the northern hemisphere. They are therefore unconstrained by central-place-foraging demands and their ocean distribution more closely tracks forage fishes (Adams et al. 2012, Phillips et al. 2017).

There were three significant bottom-up associations between overlap or abundance indices for YOY rockfishes and zooplankton and marine survival: abundance of zooplankton had a significant positive association with marine survival in two models (Fig. 3A, B), whereas overlap between YOY rockfishes and yearling Chinook Salmon had a significant negative association with marine survival in one model (Fig. 3D). As the same covariates (YOY rockfish and zooplankton prey overlap and abundance indices) were included in all four models but were found to only be significant in a subset of these models, this indicates mixed support for the importance of these bottom-up effects for marine survival. This may support previous diet and growth studies that suggest that top-down effects are more closely linked to marine survival than bottom-up effects (Miller et al. 2013, Dale et al. 2017). However, it also demonstrates the sensitivity of the results to both the different time series for the different focal predator models and the inclusion of other covariates. Given the considerable interannual variability in juvenile salmon diets (Daly and Brodeur 2015, Daly et al. 2017) and the fact that the seabird (Fig. 3A, B) and Pacific Hake (Fig. 3C, D) models had considerably different time series, this may indicate that these relationships are important under certain conditions but not others.

The positive association between zooplankton prey abundance and marine survival is consistent with bottom-up effects on survival, but it is notable that for this taxon the abundance rather than

the overlap indices were significant. This may be because zooplankton are a trophic level beneath the primary prey of predominantly piscivorous juvenile Chinook Salmon (Daly et al. 2009). Notably, the majority of prey items found in salmon diets, including various forage fishes and euphausiids (Daly et al. 2009, 2017), were not included in this study because of the short time series available for these species. However, similar indices of lower trophic level productivity from the JSOES zooplankton data have been positively correlated with adult returns of Columbia River Basin Spring Chinook Salmon (Burke et al. 2013), although that study preceded an ocean warming pattern starting in 2014 that may represent a major regime shift (Cluett et al. 2025).

The abundance of YOY rockfish was never significantly associated with marine survival across all models, but the overlap between YOY rockfish and yearling Chinook Salmon was negatively associated with marine survival in one of four models (Fig. 3D). YOY rockfishes are a major yet variable component of juvenile Chinook Salmon diets (Daly and Brodeur 2015, Daly et al. 2017), with juvenile Chinook Salmon consuming considerably more YOY rockfishes under warmer ocean conditions, which also tend to have lower marine survival (Daly and Brodeur 2015). YOY rockfishes have also been more abundant in years with higher surface temperatures, including the warm blob years of 2014-16 (Field et al. 2021), and have notoriously patchy distributions that are strongly linked to variable ocean productivity and transport (Field et al. 2021). Additionally, high coastal upwelling can push YOY rockfish further offshore (Schwing et al. 2000), thereby reducing overlap with coast-oriented juvenile Chinook Salmon. As such, YOY rockfish distributions may be representative of other oceanographic or ecological conditions that may negatively impact marine survival.

Statistically integrating multiple data sources can increase the spatiotemporal scale of inference (Zipkin et al. 2021), increase precision and predictive performance (Fletcher et al. 2016), and, as demonstrated in this analysis, can facilitate the testing of ecological hypotheses that are untestable with a single data source. However, integrating disparate data sources also comes with caveats and limitations inherent to the fact that these surveys have different designs and aims. In the case of YOY rockfish, there is significant interannual variability in the degree of spatial overlap between the PRS and PWCC surveys with the JSOES (Appendix F), which likely limited our ability to detect effects of YOY rockfishes on marine survival. Our indices of overlap were also not able to account for spatiotemporal overlap in the z-axis (depth). While this is less of a concern for our focal seabirds, as their diving feeding habits allows them to cover the upper water column where surface-oriented juvenile salmonids are found (Burger 2001, Nevins 2004), Pacific Hake tend to be found much deeper, aggregating primarily in depths of 150-250 m (Ressler et al. 2007). Differences in survey timing also require assumptions about how static distributions are in time. In the case of the Hake Survey, the study region (the Oregon and Washington shelf) is typically surveyed in August, whereas the JSOES is completed in June.

Pacific Hake feed off the coasts of Oregon, Washington, and British Columbia from April-May to September-October (Ressler et al. 2007), suggesting that this survey captures them in their feeding habitat prior to their southward migration in the fall. However, the difference in timing of these surveys means that the distribution of Pacific Hake during the early marine residence of Chinook Salmon, when salmon mortality is high and variable, is not being directly captured.

In this study, we found that finer-scale trophic interactions, as captured by abundance and overlap indices for Columbia River Basin Chinook Salmon predators and prey, were significantly associated with differences in marine survival. Furthermore, we demonstrated how using species distribution models can facilitate the integration of complementary data sources across trophic levels, and therefore the investigation of spatiotemporal predator-prey dynamics. This approach could be extended to other systems that have overlapping ecological monitoring efforts and could also be extended in this system in future studies by integrating other key taxa from surveys that could not be included in the present study. As previously reliable correlations between ecological processes and climate and ocean indices continue to break down (Litzow et al. 2020, Cluett et al. 2025) future efforts to statistically integrate existing data sources will be crucial in furthering our understanding of mechanisms that structure key ecological processes.

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3.7 References

Adams, J., C. MacLeod, R. M. Suryan, K. David Hyrenbach, and J. T. Harvey. 2012. Summer-time use of west coast US National Marine Sanctuaries by migrating sooty shearwaters (*Puffinus griseus*). *Biological Conservation* 156:105–116.

- Báez, J. C., L. Gimeno, and R. Real. 2021. North Atlantic Oscillation and fisheries management during global climate change. *Reviews in Fish Biology and Fisheries* 31:319–336.
- Beamish, R. J., and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. *Progress in Oceanography* 49:423–437.
- Beamish, R. J., C. Mahnken, and C. M. Neville. 2004. Evidence That Reduced Early Marine Growth is Associated with Lower Marine Survival of Coho Salmon. *Transactions of the American Fisheries Society* 133:26–33.
- Brosnan, I., D. Welch, E. Rechisky, and A. Porter. 2014. Evaluating the influence of environmental factors on yearling Chinook salmon survival in the Columbia River plume (USA). *Marine Ecology Progress Series* 496:181–196.
- Buren, A., M. Koen-Alonso, and W. Montevecchi. 2012. Linking predator diet and prey availability: common murre and capelin in the Northwest Atlantic. *Marine Ecology Progress Series* 445:25–35.
- Burger, A. E. 2001. Diving depths of shearwaters. *The Auk* 118:755–759.
- Burke, B. J., W. T. Peterson, B. R. Beckman, C. Morgan, E. A. Daly, and M. Litz. 2013. Multivariate Models of Adult Pacific Salmon Returns. *PLoS ONE* 8.
- Cairns, D. 1988. Seabirds as indicators of marine food supplies. *Biological oceanography* 5:261–271.
- Carroll, G., K. K. Holsman, S. Brodie, J. T. Thorson, E. L. Hazen, S. J. Bograd, M. A. Haltuch, S. Kotwicki, J. Samhouri, P. Spencer, E. Willis-Norton, and R. L. Selden. 2019. A review of methods for quantifying spatial predator–prey overlap. *Global Ecology and Biogeography* 28:1561–1577.
- Chasco, B. E., B. Burke, L. Crozier, and R. Zabel. 2021. Differential impacts of freshwater and marine covariates on wild and hatchery Chinook salmon marine survival. *PLoS ONE* 16:1–23.
- Chasco, B. E., I. C. Kaplan, A. C. Thomas, A. Acevedo-Gutiérrez, D. P. Noren, M. J. Ford, M. B. Hanson, J. J. Scordino, S. J. Jeffries, K. N. Marshall, A. O. Shelton, C. Matkin, B. J. Burke, and E. J. Ward. 2017. Competing tradeoffs between increasing marine mammal predation and fisheries harvest of Chinook salmon. *Scientific Reports* 7:1–14.
- Cluett, A. A., S. J. Bograd, M. G. Jacox, M. P. Buil, and E. L. Hazen. 2025. Pan-basin warming now overshadows robust Pacific Decadal Oscillation. *Nature Climate Change* 15:1340–1347.
- Collis, K., D. D. Roby, D. P. Craig, S. Adamany, J. Y. Adkins, and D. E. Lyons. 2002. Colony size and diet composition of piscivorous waterbirds on the lower Columbia River: implications for losses of juvenile salmonids to avian predation. *Transactions of the American Fisheries Society* 131:537–550.
- Dale, K. E., E. A. Daly, and R. D. Brodeur. 2017. Interannual variability in the feeding and condition of subyearling Chinook salmon off Oregon and Washington in relation to fluctuating ocean conditions. *Fisheries Oceanography* 26:1–16.

- Daly, E. A., T. D. Auth, R. D. Brodeur, and W. T. Peterson. 2013. Winter ichthyoplankton biomass as a predictor of early summer prey fields and survival of juvenile salmon in the northern California Current. *Marine Ecology Progress Series* 484:203–217.
- Daly, E. A., and R. D. Brodeur. 2015. Warming ocean conditions relate to increased trophic requirements of threatened and endangered salmon. *PLoS ONE* 10:1–23.
- Daly, E. A., R. D. Brodeur, and T. D. Auth. 2017. Anomalous ocean conditions in 2015: Impacts on spring Chinook salmon and their prey field. *Marine Ecology Progress Series* 566:168–182.
- Daly, E. A., R. D. Brodeur, and L. A. Weitkamp. 2009. Ontogenetic Shifts in Diets of Juvenile and Subadult Coho and Chinook Salmon in Coastal Marine Waters: Important for Marine Survival? *Transactions of the American Fisheries Society* 138:1420–1438.
- Davoren, G., W. Montevecchi, and J. Anderson. 2003. Distributional patterns of a marine bird and its prey: habitat selection based on prey and conspecific behaviour. *Marine Ecology Progress Series* 256:229–242.
- Di Lorenzo, E., N. Schneider, K. M. Cobb, P. J. S. Franks, K. Chhak, A. J. Miller, J. C. McWilliams, S. J. Bograd, H. Arango, E. Curchitser, T. M. Powell, and P. Rivière. 2008. North Pacific Gyre Oscillation links ocean climate and ecosystem change. *Geophysical Research Letters* 35:2–7.
- Duffy, E. J., and D. A. Beauchamp. 2011. Rapid growth in the early marine period improves the marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, Washington. *Canadian Journal of Fisheries and Aquatic Sciences* 68:232–240.
- Emmett, R. L., and G. K. Krutzikowsky. 2008. Nocturnal Feeding of Pacific Hake and Jack Mackerel off the Mouth of the Columbia River, 1998-2004: Implications for Juvenile Salmon Predation. *Transactions of the American Fisheries Society* 137:657–676.
- Emmett, R. L., and D. B. Sampson. 2007. THE RELATIONSHIPS BETWEEN PREDATORY FISH, FORAGE FISHES, AND JUVENILE SALMONID MARINE SURVIVAL OFF THE COLUMBIA RIVER: A SIMPLE TROPHIC MODEL ANALYSIS. *CalCOFI Rep* 48.
- Field, J. C., R. R. Miller, J. A. Santora, N. Tolimieri, M. A. Haltuch, R. D. Brodeur, T. D. Auth, E. J. Dick, M. H. Monk, K. M. Sakuma, and B. K. Wells. 2021. Spatiotemporal patterns of variability in the abundance and distribution of winter-spawned pelagic juvenile rockfish in the California Current. *PLoS ONE* 16:1–25.
- Fisher, J. P. 1995. Distribution, migration, and growth of juvenile Chinook salmon, *Oncorhynchus tshawytscha*, off Oregon and Washington. *Fish. Bull.* 93:274–289.
- Fisher, J. P., L. A. Weitkamp, D. J. Teel, S. A. Hinton, J. A. Orsi, E. V. Farley, J. F. T. Morris, M. E. Thiess, R. M. Sweeting, and M. Trudel. 2014. Early Ocean Dispersal Patterns of Columbia River Chinook and Coho Salmon. *Transactions of the American Fisheries Society* 143:252–272.

- Fletcher, R. J., R. A. McCleery, D. U. Greene, and C. A. Tye. 2016. Integrated models that unite local and regional data reveal larger-scale environmental relationships and improve predictions of species distributions. *Landscape Ecology* 31:1369–1382.
- Gomes, D., J. J. Ruzicka, L. G. Crozier, D. D. Huff, E. M. Phillips, P.-Y. Hervann, C. A. Morgan, R. D. Brodeur, J. E. Zamon, and E. A. Daly. 2024. An updated end-to-end ecosystem model of the Northern California Current reflecting ecosystem changes due to recent marine heat waves. *Page PLoS ONE*.
- Goodman, M. C., G. Carroll, S. Brodie, A. Grüss, J. T. Thorson, S. Kotwicki, K. Holsman, R. L. Selden, E. L. Hazen, and G. A. De Leo. 2022. Shifting fish distributions impact predation intensity in a sub-Arctic ecosystem. *Ecography* 2022:e06084.
- Gosselin, J. L., E. R. Buhle, C. Van Holmes, W. N. Beer, S. Iltis, and J. J. Anderson. 2021. Role of carryover effects in conservation of wild Pacific salmon migrating regulated rivers. *Ecosphere* 12.
- Hatch, S. A., P. M. Meyers, D. M. Mulcahy, and D. C. Douglas. 2000. SEASONAL MOVEMENTS AND PELAGIC HABITAT USE OF MURRES AND PUFFINS DETERMINED BY SATELLITE TELEMETRY.
- Johnson, J., T. Johnson, and T. Copeland. 2012. Defining life histories of precocious male parr, minijack, and jack chinook salmon using scale patterns. *Transactions of the American Fisheries Society* 141:1545–1556.
- Kass, R. E., and D. Steffey. 1989. Approximate Bayesian inference in conditionally independent hierarchical models (parametric empirical Bayes models). *Journal of the American Statistical Association* 84:717–726.
- Kilduff, D. P., E. Di Lorenzo, L. W. Botsford, and S. L. H. Teo. 2015. Changing central Pacific El Niños reduce stability of North American salmon survival rates. *Proceedings of the National Academy of Sciences* 112:10962–10966.
- Kristensen, K., A. Nielsen, C. W. Berg, H. Skaug, and B. M. Bell. 2016. TMB: Automatic differentiation and laplace approximation. *Journal of Statistical Software* 70.
- Langan, J. A., C. J. Cunningham, J. T. Watson, and S. McKinnell. 2024. Opening the black box: New insights into the role of temperature in the marine distributions of Pacific salmon. *Fish and Fisheries* 25:551–568.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943–1967.
- Lindgren, F., H. Rue, and J. Lindström. 2011. An explicit link between gaussian fields and gaussian markov random fields: The stochastic partial differential equation approach. *Journal of the Royal Statistical Society. Series B: Statistical Methodology* 73:423–498.
- Litzow, M. A., L. Ciannelli, P. Puerta, J. J. Wettstein, R. R. Rykaczewski, and M. Opiekun. 2019. Nonstationary environmental and community relationships in the North Pacific Ocean. *Ecology* 100:1–8.
- Litzow, M. A., M. E. Hunsicker, N. A. Bond, B. J. Burke, C. J. Cunningham, J. L. Gosselin, E. L. Norton, E. J. Ward, and S. G. Zador. 2020. The changing physical and ecological

- meanings of North Pacific Ocean climate indices. *Proceedings of the National Academy of Sciences of the United States of America* 117:7665–7671.
- Lyday, S. E., L. T. Ballance, D. B. Field, and K. David Hyrenbach. 2015. Shearwaters as ecosystem indicators: Towards fishery-independent metrics of fish abundance in the California Current. *Journal of Marine Systems* 146:109–120.
- Malick, M. J., S. P. Cox, F. J. Mueter, B. Dorner, and R. M. Peterman. 2017. Effects of the North Pacific Current on the productivity of 163 Pacific salmon stocks. *Fisheries Oceanography* 26:268–281.
- Malick, M. J., S. A. Siedlecki, E. L. Norton, I. C. Kaplan, M. A. Haltuch, M. E. Hunsicker, S. L. Parker-Stetter, K. N. Marshall, A. M. Berger, A. J. Hermann, N. A. Bond, and S. Gauthier. 2020. Environmentally Driven Seasonal Forecasts of Pacific Hake Distribution. *Frontiers in Marine Science* 7:1–12.
- Mantua, N. J., and S. R. Hare. 2002. The Pacific decadal oscillation. *Journal of oceanography* 58:35–44.
- Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society* 78:1069–1080.
- Marshall, J. B. 2024. Spatial Modeling of Climate-Induced Distribution Shifts: A Predictive Framework to Support Pacific Hake Fishery Management.
- Miller, J. A., D. J. Teel, A. Baptista, and C. A. Morgan. 2013. Disentangling bottom-up and top-down effects on survival during early ocean residence in a population of Chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 70:617–629.
- Miller, J. A., D. J. Teel, W. T. Peterson, and A. M. Baptista. 2014. Assessing the relative importance of local and regional processes on the survival of a threatened salmon population. *PLoS ONE* 9.
- Muir, W. D., D. M. Marsh, B. P. Sandford, S. G. Smith, and J. G. Williams. 2006. Post-hydropower system delayed mortality of transported Snake River stream-type Chinook Salmon: unraveling the mystery. *Transactions of the American Fisheries Society* 135:1523–1534.
- Nevins, H. M. 2004. Diet, demography, and diving behavior of the Common Murre (*Uria aalge*) in central California.
- Newman, M., M. A. Alexander, T. R. Ault, K. M. Cobb, C. Deser, E. Di Lorenzo, N. J. Mantua, A. J. Miller, S. Minobe, H. Nakamura, N. Schneider, D. J. Vimont, A. S. Phillips, J. D. Scott, and C. A. Smith. 2016. The Pacific Decadal Oscillation, Revisited. *Journal of Climate* 29:4399–4427.
- NMFS (National Marine Fisheries Service). 2005. Endangered and threatened species: final listing determinations for 16 ESUs of West Coast salmon, and final 4 (d) protective regulations for threatened salmonid ESUs. *Federal Register* 70:37160–37204.

- Parrish, J. K., and S. G. Zador. 2003. Seabirds as indicators: An exploratory analysis of physical forcing in the Pacific Northwest coastal environment. *Estuaries* 26:1044–1057.
- Pearcy, W. G., and J. P. Fisher. 1990. Distribution and abundance of juvenile salmonids off Oregon and Washington, 1981–1985.
- Pebesma, E. J. 2018. Simple features for R: standardized support for spatial vector data. *R J.* 10:439.
- Peterson, W. T., J. L. Fisher, J. O. Peterson, C. A. Morgan, B. J. Burke, and K. L. Fresh. 2014. Applied fisheries oceanography: Ecosystem indicators of ocean conditions inform fisheries management in the California Current. *Oceanography* 27:80–89.
- Petrosky, C. E., H. A. Schaller, E. S. Tinus, T. Copeland, and A. J. Storch. 2020. Achieving Productivity to Recover and Restore Columbia River Stream-Type Chinook Salmon Relies on Increasing Smolt-To-Adult Survival. *North American Journal of Fisheries Management* 40:789–803.
- Phillips, E. M., J. K. Horne, and J. E. Zamon. 2017. Predator–prey interactions influenced by a dynamic river plume. *Canadian Journal of Fisheries and Aquatic Sciences* 74:1375–1390.
- Phillips, E. M., J. K. Horne, and J. E. Zamon. 2021. Characterizing juvenile salmon predation risk during early marine residence. *PLoS ONE* 16:1–22.
- Pianka, E. R. 1973. The Structure of Lizard Communities. *Annual Review of Ecology and Systematics* 4:53–74.
- Piatt, I., and W. Sydeman. 2007. Seabirds as indicators of marine ecosystems. *Marine Ecology Progress Series* 352:199–204.
- Quinn, T. P. 2018. The behavior and ecology of Pacific salmon and trout. University of Washington press.
- Rechisky, E. L., D. W. Welch, A. D. Porter, M. C. Jacobs-Scott, P. M. Winchell, and J. L. McKern. 2012. Estuarine and early-marine survival of transported and in-river migrant Snake River spring Chinook salmon smolts. *Scientific Reports* 2:448.
- Ressler, P. H., J. A. Holmes, G. W. Fleischer, R. E. Thomas, and K. C. Cooke. 2007. Pacific hake, *Merluccius productus*, autecology: a timely review. *Marine Fisheries Review* 69:1.
- Scheuerell, M. D., R. W. Zabel, and B. P. Sandford. 2009. Relating juvenile migration timing and survival to adulthood in two species of threatened Pacific salmon (*Oncorhynchus* spp.). *Journal of Applied Ecology* 46:983–990.
- Schmitz, O. J., J. R. B. Miller, A. M. Trainor, and B. Abrahms. 2017. Toward a community ecology of landscapes: predicting multiple predator–prey interactions across geographic space. *Ecology* 98:2281–2292.
- Schrimpf, M., J. Parrish, and S. Pearson. 2012. Trade-offs in prey quality and quantity revealed through the behavioral compensation of breeding seabirds. *Marine Ecology Progress Series* 460:247–259.
- Schwing, F. B., S. Ralston, C. S. Moore, and K. M. Sakuma. 2000. RECORD COASTAL UPWELLING IN THE CALIFORNIA CURRENT IN 1999 41.

- Shono, H. 2008. Application of the Tweedie distribution to zero-catch data in CPUE analysis. *Fisheries Research* 93:154–162.
- Skirving, W., B. Marsh, J. De La Cour, G. Liu, A. Harris, E. Maturi, E. Geiger, and C. M. Eakin. 2020. CoralTemp and the coral reef watch coral bleaching heat stress product suite version 3.1. *Remote Sensing* 12:3856.
- Teel, D. J., B. J. Burke, D. R. Kuligowski, C. A. Morgan, and D. M. Van Doornik. 2015. Genetic identification of chinook salmon: Stock-specific distributions of juveniles along the Washington and oregon coasts. *Marine and Coastal Fisheries* 7:274–300.
- Tenney, J., N. Tancroto, G. Axel, and S. Livingston. 2023. Columbia Basin PIT Tag Information System, 1/1/2023 - 12/31/2023 Annual Report, 1990-080-00.
- Thomas, S. M., and J. E. Lyons. 2017. POPULATION TRENDS AND DISTRIBUTION OF COMMON MURRE *URIA AALGE* COLONIES IN WASHINGTON, 1996–2015.
- Thorson, J. T., A. Rindorf, J. Gao, D. H. Hanselman, and H. Winker. 2016. Density-dependent changes in effective area occupied for sea-bottom-associated marine fishes. *Proceedings of the Royal Society B: Biological Sciences* 283.
- Thorson, J. T., A. O. Shelton, E. J. Ward, and H. J. Skaug. 2015. Geostatistical delta-generalized linear mixed models improve precision for estimated abundance indices for {West} {Coast} groundfishes. *ICES Journal of Marine Science* 72:1297–1310.
- Vaida, F., and S. Blanchard. 2005. Conditional Akaike information for mixed effects models. *Corrado Lagazio, Marco Marchi (Eds)* 101.
- Varoujean, D. H., and D. R. Matthews. 1983. Distribution, abundance, and feeding habits of seabirds off the Columbia River, May-June, 1982. University of Oregon Institute of Marine Biology.
- Vasbinder, K., J. Fiechter, J. A. Santora, J. J. Anderson, N. Mantua, S. T. Lindley, D. D. Huff, and B. K. Wells. 2024. Size-selective predation effects on juvenile Chinook salmon cohort survival off Central California evaluated with an individual-based model. *Fisheries Oceanography* 33:e12654.
- Weitkamp, L. A., P. J. Bentley, and M. N. Litz. 2012. Seasonal and interannual variation in juvenile salmonids and associated fish assemblage in open waters of the lower Columbia River estuary. *Fishery Bulletin* 110.
- Wells, B. K., D. D. Huff, T. P. Quinn, J. A. Santora, D. G. E. Gomes, K. Vasbinder, K. A. Barnas, B. J. Burke, M. B. Courtney, L. G. Crozier, J. Fiechter, K. D. Friedland, S. A. Hayes, M. E. Hunsicker, F. Juanes, N. J. Mantua, C. J. Michel, E. M. Phillips, B. L. Sanderson, W. H. Satterthwaite, A. C. Seitz, T. F. Sheehan, J. D. Stewart, and M. Trudel. 2025. When, where, and why salmon become vulnerable to predation. *ICES Journal of Marine Science* 82:fsaf162.
- Wells, B. K., J. A. Santora, J. J. Bizzarro, A. Billings, R. D. Brodeur, E. A. Daly, J. C. Field, K. E. Richerson, and J. T. Thorson. 2024. Trophoscapes of predatory fish reveal biogeographic structuring of spatial dietary overlap and inform fisheries bycatch patterns. *Marine Ecology Progress Series* 741:47–70.

- Wells, B. K., J. A. Santora, M. J. Henderson, P. Warzybok, J. Jahncke, R. W. Bradley, D. D. Huff, I. D. Schroeder, P. Nelson, J. C. Field, and D. G. Ainley. 2017. Environmental conditions and prey-switching by a seabird predator impact juvenile salmon survival. *Journal of Marine Systems* 174:54–63.
- Wiens, J. A., and J. M. Scott. 1975. Model Estimation of Energy Flow in Oregon Coastal Seabird Populations. *The Condor* 77:439.
- Wood, S. N. 2017. Generalized additive models: an introduction with R. Chapman and Hall/CRC.
- Zamon, J. E., E. M. Phillips, and T. J. Guy. 2014. Marine bird aggregations associated with the tidally-driven plume and plume fronts of the Columbia River. *Deep Sea Research Part II: Topical Studies in Oceanography* 107:85–95.
- Zamon, J. E., N. Tolimieri, B. E. Chasco, M. E. Hunsicker, D. M. Van Doornik, B. J. Burke, D. J. Teel, and E. M. Phillips. 2024. Stock-specific spatial overlap among seabird predators and Columbia River juvenile Chinook Salmon suggests a mechanism for predation during early marine residence. *Marine and Coastal Fisheries* 16.
- Zheng, N., N. Cadigan, and J. T. Thorson. 2024, November 21. A note on numerical evaluation of conditional Akaike information for nonlinear mixed-effects models. *arXiv*.
- Zipkin, E. F., E. R. Zylstra, A. D. Wright, S. P. Saunders, A. O. Finley, M. C. Dietze, M. S. Itter, and M. W. Tingley. 2021. Addressing data integration challenges to link ecological processes across scales. *Frontiers in Ecology and the Environment* 19:30–38.
- Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer.

Chapter 4. Spatially explicit recruitment modeling in Sablefish (*Anoplopoma fimbria*) on the U.S. West Coast

4.1 Abstract

Understanding the drivers of variability in fisheries recruitment has been a core challenge for over a century. Recruitment appears to be more strongly linked to the environment than to spawning stock biomass for most stocks, but correlations between recruitment and the environment are notoriously fickle. However, analyses of recruitment have historically looked at recruitment and its drivers at the stock level, ignoring the spatial variability that is commonly seen in this process. In this study, we analyzed recruitment in Sablefish (*Anoplopoma fimbria*) on the U.S. West Coast in a spatially explicit analytical framework. By leveraging length compositions from the West Coast Groundfish Bottom Trawl Survey, we characterized the distribution of both spawning females and age-0 recruits. We then analyzed the distribution of age-0 recruits using spatiotemporal generalized linear mixed effects models, with separate models for the encounter probability and positive catch components. In these submodels, we investigated the support for oceanographic and environmental covariates as well as the effect of spawning stock biomass at different spatial scales. We found that while the presence or absence of age-0 recruits was poorly characterized by our covariates, the positive catch of age-0 recruits was related to several environmental factors. In particular, higher coastwide spawning stock biomass, cooler temperatures and higher net primary productivity in both the larval and pelagic juvenile phase, and cooler temperatures experienced by spawners during their preconditioning period were associated with higher recruit abundance. This study presents a framework for identifying drivers of spatiotemporal variability in recruitment while furthering our knowledge of drivers of Sablefish recruitment.

4.2 Introduction

Understanding the drivers of variability in fisheries recruitment has been a core challenge of fisheries science for over a century, beginning with Johan Hjort's observation that variability in year class strength drove variability in landings in Norwegian Herring (Hjort, 1914). The study of recruitment variability has focused on the roles of two key drivers: spawning stock biomass (SSB) and the environment. The assumption of a relationship between stock and recruitment fundamentally underpins the concept of maximum sustainable yield in fisheries management, as fisheries are often managed with the target of maintaining biomass at B_{msy} , or the biomass that theoretically supports the highest recruitment rate and therefore the maximum sustainable yield (Hilborn & Walters, 1992). However, across the observed range of stock sizes for most stocks,

there is little evidence of a relationship between spawning biomass and recruitment, suggesting stronger control by the environment (Szuwalski et al., 2015). Despite this, identifying environmental drivers of recruitment has been notoriously difficult. Correlations between environmental indices and recruitment are unstable (Myers, 1998), with many of these relationships proving to be non-stationary (Litzow et al., 2019).

However, analyses of relationships between stock, environment, and recruitment have typically examined year class strength across the full range of the stock, thus ignoring spatial heterogeneity, which is frequently acknowledged but rarely modeled. Recruitment often occurs in spatially discrete pulses (Hamer & Jenkins, 2004; Tolimieri et al., 2020), underscoring the importance of local processes including transport patterns (Schroeder et al., 2019), larval retention areas (Iles & Sinclair, 1982), and the availability of suitable habitat (Lilley & Unsworth, 2014; Rijnsdorp et al., 1992). Spawning fish also have variable and often patchy distributions (Ward & Tolimieri, 2025), suggesting that viewing spawning stock biomass as a scalar value may also obscure relationships between spawners and recruits at finer spatial scales. There are, however, several reasons that space is rarely accounted for in recruitment dynamics, from the scales of management and assessment to practical data considerations. Fisheries management and assessment primarily operate on the scale of individual stocks, causing stock assessments to collapse spatial variability in metrics like SSB, recruitment, and age structure into single stock-wide estimates. To align with the univariate time series of SSB and recruitment, environmental covariates in recruitment analyses have also typically been univariate time series, such as indices of temperature (e.g., Lindegren & Checkley, 2013), prey abundance (e.g., Feddern et al., 2026), or basin-scale indices of oceanographic conditions (e.g., Báez et al., 2021). Data availability also restricts the feasibility of analyzing spatial variability in recruitment: observations of recent recruits are rare, as recruits are not often encountered in the fishery and fishery-independent surveys are typically designed to target the fished stock, with higher selectivity for older age classes (Keller et al., 2017; Tolimieri et al., 2020).

Life history differences among groundfishes on the U.S. West Coast lead to differences in sampling efficacy for younger age classes by the West Coast Groundfish Bottom Trawl Survey (WCGBTS), which is the primary survey used to estimate indices of abundance for stock assessments. For example, while midwater-associated Yellowtail Rockfish are not typically encountered until age-4 (Oken et al., 2025), many other species are encountered as age-0 or age-1 fish (Tolimieri et al., 2020). When stocks are both encountered as recent recruits and are sampled for length and age compositions due to their management importance, the distribution of recent recruits can be characterized. This is the case for Sablefish (*Anoplopoma fimbria*), which is one of the stocks with the most age and length data from the WCGBTS (Ward & Tolimieri, 2025), and one that has a life history where age-0 fish are encountered in the trawl survey. On the U.S. West Coast, Sablefish spawning peaks in January and February in deep waters (>300 m)

(Guzmán et al., 2017). Eggs remain at depth for 2-3 weeks before hatching into larvae, which rise to the surface and transition into pelagic juveniles which are found in the nearshore by summer (Kendall Jr & Matarese, 1987). After this point, juveniles settle to the benthos as age-0 recruits and are encountered primarily in depths <250 m in the summer and early fall by the WCGBTS (Head et al., 2014). Therefore, Sablefish present a unique opportunity to spatially investigate the influence of spawning stock biomass and the environment on the abundance and distribution of age-0 recruits.

In this study, we present a new conceptual and statistical framework that accounts for spatiotemporal variability in the drivers of fisheries recruitment. With this framework, we sought to address whether accounting for spatial heterogeneity in recruitment dynamics would reveal new links between recruitment and both spawning stock biomass and the environment. Applying this framework to Sablefish on the U.S. West Coast, we used age and length data to model the distribution of both age-0 recruits and likely spawning females and explored alternative hypotheses for the effect of spawning stock biomass on recruitment at different spatial resolutions. Additionally, we used an oceanographic modeling hindcast to model environmental drivers of recruitment along the coast. A conceptual life-history based approach was used to link covariates characterizing oceanographic conditions (e.g., temperature, transport, and primary productivity) at different life history stages (from pre-conditioning of spawning females through the egg, larval, and juvenile stages) to both the presence of age-0 recruits and their relative abundance. Ultimately, this study provides new insights into Sablefish recruitment dynamics while demonstrating how spatiotemporal models can be used to investigate drivers of recruitment at finer spatial scales.

4.3 Methods

We model drivers of the abundance and distribution of age-0 Sablefish recruits caught in the West Coast Groundfish Bottom Trawl Survey using spatiotemporal generalized linear mixed effects models fit with the sdmTMB package (Anderson et al., 2022). As we hypothesized that different processes governed the presence of age-0 Sablefish recruits and their density, we modeled catches using a hurdle model, with separate covariates included in the encounter probability and positive catch models. For the encounter probability model, we included covariates that we hypothesized to influence the distribution of recruits (i.e., larval transport and retention covariates), while for the positive catch model we included covariates that we hypothesized to influence the abundance of recruits (i.e., SSB, temperature, and primary productivity). We used a model selection process to identify the most influential covariates and their relative importance.

4.3.1 West Coast Groundfish Bottom Trawl Survey

The West Coast Groundfish Bottom Trawl Survey (WCGBTS) is an annual fishery-independent bottom trawl survey covering the entire U.S. West Coast from Canada to Mexico and depths from 55 m to 1,280 m. A stratified random sampling design is used to select stations, which are then fished for approximately 15 minutes each. The full survey region is covered from north to south in two passes, with pass 1 occurring from May-July and pass 2 occurring from August-October. Sablefish caught in the survey are randomly subsampled (maximum of 50 per haul) for fork length (cm), weight (kg), and sex. A smaller subset of these fish are also aged from otoliths (Beamish & Chilton, 1982). More details on the survey design can be found in Keller et al., 2017.

We used length-based cutoffs to identify spawning-size females and age-0 recruits from the WCGBTS data. We classified female fish that were at least 55 cm in fork length as potential spawners, based on the U.S. West Coast coastwide L_{50} of 54.64 cm found in Head et al., 2014. We classified fish as age-0 recruits based on a time-varying length cutoff for age-0 fish. This cutoff was calculated separately for each year using a logistic regression fit to data from age-0 and age-1 Sablefish, with fork length as the sole predictor of age (Appendix A). We used a time-varying length-based cutoff instead of a fixed one because of evidence indicating that growth for age-0 recruits can vary considerably, possibly due to density dependence during years of high abundance (Leising et al., 2024). We then expanded the subsampled length data up to the tow level to estimate the total number of age-0 and spawning females in each tow.

4.3.2 Oceanographic covariates

Oceanographic variables were drawn from two global oceanographic modeling products from the Copernicus Marine and Environmental Monitoring Service (CMEMS): the Global Ocean Physics Reanalysis (GLORYS) 12V1 model and the Global Ocean Biogeochemistry Hindcast (GOBH). GLORYS is a $1/12^\circ$ horizontal resolution oceanographic model with 50 vertical levels, covering 1993-2026 (E.U. Copernicus Marine Service Information (CMEMS), 2026b; Jean-Michel et al., 2021). From the GLORYS product, we extracted four variables: cross-shelf transport (eastward), longshore transport (northward), sea surface temperature, and bottom temperature. GOBH is a $1/4^\circ$ horizontal resolution biogeochemical hindcast with 75 vertical levels, covering 1993-2026 (E.U. Copernicus Marine Service Information (CMEMS), 2026a). From the GOBH product, we extracted two variables: chlorophyll and net primary productivity (NPP).

4.3.3 Modeling the distribution of adult female spawners

For the influence of SSB, we used sdmTMB to characterize the distribution and abundance of spawning-sized female fish based on our length cutoff, which we used to evaluate hypotheses of the spatial scale of the influence of female spawning biomass on age-0 recruits. We fit a hurdle model for the distribution of adult female spawners with a Gamma distribution with a log link for the catch-rate component (in kg) and a binomial distribution using a logit link for the encounter probability. Spatial and spatiotemporal random effects were included with anisotropy, with the spatiotemporal effects evolving as an autoregressive process. The random effects structure was selected using conditional AIC (cAIC) as our information criterion (Vaida & Blanchard, 2005), estimated using the formula presented in equation 6 of Zheng et al., 2024. Spatial and spatiotemporal variation were estimated with a mesh with a minimum cutoff of 15 km between vertices. The effects of survey pass and depth were included, in addition to a year-specific intercept. The log of the area swept (in km²) was included as an offset.

Indices of abundance were estimated using the fitted model for adult female spawners. Specifically, indices were calculated for the survey region from Point Conception (34.45° N) to the northern edge of the survey region (48.5° N), as well as separate indices for this region north and south of Cape Mendocino (40.43° N).

4.3.4 Hypothesized drivers of age-0 recruit presence and abundance

We developed hypotheses for drivers of age-0 recruit abundance and distribution from a conceptual model of the Sablefish life history, which was previously reviewed by Tolimieri et al. (2018). These hypotheses were then formalized as covariates for the encounter probability or positive catch models (or both), depending on the hypothesized mechanisms. Following previous conceptual life-history-based recruitment studies (Tolimieri et al., 2018), we identified potential drivers of Sablefish recruitment from the female preconditioning stage to when age-0 recruits are found on the benthos (and encountered by the trawl survey). We also attempted to link these hypotheses spatially to the distribution of female spawners or recruits. We categorize our hypotheses into the following: 1) environmental conditions experienced by spawning females; 2) biomass of spawning females; 3) prey and temperature conditions for feeding larvae and juveniles; 4) transport and retention conditions for eggs, larvae, and juveniles; and 5) benthic conditions for age-0 recruits. Hypotheses for the encounter probability model can be found in Table 1 and hypotheses for the positive catch model can be found in Table 2.

4.3.4.1 Environmental conditions experienced by spawning females

The strength of the Sablefish year class may begin to be determined long before spawning when females are in the pre-conditioning period, which is typically classified as the period from June to December prior to spawning. As Sablefish have been observed to skip spawning (Rodgveller et al., 2016), possibly related to poor body condition brought on by increased metabolic demands or prey availability, we included temperature during the pre-conditioning period as one of our drivers of the positive catch component (H2.1). We also included temperature during the spawning period (December – March) as a potential other driver of the positive catch component (H2.2). In each case, we hypothesized that temperature would have a negative impact on eventual recruitment, as increased metabolic demands would decrease the likelihood of spawning. Both of these covariates were estimated as the mean temperature across the focal time period, weighted to the distribution of spawning females estimated by the female spawner SDM.

4.3.4.2 Biomass of spawning females

We tested three different spatial hypotheses for the influence of female spawning biomass: that the coastwide female spawning biomass acts as a spatially uniform source of recruits (H2.3); that the coastwide female spawning biomass acts as a source of recruits, but that the influence of female spawning biomass on recruits has a persistent spatial pattern that we estimate from the age-0 recruit data (H2.4); an intermediate hypothesis, where the female spawning biomass in each of three biogeographic provinces (with breakpoints at Cape Mendocino and Point Conception) serves as a source of recruits in the same biogeographic province (H2.5).

4.3.4.3 Prey and temperature conditions for feeding larvae and juveniles

We included the effect of chlorophyll (H2.7, H2.10), NPP (H2.8, H2.11), and sea surface temperature (H2.9, H2.12) during the larval and pelagic juvenile stages as drivers of the positive catch component. For each of these effects, we took the mean value of the covariate in each 1.0° latitude bin across the time period corresponding to either the larval or pelagic stage and matched these summaries to the trawl tows within those latitude bins. Sablefish exhibit exceptionally high growth rates (Sigler et al., 2001; Sogard, 2011) and are voracious and flexible predators, with juveniles found to prey primarily upon various zooplankton in the California Current (Daly et al., 2024; McFarlane & Beamish, 1992) and forage fishes in Southeast Alaska (Callahan et al., 2021). However, data on direct prey of young-of-year Sablefish is not available spatially in the California Current. Therefore, we included chlorophyll and NPP as spatially resolved indices of feeding conditions. Temperature during the larval and pelagic juvenile stages of Sablefish is also hypothesized to be a driver of survival but may act through mechanisms with opposing directions of effects. While warmer temperatures are linked to faster growth that may allow juvenile Sablefish to escape predation (Anderson, 1988; Bailey & Houde, 1989; Miller et al., 1988),

warmer waters also increase metabolic demands, potentially increasing the chance of starvation. One study of Sablefish growth under different laboratory conditions found that age-0 Sablefish growth was maximized at 12-16.8 °C, indicating a thermal optimum (Krieger et al., 2020). Furthermore, as the California Current is an upwelling-driven system (Checkley & Barth, 2009), where upwelled waters are cool and nutrient-rich, warmer temperatures may also be associated with lower upwelling and therefore poorer feeding conditions.

4.3.4.4 Transport and retention conditions for eggs, larvae, and juveniles

We included the interaction between longshore (northward) transport at depth and spawning latitude as a covariate for both the encounter probability (H1.1) and positive catch (H2.6) models, where latitude was centered relative to the center of gravity of the distribution of female spawners. We included this effect in both models because of two hypothesized mechanisms acting on the egg and early larval stages of Sablefish. Sablefish eggs are buoyant and are most commonly found between 240 and 480 m, sink post-hatch as yolk-sac larvae, and eventually rise to the surface as feeding larvae (Moser et al., 1994). We included the interaction between transport strength and latitude as a covariate for the encounter probability model, as we expected stronger northward transport to bring recruits from the southern to the northern reaches of the study region. We included this same interaction as a covariate for the positive catch model because Sablefish recruitment strength has been linked to overlap with northern copepods, which requires that eggs and larvae are transported northward (McFarlane & Beamish, 1992; Tolimieri et al., 2018). The strength of northward transport at depth was calculated as the mean northward transport in the survey area, north of Point Conception and at >242 m depth (aligned with the distribution of eggs and larvae, with this bound determined by the cell dimensions from the GLORYS model), over the time period aligned to the egg and yolk-sac larval stages.

We also included the effect of cross-shelf transport in the presence/absence model, processed in different ways to align with the hypothesized mechanisms around transport of eggs, larvae, and juveniles to suitable nearshore habitat. First, we included the effect of cross-shelf transport at depth (>242 m) over the egg and yolk-sac larvae period (H1.2). Second, we included the effect of cross-shelf transport in the upper 20 m of the water column over both the larval (H1.3) and pelagic juvenile (H1.5) stages. This depth range was chosen based on information on the vertical distribution of pelagic juvenile Sablefish caught in suspended pots and pelagic surface trawls (Daly et al., 2024; Rutecki & Varosi, 1997); however, pelagic juveniles have also been found in deeper waters (Callahan et al., 2021). These cross-shelf transport covariates were calculated as the mean eastward transport over the corresponding life history stages, summarized into 1.0° latitude bins, and matched these summaries to the trawl tows within those latitude bins. Third, we calculated the horizontal divergence in the surface waters (0-20m) in each cell. Horizontal divergence is calculated using the flow rates into and out of cells to estimate the degree of water

convergence (leading to downwelling and retention) vs. divergence (leading to upwelling and dispersal) (Vallis, 2017). We hypothesized that retention of both larvae (H1.4) and pelagic juveniles (H1.6) in cells was necessary for recruitment.

4.3.4.5 Benthic conditions for age-0 recruits

We hypothesized that age-0 Sablefish may select for suitable benthic thermal habitat, thereby affecting their encounter probability (H1.9), and also that temperature may affect survival, thereby affecting abundance (H2.15). We included temperature as a linear effect in each model. Age-0 Sablefish settle to the benthos beginning in May and peaking in August and September, primarily in shallow depths <250 m, as is seen in the trawl survey catches (Appendix B). Therefore, because of the phenology and ontogenetic depth preferences of age-0 Sablefish, we included depth as a linear effect and survey pass as an intercept (with pass 1 being May-July and pass 2 being August-October) in all candidate models for both encounter probability (H1.7 and H1.8) and positive catch (H2.13 and H2.14).

Table 1. Oceanographic and bathymetric conditions hypothesized to influence the encounter probability of age-0 recruits. Any hypotheses marked by an asterisk in the abbreviation column are also included in the positive catch model (Table 2).

Life-history stage	Hypothesis	Time period	Water column depth	Abbreviation	Covariates	Effect type, shape	Data Source	Spatiotemporal dimension
Eggs, yolk-sac larvae	(H1.1) Northward transport of eggs and larvae influences eventual latitudinal distribution	Jan-May (Yr 1)	242 m to seafloor	E-LST*lat	Mean long-shore transport north of Point Conception multiplied by latitude, centered at the center of gravity of female spawners	Fixed, linear	CMEMS	Mean northward transport in the survey area, north of Point Conception
Eggs, yolk-sac larvae	(H1.2) Onshore transport of eggs and yolk-sac larvae influences	Jan-May (Yr 1)	242 m to seafloor	E-CST	Mean cross-shelf transport	Fixed, linear	CMEMS	Cross-shelf transport for the survey area is binned into 1.0° latitudinal bins and linked to cells in the age-0 SDM

	eventual distribution							
Larvae (feeding)	(H1.3) Onshore transport is required to bring age-0 recruits to suitable habitat	Feb-May (Yr 1)	Surface (0-20 m)	L-CST	Mean cross-shelf transport	Fixed, linear	CMEMS	Cross-shelf transport for the survey area is binned into 1.0° latitudinal bins and linked to cells in the age-0 SDM
Larvae (feeding)	(H1.4) Age-0 recruits must be retained by surface currents	Feb-May (Yr 1)	Surface (0-20 m)	L-RET	Mean horizontal divergence	Fixed, linear	CMEMS	Mean horizontal divergence in each cell
Pelagic juveniles	(H1.5) Onshore transport is required to bring age-0 recruits to suitable habitat	Jun-Sep (Yr 1)	Surface (0-20 m)	P-CST	Mean cross-shelf transport	Fixed, linear	CMEMS	Cross-shelf transport for the survey area is binned into 1.0° latitudinal bins and linked to cells in the age-0 SDM
Pelagic juveniles	(H1.6) Age-0 recruits must be retained by surface currents	Jun-Sep (Yr 1)	Surface (0-20 m)	P-RET	Mean horizontal divergence	Fixed, linear	CMEMS	Mean horizontal divergence in each cell

Benthic age-0 recruits	(H1.7) Recruits settle in shallower depths	NA	Bottom	Depth*	Depth	Fixed, linear	WCGBTS	CMEMS output matched to trawl tows in age-0 SDM
Benthic age-0 recruits	(H1.8) Recruits settle in the late summer and fall	NA	Bottom	Pass*	Pass 1 (May-July) or Pass 2 (August-October)	Fixed, intercept	WCGBTS	Coastwide effect
Benthic age-0 recruits	(H1.9) Recruits preferentially select suitable thermal habitat	May-Oct (Yr 1)	Bottom	R-BT*	Mean temperature	Fixed, linear	CMEMS	CMEMS output matched to trawl tows in age-0 SDM

Table 2. Oceanographic, bathymetric, and biological conditions hypothesized to influence the abundance of age-0 recruits, conditional on encounter. Any hypotheses marked by an asterisk in the abbreviation column are also included in the encounter probability model (Table 1).

Life-history stage	Hypothesis	Time period	Water column depth	Abbreviation	Covariates	Effect type, shape	Data Source	Spatiotemporal dimension
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Preconditioning of spawning females	(H2.1) Higher temperatures increase food demand resulting in lower egg production, egg quality, or probability of spawning	Jun – Dec (Yr 0)	Bottom	PS-BT	Mean temperature, weighted to the distribution of female spawning biomass estimated in sdmTMB	Fixed, linear	CMEMS, WCGBTS	Coastwide effect
Spawning females	(H2.2) Temperature acts as a spawning cue with fish less likely to spawn at higher temperatures	Dec (Yr 0) – Mar (Yr 1)	Bottom	S-BT	Mean temperature, weighted to the distribution of female spawning biomass estimated in sdmTMB	Fixed, linear	CMEMS, WCGBTS	Coastwide effect
Spawning of spawning females	(H2.3) Biomass of female spawners north of Point Conception is a spatially uniform source of age-0 recruits.	May-Oct (Yr 1)	Bottom	SSB-coast	sdmTMB estimated biomass of spawning females	Fixed, linear	WCGBTS	Point Conception (32.45° N) to U.S.-Canada border (48.5° N)

Spawning of spawning females	(H2.4) Biomass of female spawners north of Point Conception is a spatially varying source of age-0 recruits.	May-Oct (Yr 1)	Bottom	SSB-svc	sdmTMB estimated biomass of spawning females	Spatially varying coefficient	WCGBTS	Point Conception (32.45° N) to U.S.-Canada border (48.5° N)
Spawning of spawning females	(H2.5) Cape Mendocino serves as a biogeographic break, where the biomass of female spawners north of Cape Mendocino are a spatially uniform source of age-0 recruits north of Cape Mendocino, while the biomass of female spawners south of Cape Mendocino are a spatially uniform source of age-0 recruits south of Cape Mendocino	May-Oct (Yr 1)	Bottom	SSB-prov	sdmTMB estimated biomass of spawning females	Fixed, linear	WCGBTS	Point Conception (32.45° N) to Cape Mendocino (40.43° N) / Cape Mendocino (40.43° N) to U.S.-Canada border (48.5° N)
Eggs, yolk-sac larvae	(H2.6) Northward transport of eggs and larvae increases	Jan-May (Yr 1)	242 m to seafloor	E-LST*lat	Mean long-shore transport north of	Fixed, linear	CMEMS, WCGBTS	Coastwide effect

	overlap with preferred prey				Point Conception multiplied by latitude, centered at the center of gravity of female spawners			
Larvae (feeding)	(H2.7) Chlorophyll is an indicator of feeding conditions	Feb-May (Yr 1)	Surface (0-20 m)	L-CHL	Mean chlorophyll	Fixed, linear	CMEMS	Chlorophyll for the survey area is binned into 1.0° latitudinal bins and linked to cells in the age-0 SDM
Larvae (feeding)	(H2.8) Net primary productivity is an indicator of feeding conditions	Feb-May (Yr 1)	Surface (0-20 m)	L-NPP	Mean net primary productivity	Fixed, linear	CMEMS	Net primary productivity for the survey area is binned into 1.0° latitudinal bins and linked to cells in the age-0 SDM
Larvae (feeding)	(H2.9) Growth is faster in warmer waters, leading to reduced predation. Alternatively, warmer	Feb-May (Yr 1)	Surface (0-20 m)	L-ST	Mean seawater potential temperature	Fixed, linear	CMEMS	Seawater potential temperature for the survey area is binned into

	waters increase metabolic demands, increasing the risk of starvation.							1.0° latitudinal bins and linked to cells in the age-0 SDM
Pelagic juveniles	(H2.10) Chlorophyll is an indicator of feeding conditions	Jun-Sep (Yr 1)	Surface (0-20 m)	P-CHL	Mean chlorophyll	Fixed, linear	CMEMS	Chlorophyll for the survey area is binned into 1.0° latitudinal bins and linked to cells in the age-0 SDM
Pelagic juveniles	(H2.11) Net primary productivity relates to feeding conditions for pelagic juveniles by serving as food zooplankton	Jun-Sep (Yr 1)	Surface (0-20 m)	P-NPP	Mean net primary productivity	Fixed, linear	CMEMS	Net primary productivity for the survey area is binned into 1.0° latitudinal bins and linked to cells in the age-0 SDM
Pelagic juveniles	(H2.12) Growth is faster in warmer waters, leading to reduced predation. Alternatively, warmer waters increase metabolic demands, increasing the risk of starvation in the	Jun-Sep (Yr 1)	Surface (0-20 m)	P-ST	Mean seawater potential temperature	Fixed, linear	CMEMS	Seawater potential temperature for the survey area is binned into 1.0° latitudinal bins and linked to cells in the age-0 SDM

	absence of adequate prey.							
Benthic age-0 recruits	(H2.13) Recruits settle in shallower depths	NA	Bottom	Depth*	Depth	Fixed, linear	WCGBTS	CMEMS output matched to trawl tows in age-0 SDM
Benthic age-0 recruits	(H2.14) Recruits settle in the late summer and fall	NA	Bottom	Pass*	Pass 1 (May-July) or Pass 2 (August-October)	Fixed, intercept	WCGBTS	Coastwide effect
Benthic age-0 recruits	(H2.15) Growth is faster in warmer waters, leading to reduced predation. Alternatively, warmer waters increase metabolic demands, increasing the risk of starvation in the absence of adequate prey.	May – Oct (Yr 1)	Bottom	R-BT*	Mean temperature	Fixed, linear	CMEMS	CMEMS output matched to trawl tows in age-0 SDM

4.3.5 Statistical model

We modeled the observations of age-0 Sablefish recruits using a two-part (hurdle) model, with separate models for the encounter probability and positive catch datasets. The observations were highly zero-inflated, as while the encounter probability dataset had 8,361 observations, the positive catch dataset had only 552 observations (6.6% of the total dataset). We chose to model age-0 Sablefish observations with a hurdle model as we believed that the presence or absence of age-0 recruits was driven by a separate process than the abundance of age-0 recruits.

Specifically, we hypothesized that oceanographic transport or retention covariates would explain the presence or absence of age-0 recruits, but that the abundance would be controlled by a set of covariates that would affect the abundance and survival of recruits at each stage, including feeding conditions, temperature, and spawning stock biomass.

We first examined the correlation among possible predictors (Appendix C) and ensured that no predictors that had a correlation coefficient of greater than 0.7 were included in the same model. For the encounter probability dataset, the only two predictors that had a correlation coefficient of >0.7 were depth and bottom temperature; we decided to only retain depth in each model due to the known ontogenetic movement of Sablefish into deeper waters and the high preference of age-0 benthic recruits for shallower waters (Head et al., 2014). For the positive catch dataset, NPP and chlorophyll were highly correlated (>0.9) in each of the two time periods examined. Chlorophyll was also negatively correlated (-0.75) with surface temperature in the pelagic juvenile stage. Therefore, we chose to remove chlorophyll from our set of candidate covariates and retained NPP, as it is more proximately related to food conditions for Sablefish. The bottom temperature experienced by female spawners during the pre-conditioning period and bottom temperature experienced by female spawners during the spawning period was also highly correlated (>0.96). We chose to retain the pre-conditioning period temperature, as a previous study found greater evidence for its importance (Tolimieri et al., 2018).

Each covariate except for the interaction between northward transport and latitude was z-scored prior to model fitting. We did not z-score the transport metric or latitude because the values were inherently meaningful based on how they were centered. Each candidate model for both the probability of encounter and the positive catch models included an effect of both depth and survey pass, as these are both strongly supported by the ontogenetic movement of Sablefish to deeper waters with age and the timing of benthic settlement. For the encounter probability model, six oceanographic covariates were evaluated (Table 1). For the positive catch model, seven oceanographic covariates and four different potential effects of SSB (mutually exclusive) were tested (Table 2). Therefore, we had 64 candidate models for the encounter probability model and 512 candidate models for the positive catch model.

We modeled the encounter probability of age-0 Sablefish at location s and time t using a Binomial observation model with a logit link and an offset for the log of area swept using the following equation:

$$\text{logit}(p_{s,t}) = \mathbf{X}_{s,t}\boldsymbol{\beta} + \omega_s + \varepsilon_{s,t}$$

$$\omega_s \sim \text{MVN}(0, \sigma_\omega^2 \mathbf{R}_\omega)$$

$$\varepsilon_{s,t} \sim \text{MVN}(0, \sigma_\varepsilon^2 \mathbf{R}_\varepsilon)$$

Where $p_{s,t}$ represents the probability of encounter of recruits at location s and time t , $\mathbf{X}_{s,t}$ is a vector of fixed effects corresponding to location s and time t (drawn from the hypotheses in Table 1), and $\boldsymbol{\beta}$ is a vector of estimated coefficients. ω_s are the spatial random effects drawn from a multivariate normal distribution with mean 0 and variance given by the covariance matrix $\sigma_\omega^2 \mathbf{R}_\omega$, where σ_ω is the spatial variance and $\mathbf{R}_\omega$ is the spatial correlation. $\varepsilon_{s,t}$ are the spatiotemporal random effects drawn from a multivariate normal distribution with mean 0 and variance given by the covariance matrix $\sigma_\varepsilon^2 \mathbf{R}_\varepsilon$, where σ_ε is the spatiotemporal variance and $\mathbf{R}_\varepsilon$ is the spatiotemporal correlation.

We modeled the positive catch of age-0 Sablefish at location s and time t , conditional on their encounter, using a Gamma observation model with a log link and an offset for the log of area swept using the following equation:

$$\ln(\mu_{s,t}) = \mathbf{Y}_{s,t}\boldsymbol{\alpha} + \mathbf{Y}_{s,t}^{svc} \boldsymbol{\zeta}_s + \eta_{s,t}$$

$$\eta_{s,t} \sim \text{MVN}(0, \tau_\eta^2 \boldsymbol{\rho}_\eta)$$

Where $\mu_{s,t}$ represents the number of recruits at location s and time t , $\mathbf{Y}_{s,t}$ is a vector of fixed effects corresponding location s and time t (drawn from the hypotheses in Table 2), $\boldsymbol{\alpha}$ is a vector of estimated coefficients, $\mathbf{Y}_{s,t}^{svc}$ is a vector of spatially varying effects corresponding to location s and time t (which only contains coastwide value of SSB estimated in each year and is only included in models with a spatially-varying effect of SSB), $\boldsymbol{\zeta}_s$ is a vector of spatially varying coefficients following a random field (only included in models with a spatially-varying effect of SSB), and $\eta_{s,t}$ are the spatiotemporal random effects drawn from a multivariate normal distribution with mean 0 and variance given by the covariance matrix $\tau_\eta^2 \boldsymbol{\rho}_\eta$, where τ_η is the

spatiotemporal variance and ρ_η is the spatial correlation. A spatial random effect was not included in the best supported random effects structure. A probability density function for the gamma distribution using the estimated values from the best fit model is shown in Appendix D.

We evaluated different candidate models for both the encounter probability and positive catch models using the “top-down” strategy for model selection (Zuur et al., 2009). However, when selecting the best structure of the random effects and the fixed effects, we used two different information criteria: conditional AIC, or cAIC (Vaida & Blanchard, 2005) for the random effects, and marginal AIC (Akaike, 1974) for the fixed effects. While these two information criteria have the same two basic components (a term for the fit of the model to the data based on the log likelihood and a penalty term for the degrees of freedom), these components are computed differently. Most importantly for our purposes, the degrees of freedom term in marginal AIC is based only on the number of parameters in the model, whereas in cAIC it is the effective degrees of freedom, which accounts for the number of random effects estimated based on the extent to which they act as parameters (Vaida & Blanchard, 2005). This makes cAIC a more appropriate information criterion for comparing different random effects structures, while AIC is more appropriate when the random effects are fixed and we are most interested in the best supported structure of fixed effects. To estimate cAIC we implemented the formula presented in equation 6 of Zheng et al., 2024. Therefore, we used the following process:

1. Starting with a model with saturated fixed effects, tune the structure of the spatial and spatiotemporal random effects using cAIC as the information criterion.
2. Keeping the random effects structure identified in the previous step, identify the fixed effects structure for our covariates using AIC (marginal) as the information criterion.

The best fit random effects structures for both the encounter probability and positive catch models are found in Appendix E.

Because of the high number of candidate models, we present model-averaged parameter estimates and relative variable importance (RVI) estimates for our covariates of interest for both the encounter probability model and the positive catch model. We calculate the average coefficient values for each of our covariates using model averaging with Akaike weights (Burnham & Anderson, 2002) using the following formula:

$$\hat{\theta} = \sum_{i=1}^R w_i \hat{\theta}_i$$

where $\hat{\theta}$ denotes the model average estimate of coefficient θ , i indicates model from candidate set R , w_i is the Akaike weight of model i , and $\hat{\theta}_i$ is the estimate of coefficient θ in model i . This approach is the so-called “natural average” method, where the candidate set of models also includes the models where the term is not included, and those models where the term is not included serve as a regularization penalty that pulls the coefficient estimate towards zero (Burnham & Anderson, 2002). However, method requires a balanced set of models (i.e., an equal number of models where the term is vs. is not included), otherwise the coefficient estimate will be biased (Grueber et al., 2011). Therefore, while the full set of candidate models was used to calculate coefficient estimates, the four mutually exclusive terms for an effect of SSB in the encounter probability model meant that the full set of candidate models was unbalanced. Therefore, coefficient estimates for these models were calculated on three different truncated sets of candidate models, where each set included the models with no effect of SSB (null model) and the models with one of the three spatial effects of SSB (coastwide, by province, or spatially varying).

We calculate the variance of these terms using the following formula:

$$\widehat{var}(\hat{\theta}) = \left[\sum_{i=1}^R w_i \sqrt{\widehat{var}(\hat{\theta}_i | g_i) + (\hat{\theta}_i - \hat{\theta})^2} \right]^2$$

where $\hat{\theta}$ denotes the model average estimate of coefficient θ , i indicates model from candidate set R , w_i is the Akaike weight of model i , and $\hat{\theta}_i$ is the estimate of coefficient θ in model i , and g_i is the model.

4.4 Results

4.4.1 Overview

Support for our hypothesized covariates (Tables 1 and 2) was greater for the positive catch model than for the encounter probability model. While variability in the encounter probability was best characterized by a model with only spatial and spatiotemporal random effects, the positive catch model showed higher expected catches with cooler surface temperatures and higher NPP during the larval and pelagic juvenile stages, and cooler temperatures experienced by spawners during the pre-conditioning period. When the predictions from the two sub-models were combined, recruitment exhibited boom and bust cycles, with the northern and central regions showing boom events that are occasionally synchronous and occasionally asynchronous

(Fig. 1). The southern region consistently had very low recruitment, despite containing a considerable portion of the total female spawning biomass (Fig. 2). The distribution of female spawners shows most of the biomass north of Cape Mendocino, with some persistent hotspots through time (Appendix F).

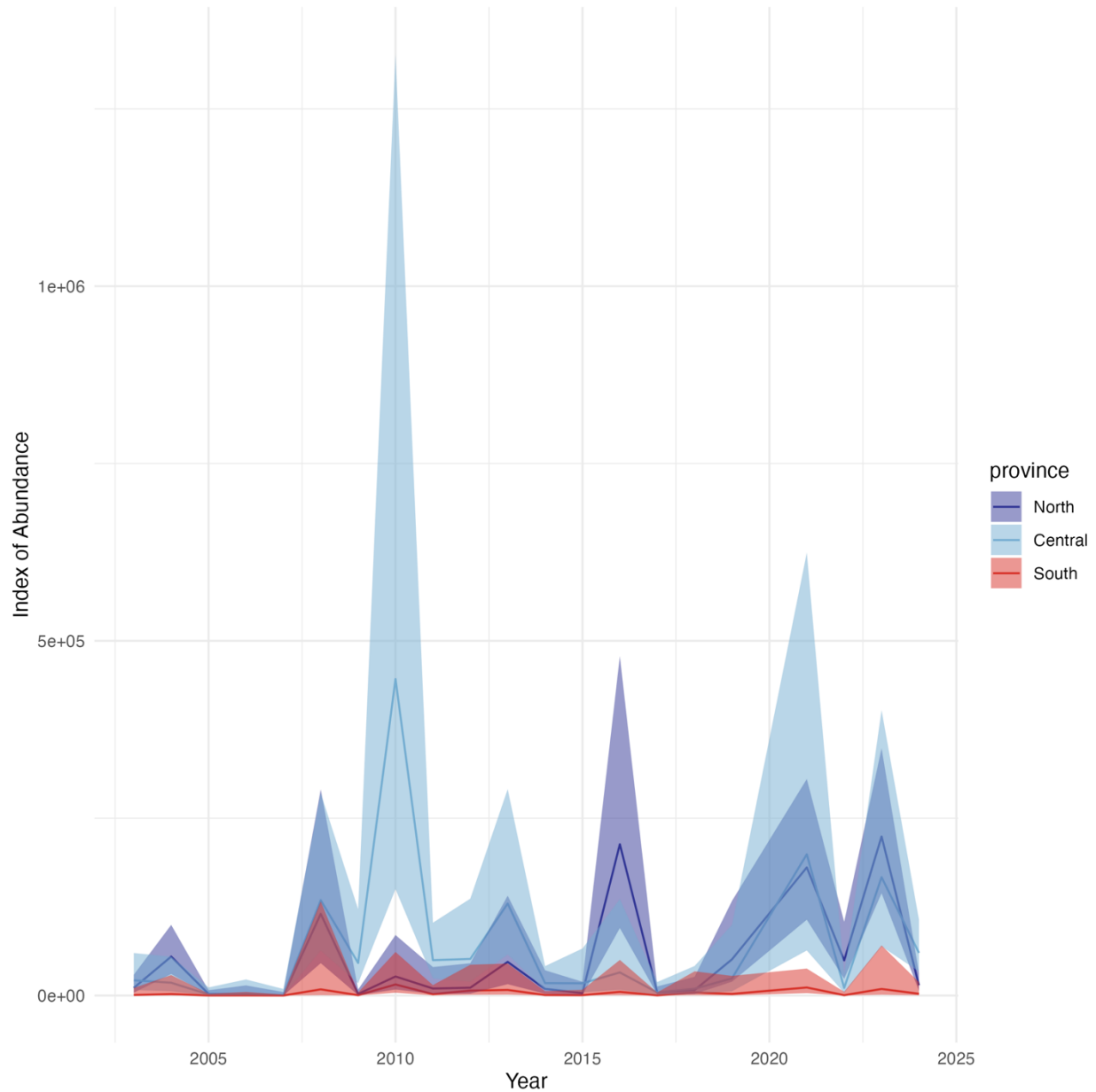


Figure 1. Estimated indices of age-0 recruit abundance in the three provinces based on the combined predictions from the encounter probability and positive catch models.

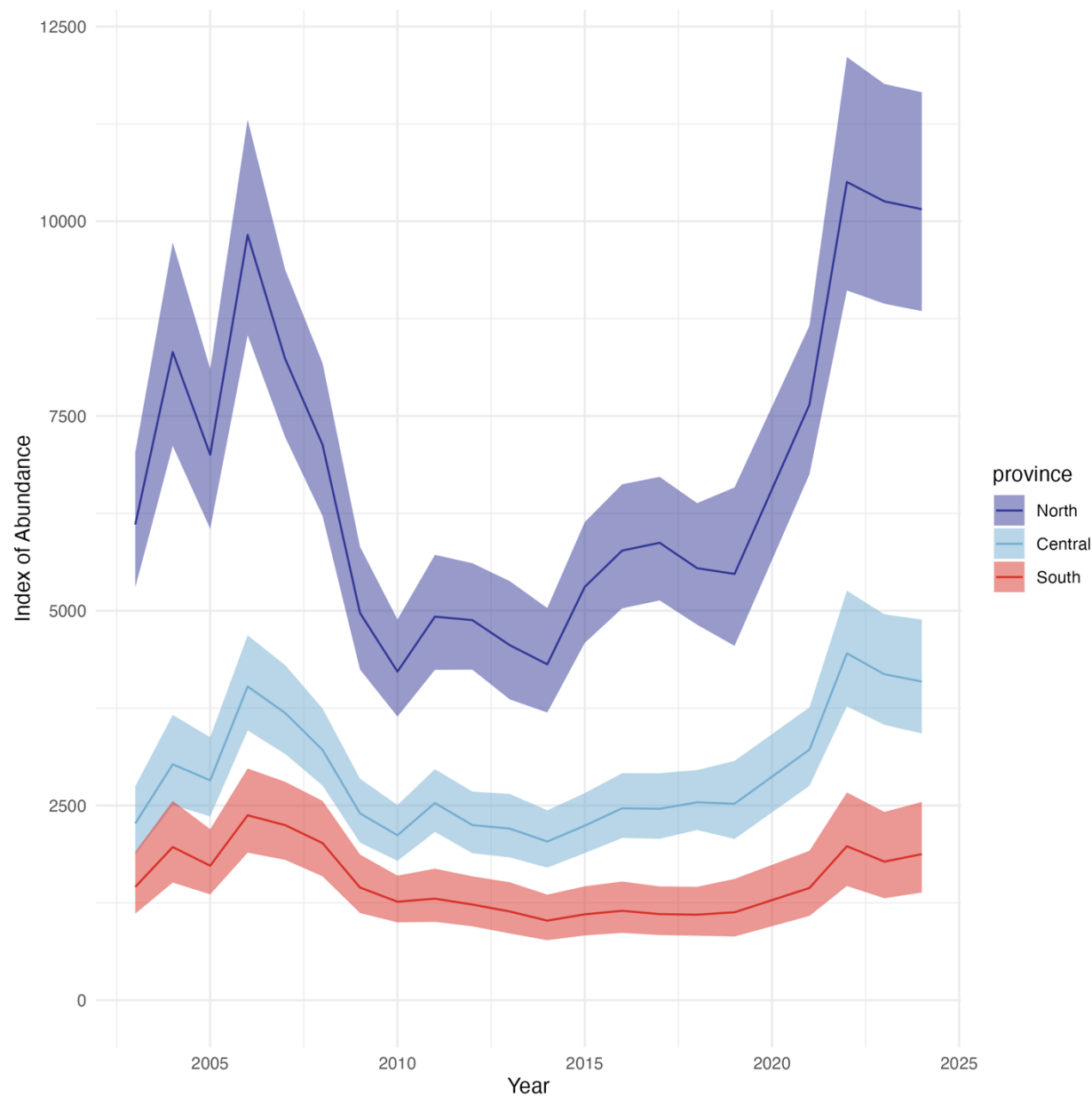


Figure 2. Estimated indices of abundance for female spawner biomass in the three provinces: North (Cape Mendocino to the Canadian border), Central (Point Conception to Cape Mendocino), and South (Mexican border to Point Conception).

4.4.2 Encounter probability model

Overall, our model selection process did not indicate that our candidate oceanographic predictors were associated with the encounter probability of age-0 Sablefish. The best supported model for

encounter probability included anisotropic spatial and spatiotemporal (IID, no autoregressive component) random effects (Appendix E). It did not include any fixed effects besides the effects of depth and survey pass (Table 3). However, the candidate models with $\Delta AIC < 2$ (Table 4) besides the best fit model each included one of the potential covariates. The RVI scores were generally low for all predictors, with the most important variable being E-CST (cross-shore transport during the egg stage), with a score of 0.337 (Table 4). While our candidate fixed effects were generally not supported for the encounter probability model, the estimated spatial random fields indicate strong and consistent spatial patterns in encounter probability (Appendix G). Additionally, the estimated spatiotemporal random fields led to considerable differences in encounter probability across years (Appendix G).

4.4.3 Positive catch model

In contrast to the encounter probability model, the inclusion of multiple covariates was supported for the positive catch model (Table 5), with both SSB and oceanographic covariates being associated with the catch of age-0 Sablefish. Every candidate covariate except for SSB-svc was included in at least one of the models with $\Delta AIC < 2$ (Table 5), but the RVI scores indicate that SSB-coast and SSB-prov were the most important covariates, each having a positive effect on predicted catch (Table 6). The coefficient estimates for oceanographic covariates indicated that age-0 recruitment was higher when surface temperature was cooler during the larval and pelagic juvenile stages and when NPP was higher during the larval and pelagic juvenile stages (Table 6). They also indicated that age-0 recruitment was higher when preconditioning temperatures were cooler for spawning adults. Additionally, the best supported random effects structure for the positive catch model included isotropic spatiotemporal (IID, no autoregressive component) random effects, but no spatial random effects (Appendix E).

When comparing the different spatial hypotheses for the effect of spawning stock biomass, the RVI scores were 0.536 for the coastwide effect of SSB, 0.372 for the province-specific effect of SSB, and 0.092 for the spatially-varying effect of SSB. This indicates that the data supports either a coastwide or a province-specific effect of SSB, with more support for the coastwide effect. Among the oceanographic covariates, RVI scores varied when comparing the model sets for the three different SSB covariates, although patterns were generally consistent (Table 6). However, when comparing RVI scores for the models with SSB-coast (the most supported structure for SSB), L-ST and P-NPP stage had the highest RVI scores, followed by P-ST, L-NPP, and PS-BT. E-LST*lat and R-BT had lower RVI scores.

Table 3. Models for the encounter probability of age-0 recruits with a $\Delta AIC < 2$. Terms correspond to the terms in Table 1.

Candidate Model	ΔAIC
Pass + Depth	0
Pass + Depth + E-CST	1.37
Pass + Depth + L-CST	1.4
Pass + Depth + P-RET	1.76
Pass + Depth + P-CST	1.78
Pass + Depth + L-RET	1.94
Pass + Depth + E-LST*lat	2

Table 4. Relative importance, model-averaged coefficient estimates, and model-averaged coefficient SE estimates for the covariates in the encounter probability model.

Covariate	Covariate description	Relative Importance	Coefficient	SE
L-CST	Larval stage, cross-shore transport	0.326	-0.028	0.062
E-CST	Egg stage, cross-shore transport	0.337	0.036	0.074
P-CST	Pelagic juvenile stage, cross-shore transport	0.286	-0.016	0.053
L-RET	Larval stage, retention	0.286	0.007	0.025
P-RET	Pelagic juvenile stage, retention	0.302	-0.011	0.029
E-LST*lat	Egg stage, interaction between long-shore transport and latitude	0.27	0.038	0.871

Table 5. Models for the positive catch of age-0 recruits with a $\Delta AIC < 2$. Terms correspond to the terms in Table 1.

Candidate Model	ΔAIC
Pass + Depth + SSB-coast + PS-BT + L-NPP + P-ST	0
Pass + Depth + SSB-coast + L-NPP + P-ST	0.58
Pass + Depth + SSB-coast + P-NPP	0.92
Pass + Depth + SSB-coast + PS-BT + P-NPP	0.92
Pass + Depth + SSB-prov + L-NPP + P-ST	0.93
Pass + Depth + SSB-coast + PS-BT + P-NPP + L-ST	1.26
Pass + Depth + SSB-prov + PS-BT + L-NPP + P-ST	1.35
Pass + Depth + SSB-prov + L-NPP + P-NPP	1.54
Pass + Depth + SSB-coast + P-NPP + L-ST	1.57
Pass + Depth + SSB-prov + L-NPP	1.58
Pass + Depth + SSB-prov + PS-BT + L-NPP	1.59
Pass + Depth + SSB-coast + P-NPP + L-ST + E-LST*lat	1.7
Pass + Depth + SSB-coast + PS-BT + L-NPP + L-ST + P-ST	1.71
Pass + Depth + SSB-coast + PS-BT + L-NPP + P-NPP + L-ST	1.75
Pass + Depth + SSB-coast + PS-BT + L-NPP + L-ST	1.79
Pass + Depth + L-ST + E-LST*lat	1.81
Pass + Depth + P-NPP + L-ST + E-LST*lat	1.82
Pass + Depth + SSB-coast + PS-BT + P-NPP + L-ST + E-LST*lat	1.82

Pass + Depth + SSB-prov + L-NPP + P-ST + E-LST*lat	1.88
Pass + Depth + SSB-prov + PS-BT + L-NPP + P-NPP	1.95
Pass + Depth + SSB-coast + PS-BT + L-NPP + P-NPP + P-ST	1.95
Pass + Depth + SSB-prov + P-NPP + L-ST + E-LST*lat	1.96
Pass + Depth + SSB-coast + PS-BT + R-BT + L-NPP + P-ST	1.96
Pass + Depth + SSB-coast + PS-BT + P-NPP + P-ST	2
Pass + Depth + SSB-coast + PS-BT + L-NPP + P-ST + E-LST*lat	2

Table 6. Relative importance, model-averaged coefficient estimates, and model-averaged coefficient SE estimates for the covariates in the positive catch of age-0 recruits models. Each covariate is presented three times, where its relative importance, coefficient estimate, and coefficient SE is calculated separately for each of the three SSB inclusion structures compared to the null model.

Covariate	Covariate Description	Relative Importance			Coefficient (SE)		
		SSB-coast	SSB-prov	SSB-svc	SSB-coast	SSB-prov	SSB-svc
SSB-coast	Spawning stock biomass (coastwide)	0.691	NA	NA	0.114 (0.105)	NA	NA
SSB-prov	Spawning stock biomass (by province)	NA	0.608	NA	NA	0.125 (0.139)	NA
SSB-svc	Spawning stock biomass (spatially-varying covariate)	NA	NA	0.277	NA	NA	0.046 (0.076)
PS-BT	Pre-spawning stage, bottom temperature	0.453	0.364	0.355	-0.05 (0.079)	-0.027 (0.052)	-0.021 (0.047)
E-LST*lat	Egg stage, interaction between long-shore transport and latitude	0.387	0.449	0.421	-0.32 (0.669)	-0.583 (0.929)	-0.414 (0.759)
L-NPP	Larval stage, net primary productivity	0.471	0.56	0.423	0.062 (0.092)	0.107 (0.132)	0.049 (0.082)

L-ST	Larval stage, surface temperature	0.511	0.497	0.576	-0.079 (0.108)	-0.078 (0.112)	-0.103 (0.121)
P-NPP	Pelagic juvenile stage, net primary productivity	0.508	0.466	0.482	0.066 (0.092)	0.055 (0.084)	0.059 (0.087)
P-ST	Pelagic juvenile stage, surface temperature	0.482	0.445	0.456	-0.061 (0.095)	-0.049 (0.084)	-0.052 (0.089)
R-BT	Benthic recruit stage, bottom temperature	0.306	0.311	0.32	0.008 (0.042)	0.016 (0.048)	0.016 (0.049)

4.5 Discussion

In this study, we found that the spatial distribution and abundance of age-0 Sablefish recruits is characterized by high interannual variability and that the presence or absence of age-0 recruits is poorly explained by oceanographic covariates. However, we found evidence of a link between SSB and age-0 recruit catch, with the strongest evidence for a link between coastwide SSB and catch. Furthermore, we found evidence of higher recruitment with lower preconditioning temperatures for spawning females, cooler surface temperatures for larval and juvenile Sablefish, and higher net primary productivity. Overall, this supports our hypothesis that finer scale spatial processes influence recruitment, and that while the distribution of eventual recruits is a highly stochastic and unpredictable process, recruit abundance may relate to oceanographic covariates.

In our positive catch model, our top models indicated strong support for the inclusion of oceanographic covariates, as well as an effect of spawning stock biomass either at the coastwide or biogeographic province scale (Table 6). Previous studies of oceanographic drivers of recruitment in Sablefish in the California Current used annual deviations from the stock recruitment curve as their response variable (Tolimieri et al., 2018; Tolimieri & Haltuch, 2023; Wetzel et al., 2025), making their results more comparable to our positive catch model than our encounter probability model. As in Tolimieri et al. (2018), we found evidence for a negative effect of temperature on the positive catch of age-0 recruits during both the preconditioning stage and the larval stage. However, this analysis was recently re-done with a longer time series in the most recent U.S. West Coast Sablefish stock assessment, and these relationships no longer existed (Wetzel et al., 2025). This new analysis found the greatest support for a negative relationship with cross-shelf surface transport during the pelagic juvenile stage and a positive relationship with cross-shelf transport from 0-250 m depth during the benthic juvenile stage (Wetzel et al., 2025). The contrasting direction of effects was interpreted as surface cross-shelf transport during the pelagic juvenile stage serving as a proxy for upwelling, whereas cross-shelf transport through the water column during the benthic juvenile stage helped individuals recruit to suitable habitat. We did find an association between higher NPP (likely driven by upwelling) and catch of recruits, aligning with their finding of a negative relationship with cross-shelf surface

transport during the pelagic juvenile stage. However, other transport coefficients used in these past analyses are hard to directly compare to our mostly null findings for transport effects in our presence/absence model.

Sablefish recruitment drivers have also been investigated in the northern part of their range that extends up to the Aleutian Islands and the Bering Sea. With increasing surface temperatures throughout the Northeast Pacific beginning with the warm blob of 2014-2016 (Cavole et al., 2016), the role of temperature has been a major focus. In Alaska, higher Sablefish recruitment has been associated with warmer sea surface temperatures, with extremely high recruitment coinciding with the warm blob in the Northeast Pacific (Goethel et al., 2023). Previous analyses have suggested that with adequate prey, juvenile Sablefish may thrive with warming oceans (Krieger et al., 2020). While this initially appears to contrast with our finding of higher age-0 recruit catch occurring in areas with cooler surface temperatures in the California Current, there are important differences between these systems that may explain these differing conclusions. First, as a lower latitude system, the California Current is typically warmer than the Gulf of Alaska, suggesting that cool temperatures in the California Current may be similar to warm temperatures in the Gulf of Alaska. Second, while both systems are highly biologically productive, productivity in the California Current is linked to the upwelling of cool, nutrient-rich waters (Checkley & Barth, 2009), while the direction of the dominant surface winds in the Alaska Current typically lead to downwelling (Weingartner et al., 2009). As such, there is a negative relationship between food availability and temperature in the California Current but not in the Alaska Current. However, even within the California Current, the effect of temperature may be spatially variable, as in the Northern California Current, the density of pelagic juvenile Sablefish has been positively associated with surface temperature (Daly et al., 2024).

Our encounter probability model had relatively low support for the inclusion of the candidate covariates, instead supporting a best fit model where spatial and spatiotemporal random effects characterized a variable recruitment landscape. The California Current is a highly dynamic system, with features like fronts and eddies frequently forming and subsiding (Kurian et al., 2011), jets originating from coastal upwelling (Barth et al., 2000), and many other sources of variability operating at various timescales (Checkley & Barth, 2009). It is therefore perhaps unsurprising that there was little support for our summaries of transport patterns and water retention that only captured broad patterns over sections of the life history (Table 1) in predicting the presence or absence of age-0 Sablefish recruits. However, a promising future direction for this work could be modeling the dispersal of Sablefish eggs and larvae using Lagrangian analysis, where the movement of virtual particles is driven by ocean circulation models (Van Sebille et al., 2018). These analyses can integrate larval behavior, allowing realistic dispersal patterns to be modeled (Drake et al., 2013; Engel et al., 2025). Starting with the distribution of spawning females estimated here and incorporating the densities of Sablefish eggs and larvae

(McFarlane & Beamish, 1992), their changing position in the water column with developmental stage (Moser et al., 1994), and their durations in each stage (Tolimieri et al., 2018), we could estimate larval dispersal in each year. The final distribution of larvae from a Lagrangian analysis could be used as a predictor of presence/absence in this modeling framework and also be evaluated as an alternative way to link SSB to age-0 recruits.

For the effects of covariates on both the encounter probability and positive catch of age-0 recruits, alternative ways of processing the data or modeling its effect could also be explored in future analyses. Temperature could be processed as degree days, or the cumulative temperature above a threshold value (Chezik et al., 2014), to explore cumulative effects on growth or pre-conditioning spawning females. Sablefish also exhibit an optimum temperature range for growth (Krieger et al., 2020), suggesting that non-linear and non-monotonic effects of temperature or other covariates like depth could be explored within these models. Interactions between covariates, such as temperature and NPP, could also be explored to investigate hypothesized food limitation at higher temperatures.

Another future direction is a deeper investigation of alternative model structures for the observations of age-0 Sablefish. Specifically, our use of a hurdle model does not differentiate the different sources of zeros in our trawl survey dataset (Blasco-Moreno et al., 2019), and assumes that the zeros are all “true zeros” that emerge from the same process (Martin et al., 2005). These “true zeros” emerge due to either random chance or the ecological processes of interest (i.e., our covariates for the encounter probability model) and are differentiated from “false zeros” that occur either due to observer error or design error (Zuur et al., 2009). However, this assumption may be violated in our trawl survey dataset as some of the zeros may indeed be these “false zeros” originating from the design of the survey. For example, false zeros may originate from the subsampling protocol, wherein a maximum of only 20 individual Sablefish are measured (thus leading to the potential for age-0 fish to be missed in large tows), or the timing of the survey (wherein potentially suitable habitat may be trawled in the summer prior to the settling of age-0 recruits on the benthos in the fall). Furthermore, the shallowest depth surveyed by the WCGBTS is 55 m, with previous studies finding the highest density of recent recruits around 25 m (Callahan et al., 2021). In future model structures, zero-inflated mixture models could be used to model “true” and “false” zeros coming from different processes, with “true zeros” originating from the count process and “false zeros” being modeled separately with a binomial model. As failing to account for the source of zeros can hinder our ability to detect relationships (Martin et al., 2005), a further exploration of alternative models for our observation process may reveal alternative effects of the environment and SSB on recruitment.

Understanding the drivers of recruitment variability remains one of the great challenges of fisheries science. Recruitment analyses typically investigate correlations between different

covariates and recruitment at the stock level, thereby ignoring the mechanisms governing recruitment at finer spatial scales. In this study, we suggest an alternative way of investigating the connections between stock, environment, and recruitment in a spatially explicit way, connecting these covariates to recruitment at a local scale. While many opportunities exist to refine the analytical approach presented here, we nonetheless found connections between Sablefish recruitment and local processes, including that Sablefish recruitment is higher in regions that are cooler and more productive. Future refinements of this work with increased ecological realism could help elucidate the variable patterns of recruitment hotspots and inform juvenile Sablefish bycatch avoidance measures and recruitment forecasts in stock assessments. More generally, this framework for studying recruitment could be used to investigate mechanisms driving the recruitment of marine fishes in ecosystems where recent recruits are captured by fisheries surveys.

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4.7 References

- Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, 19(6), 716–723.
- Anderson, J. T. (1988). A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. *Journal of Northwest Atlantic Fishery Science*, 8, 55–66.
- Anderson, S. C., Ward, E. J., English, P. A., & Barnett, L. A. K. (2022). sdmTMB: an R package for fast, flexible, and user-friendly generalized linear mixed effects models with spatial and spatiotemporal random fields. *bioRxiv*, 2022.03.24, 1–17.
- Báez, J. C., Gimeno, L., & Real, R. (2021). North Atlantic Oscillation and fisheries management during global climate change. *Reviews in Fish Biology and Fisheries*, 31(2), 319–336. <https://doi.org/10.1007/s11160-021-09645-z>
- Bailey, K. M., & Houde, E. D. (1989). Predation on eggs and larvae of marine fishes and the recruitment problem. In *Advances in marine biology* (Vol. 25, pp. 1–83). Elsevier.
- Barth, J. A., Pierce, S. D., & Smith, R. L. (2000). A separating coastal upwelling jet at Cape Blanco, Oregon and its connection to the California Current System. *Deep Sea Research Part II: Topical Studies in Oceanography*, 47(5–6), 783–810.

- Beamish, R. J., & Chilton, D. E. (1982). Preliminary evaluation of a method to determine the age of sablefish (*Anoplopoma fimbria*). *Canadian Journal of Fisheries and Aquatic Sciences*, 39(2), 277–287.
- Blasco-Moreno, A., Pérez-Casany, M., Puig, P., Morante, M., & Castells, E. (2019). What does a zero mean? Understanding false, random and structural zeros in ecology. *Methods in Ecology and Evolution*, 10(7), 949–959. <https://doi.org/10.1111/2041-210X.13185>
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. Springer.
- Callahan, M. W., Beaudreau, A. H., Heintz, R. A., Mueter, F. J., & Rogers, M. C. (2021). Temporal and Age-Based Variation in Juvenile Sablefish Diet Composition and Quality: Inferences from Stomach Contents and Stable Isotopes. *Marine and Coastal Fisheries*, 13(4), 396–412. <https://doi.org/10.1002/mcf2.10173>
- Cavole, L. M., Demko, A. M., Diner, R. E., Giddings, A., Koester, I., Pagniello, C. M. L. S., Paulsen, M. L., Ramirez-Valdez, A., Schwenck, S. M., Yen, N. K., Zill, M. E., & Franks, P. J. S. (2016). Biological impacts of the 2013–2015 warm-water anomaly in the northeast Pacific: Winners, Losers, and the Future. *Oceanography*, 29(2), 273–285. <https://doi.org/10.5670/oceanog.2016.32>
- Checkley, D. M., & Barth, J. A. (2009). Patterns and processes in the California Current System. *Progress in Oceanography*, 83(1–4), 49–64. <https://doi.org/10.1016/j.pocean.2009.07.028>
- Chezik, K. A., Lester, N. P., & Venturelli, P. A. (2014). Fish growth and degree-days I: selecting a base temperature for a within-population study. *Canadian Journal of Fisheries and Aquatic Sciences*, 71(1), 47–55.
- Daly, E. A., Chasco, B. E., Morgan, C. A., Burke, B. J., Osborne, K. E., & Draper, D. L. (2024). Implications of increased spatial and trophic overlap between juvenile Pacific salmon and Sablefish in the northern California Current. *Marine and Coastal Fisheries*, 16(6). <https://doi.org/10.1002/mcf2.10325>
- Drake, P. T., Edwards, C. A., Morgan, S. G., & Dever, E. P. (2013). Influence of larval behavior on transport and population connectivity in a realistic simulation of the California Current System. *Journal of Marine Research*, 71(4), 317–350. <https://doi.org/10.1357/002224013808877099>
- Engel, L., Premathilake, L., Barrier, N., Khangaonkar, T., & Garavelli, L. (2025). Larval connectivity for European green crab management in the Salish Sea and surrounding waters. *Marine Ecology Progress Series*, 754, 77–92. <https://doi.org/10.3354/meps14778>
- E.U. Copernicus Marine Service Information (CMEMS). (2026a). *Global Ocean Biogeochemistry Hindcast* (Marine Data Store (MDS) <https://doi.org/10.48670/moi-00019>).
- E.U. Copernicus Marine Service Information (CMEMS). (2026b). *GLORYS12V1* (Marine Data Store (MDS) <https://doi.org/10.48670/moi-00021>).

- Fedder, M. L., Darby, A., Oken, K., & Tolimieri, N. (2026). Stage-Specific Indicators of Northern Yellowtail Rockfish (*Sebastes flavidus*) Recruitment in the California Current Ecosystem. *Fisheries Oceanography*, fog.70041. <https://doi.org/10.1111/fog.70041>
- Goethel, D. R., Hanselman, D., Rodgveller, C., Echave, K., Williams, B., Shotwell, S., Sullivan, J., Hulson, P., Malecha, P., & Siwicke, K. (2023). Assessment of the sablefish stock in Alaska. *North Pacific Fishery Management Council: Anchorage, AK, USA*.
- Grueber, C. E., Nakagawa, S., Laws, R. J., & Jamieson, I. G. (2011). Multimodel inference in ecology and evolution: Challenges and solutions: Multimodel inference. *Journal of Evolutionary Biology*, 24(4), 699–711. <https://doi.org/10.1111/j.1420-9101.2010.02210.x>
- Guzmán, J. M., Luckenbach, J. A., Middleton, M. A., Masee, K. C., Jensen, C., Goetz, F. W., Jasonowicz, A. J., & Swanson, P. (2017). Reproductive life history of sablefish (*Anoplopoma fimbria*) from the U.S. Washington coast. *PLOS ONE*, 12(9), e0184413. <https://doi.org/10.1371/journal.pone.0184413>
- Hamer, P. A., & Jenkins, G. P. (2004). High levels of spatial and temporal recruitment variability in the temperate sparid *Pagrus auratus*. *Marine and Freshwater Research*, 55(7), 663–673.
- Head, M. A., Keller, A. A., & Bradburn, M. (2014). Maturity and growth of sablefish, *Anoplopoma fimbria*, along the U.S. West Coast. *Fisheries Research*, 159, 56–67. <https://doi.org/10.1016/j.fishres.2014.05.007>
- Hilborn, R., & Walters, C. J. (1992). *Quantitative fisheries stock assessment: Choice, dynamics and uncertainty*. Springer Science & Business Media.
- Hjort, J. (1914). Fluctuations in the great fisheries of Northern Europe. *Rapports et Procès-Verbaux*, 20, 1–228.
- Iles, T. D., & Sinclair, M. (1982). Atlantic herring: Stock discreteness and abundance. *Science*, 215(4533), 627–633.
- Jean-Michel, L., Eric, G., Romain, B.-B., Gilles, G., Angélique, M., Marie, D., Clément, B., Mathieu, H., Olivier, L. G., Charly, R., Tony, C., Charles-Emmanuel, T., Florent, G., Giovanni, R., Mounir, B., Yann, D., & Pierre-Yves, L. T. (2021). The Copernicus Global 1/12° Oceanic and Sea Ice GLORYS12 Reanalysis. *Frontiers in Earth Science*, 9, 698876. <https://doi.org/10.3389/feart.2021.698876>
- Keller, A. A., Wallace, J. R., & Methot, R. D. (2017). The Northwest Fisheries Science Center's West Coast Groundfish Bottom Trawl Survey: History, Design, and Description. *NOAA Technical Memorandum*, (January), 47. <https://doi.org/10.7289/V5/TM-NWFSC-136>
- Kendall Jr, A. W., & Matarese, A. C. (1987). Biology of eggs, larvae, and epipelagic juveniles of sablefish, *Anoplopoma fimbria*, in relation to their potential use in management. *Mar. Fish. Rev*, 49(1), 1–13.
- Krieger, J. R., Beaudreau, A. H., Heintz, R. A., & Callahan, M. W. (2020). Growth of young-of-year sablefish (*Anoplopoma fimbria*) in response to temperature and prey quality:

- Insights from a life stage specific bioenergetics model. *Journal of Experimental Marine Biology and Ecology*, 526, 151340. <https://doi.org/10.1016/j.jembe.2020.151340>
- Kurian, J., Colas, F., Capet, X., McWilliams, J. C., & Chelton, D. B. (2011). Eddy properties in the California Current System. *Journal of Geophysical Research*, 116(C8), C08027. <https://doi.org/10.1029/2010JC006895>
- Leising, A., Hunsicker, M., Tolimieri, N., Williams, G., & Harley, A. (2024). 2023-2024 CALIFORNIA CURRENT ECOSYSTEM STATUS REPORT A report of the NOAA California Current Integrated Ecosystem.
- Lilley, R. J., & Unsworth, R. K. (2014). Atlantic Cod (*Gadus morhua*) benefits from the availability of seagrass (*Zostera marina*) nursery habitat. *Global Ecology and Conservation*, 2, 367–377.
- Lindegren, M., & Checkley, D. M. (2013). Temperature dependence of Pacific sardine (*Sardinops sagax*) recruitment in the California Current Ecosystem revisited and revised. *Canadian Journal of Fisheries and Aquatic Sciences*, 70(2), 245–252. <https://doi.org/10.1139/cjfas-2012-0211>
- Litzow, M. A., Ciannelli, L., Puerta, P., Wettstein, J. J., Rykaczewski, R. R., & Opiekun, M. (2019). Nonstationary environmental and community relationships in the North Pacific Ocean. *Ecology*, 100(8), 1–8. <https://doi.org/10.1002/ecy.2760>
- Martin, T. G., Wintle, B. A., Rhodes, J. R., Kuhnert, P. M., Field, S. A., Low-Choy, S. J., Tyre, A. J., & Possingham, H. P. (2005). Zero tolerance ecology: Improving ecological inference by modelling the source of zero observations. *Ecology Letters*, 8(11), 1235–1246. <https://doi.org/10.1111/j.1461-0248.2005.00826.x>
- McFarlane, G. A., & Beamish, R. J. (1992). Climatic Influence Linking Copepod Production with Strong Year-Classes in Sablefish, *Anoplopoma fimbria*. *Canadian Journal of Fisheries and Aquatic Sciences*, 49(4), 743–753. <https://doi.org/10.1139/f92-083>
- Miller, T. J., Crowder, L. B., Rice, J. A., & Marschall, E. A. (1988). Larval size and recruitment mechanisms in fishes: Toward a conceptual framework. *Canadian Journal of Fisheries and Aquatic Sciences*, 45(9), 1657–1670.
- Moser, H. G., Chakter, R. L., Smith, P. E., Lo, N. C. H., & Ambrose, D. A. (1994). EARLY LIFE HISTORY OF SABLEFISH, *ANOPOLOPOMA FIMBRIA*, OFF WASHINGTON, OREGON, AND CALIFORNIA, WITH APPLICATION TO BIOMASS ESTIMATION. 35.
- Myers, R. A. (1998). When do environment-recruitment correlations work? *Reviews in Fish Biology and Fisheries*, 8(3), 285–305. <https://doi.org/10.1023/A:1008828730759>
- Oken, K. L., Taylor, I. G., Feddern, M. L., & Whitman, A. D. (2025). Status of the Yellowtail Rockfish Stock off the U.S. West Coast North of 40°10' in 2025. *Pacific Fishery Management Council, Portland, Oregon*, 175 p.
- Rijnsdorp, A., Van Beek, F., Flatman, S., Millner, R., Riley, J., Giret, M., & De Clerck, R. (1992). Recruitment of sole stocks, *Solea solea* (L.), in the Northeast Atlantic. *Netherlands Journal of Sea Research*, 29(1–3), 173–192.

- Rodgveller, C. J., Stark, J. W., Echave, K. B., & Hulson, P.-J. F. (2016). Age at maturity, skipped spawning, and fecundity of female sablefish (*Anoplopoma fimbria*) during the spawning season. *Fishery Bulletin*, 114(1), 89–102. <https://doi.org/10.7755/FB.114.1.8>
- Rutecki, T. L., & Varosi, E. (1997). Distribution, age, and growth of juvenile sablefish, *Anoplopoma fimbria*, in Southeast Alaska. *NOAA Technical Report NMFS*, 130, 45–54.
- Schroeder, I. D., Santora, J. A., Bograd, S. J., Hazen, E. L., Sakuma, K. M., Moore, A. M., Edwards, C. A., Wells, B. K., & Field, J. C. (2019). Source water variability as a driver of rockfish recruitment in the California current ecosystem: Implications for climate change and fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences*, 76(6), 950–960. <https://doi.org/10.1139/cjfas-2017-0480>
- Sigler, M., Rutecki, T., Courtney, D., Karinen, J., & Yang, M. (2001). Young of the year sablefish abundance, growth, and diet in the Gulf of Alaska. *Alaska Fishery Research Bulletin*, 8(1), 57–70.
- Sogard, S. M. (2011). Interannual variability in growth rates of early juvenile sablefish and the role of environmental factors. *Bulletin of Marine Science*, 87(4), 857–872.
- Szuwalski, C. S., Vert-pre, K. A., Punt, A. E., Branch, T. A., & Hilborn, R. (2015). *Examining common assumptions about recruitment: A meta-analysis of recruitment dynamics for worldwide marine fisheries*. 633–648. <https://doi.org/10.1111/faf.12083>
- Tolimieri, N., & Haltuch, M. A. (2023). Sea-level index of recruitment variability improves assessment model performance for sablefish *Anoplopoma fimbria*. *Canadian Journal of Fisheries and Aquatic Sciences*, 80(6), 1006–1016. <https://doi.org/10.1139/cjfas-2022-0238>
- Tolimieri, N., Haltuch, M. A., Lee, Q., Jacox, M. G., & Bograd, S. J. (2018). Oceanographic drivers of sablefish recruitment in the California Current. *Fisheries Oceanography*, 27(5), 458–474. <https://doi.org/10.1111/fog.12266>
- Tolimieri, N., Wallace, J., & Haltuch, M. (2020). Spatio-temporal patterns in juvenile habitat for 13 groundfishes in the California Current Ecosystem. *PLOS ONE*, 15(8), e0237996. <https://doi.org/10.1371/journal.pone.0237996>
- Vaida, F., & Blanchard, S. (2005). Conditional Akaike information for mixed effects models. *Corrado Lagazio, Marco Marchi (Eds)*, 101.
- Vallis, G. K. (2017). *Atmospheric and oceanic fluid dynamics*. Cambridge University Press.
- Van Sebille, E., Griffies, S. M., Abernathey, R., Adams, T. P., Berloff, P., Biastoch, A., Blanke, B., Chassignet, E. P., Cheng, Y., Cotter, C. J., Deleersnijder, E., Döös, K., Drake, H. F., Drijfhout, S., Gary, S. F., Heemink, A. W., Kjellsson, J., Koszalka, I. M., Lange, M., ... Zika, J. D. (2018). Lagrangian ocean analysis: Fundamentals and practices. *Ocean Modelling*, 121, 49–75. <https://doi.org/10.1016/j.ocemod.2017.11.008>
- Ward, E. J., & Tolimieri, N. (2025). Advancing spatially explicit fisheries management with age-specific species distribution models. *Canadian Journal of Fisheries and Aquatic Sciences*, 82, 1–11. <https://doi.org/10.1139/cjfas-2025-0065>

- Weingartner, T., Eisner, L., Eckert, G. L., & Danielson, S. (2009). Southeast Alaska: Oceanographic habitats and linkages. *Journal of Biogeography*, 36(3), 387–400. <https://doi.org/10.1111/j.1365-2699.2008.01994.x>
- Wetzel, C. R., Berger, A. M., Barnes, C., Zahner, J. A., Tolimieri, N., Ward, E. J., & Head, M. (2025). Status of the sablefish (*Anoplopoma fimbria*) off the U.S. West Coast in 2025. *Pacific Fisheries Management Council, Portland, Oregon*.
- Zheng, N., Cadigan, N., & Thorson, J. T. (2024). *A note on numerical evaluation of conditional Akaike information for nonlinear mixed-effects models* (arXiv:2411.14185). arXiv. <https://doi.org/10.48550/arXiv.2411.14185>
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R* (Vol. 574). Springer.

Synthesis

Research questions in fisheries conservation span many axes of variability, including the life history strategy of the species of interest, the specific management and conservation concerns, and data availability. This dissertation, which addressed key questions for four separate study species in four separate study systems, spanned many of these axes. Confronted with little existing data but a legal requirement to ascertain the status of an ESA-listed population, Chapter 1 leveraged data-limited fishery assessment methods to estimate the status of threatened Yelloweye Rockfish in Puget Sound. Moving to fresh water, Chapter 2 used a complex movement model to estimate the combined influences of hydropower and temperature on movement decisions by ESA-listed Steelhead in the Columbia River Basin. In Chapter 3, I moved to the pelagic nearshore marine environment, integrating multiple fisheries research surveys to estimate how marine survival of fall Chinook salmon from the interior Columbia River Basin was influenced by spatiotemporal overlap with predators and prey. And finally, in Chapter 4, I took a new approach to the old problem of analyzing drivers of recruitment by modeling the spatial recruitment dynamics of Sablefish. Across the different chapters of this dissertation, a core motivation was to further our understanding of key processes by modeling increased complexity and ecological realism. By investigating research questions that spanned many axes of variability, this dissertation also revealed nuances around how the ecological process being investigated, the life history of the study species in question, and the type of long-term dataset available affects our ability to make conclusions about these processes. It also highlighted the challenges inherent to asking ecological questions of long-term observational datasets and the ubiquity and consequences of assumptions in quantitative ecology.

Fish populations and aquatic communities exhibit considerable variability as a result of multiple ecological processes operating at different temporal and spatial scales. However, research into these processes have often ignored this complexity, and instead relied on statistical analyses that model relationships with convenient proxies instead of the drivers themselves; these resulting relationships exhibit non-stationarity and often break down over time (Myers 1998, Litzow et al. 2019). In this dissertation, a core theme was modeling increased complexity in the mechanisms driving processes, with the goal of understanding how populations respond to changing conditions. Instead of modeling the influence of individual covariates at specific hydroelectric dams in the Columbia River Basin, in Chapter 2 I developed a model of the entire basin to explore how climate and hydropower interact to influence population-level movement patterns and survival. In Chapter 3, I modeled the proximate trophic drivers of salmon marine survival instead of correlating marine survival with basin-scale indices like the Pacific Decadal Oscillation or the North Pacific Gyre Oscillation (Mantua et al. 1997, Di Lorenzo et al. 2008). In Chapter 4, I modeled the relationships between spawning stock, environment, and recruitment in

space and time rather than relying on the bivariate analyses that are traditional in fisheries science (Ricker 1954, Beverton and Holt 1957). In each of these chapters, I demonstrated that increased complexity could be modeled by integrating existing datasets, and that this appreciation of complexity can shed new light on ecological processes of management and conservation concern. By doing this across different study systems, focal species, and datasets, I also demonstrated many of the challenges of modeling ecological complexity.

Although ecological research is traditionally hypothesis-driven, the types of questions that can be asked are also constrained by data availability. Furthermore, ecological processes are generally characterized by a level of complexity that greatly exceeds the temporal, spatial, or taxonomic resolution of the available data. As such, the complexity of research questions in quantitative ecology typically scales with the availability of the data, but simplifying assumptions are nonetheless present in every model (hence Box's aphorism "All models are wrong, but some models are useful"). This was evident throughout this dissertation, especially with the contrast between the first chapter and the latter three. In my first chapter, the paucity of the data (an imperfect catch history and limited demographic data) necessitated both a limited research scope (the relative stock status of ESA-listed Yelloweye Rockfish in Puget Sound) and a number of simplifying assumptions. For example, recruitment was assumed to be deterministic based on a Beverton-Holt stock-recruitment curve, an assumption known to be a significant oversimplification (notably, the entire focus of Chapter 4 is on investigating variability in this process in another species). However, with the appropriate levels of sensitivity testing across various life history parameters, such simplifying assumptions are adequate for some research questions, and are indeed necessary for assessing the world's data-limited fish stocks, which make up the majority of fish populations by number (Costello et al. 2012).

In contrast to Chapter 1, Chapters 2, 3, and 4 were all based on the analysis of data collected for over 20 years in long-term ecological monitoring efforts, which facilitated the asking of more complex questions. These long-term research efforts are key for understanding ecological communities, as long time series can capture responses of the community to perturbations, allow for signals at different scales to be discerned, and provide valuable baselines (Hampton et al. 2019). In my dissertation, the long time series were needed to capture variability in hydrosystem operations, river temperature, and Steelhead movements and survival (Chapter 2); capture variability in the spatial distribution of predators, prey, and juvenile Chinook salmon, as well as the survival of tagged Chinook salmon (Chapter 3); and capture variability in the spatial distribution of Sablefish spawners and recruits and the environmental conditions they encountered (Chapter 4). However, these chapters still required a number of simplifying assumptions, and demonstrated the limits of even these expensive and robust monitoring efforts. Furthermore, they also demonstrated the challenges of asking new questions of data collection efforts originally designed for a different purpose.

Throughout my dissertation, the datasets I analyzed were funded or collected by federal agencies to fulfill obligations either under the Endangered Species Act (ESA) or the Magnuson-Stevens Fishery Conservation and Management Act (MSA). While these laws do include some language that has been used to justify and fund more ecological studies (especially the ESA), that has not been their primary purpose. The consequence of this is that for each chapter, at least some of the datasets I used were collected to answer different questions than the ones I asked in this dissertation. In Chapter 2, the extensive Columbia River Basin PIT-tag monitoring effort was leveraged to model the movements of adult Steelhead, making use of millions of detections around the basin. However, for one of the key questions of the study (how does winter spill affect fallback of adult Steelhead?), the limitations of the PIT tag monitoring infrastructure led to results with high uncertainty. As with fish passage infrastructure in the Columbia River Basin, PIT tag antennas are designed to detect juveniles moving downstream and adults moving upstream – not adults moving downstream. As such, fallback events had to be interpolated from other tag detections, resulting in low confidence in the effect of spill for many populations. In Chapter 3, the three fisheries research surveys that were integrated were each designed to monitor the abundance and distribution of a focal species (juvenile salmon, YOY rockfishes, and adult Pacific hake), not how these focal species interact. The varying spatial footprints of the surveys could be addressed with spatiotemporal models, but the differences in survey timing required the simplifying assumption that these surveys were representative of the distribution of each taxon during the same period of early marine residence by juvenile Chinook salmon. In Chapter 4, the West Coast Groundfish Bottom Trawl Survey (WCGBTS) was designed to monitor the abundance and distribution of dozens of managed groundfish stocks (Keller et al. 2017), not age-0 Sablefish recruits. As a result, the survey depth and timing are poorly aligned with the ecology of benthic age-0 Sablefish recruits. Additionally, the summer survey timing also does not align with the winter spawning of Sablefish, requiring the simplifying assumption that the distribution of mature Sablefish in the summer is representative of their distribution in the winter. For each chapter, the best available data was used to address each question; however, the mismatches between monitoring/survey designs and research questions required both statistical/data processing solutions to these mismatches and assumptions (and a discussion of those assumptions) for those mismatches that could not be addressed analytically.

There is also a distinction between data collection in support of ESA and MSA requirements, as well as a spectrum of data collection in support of populations managed under the same law. For example, while Puget Sound Yelloweye Rockfish (Chapter 1) and Columbia River Steelhead and Chinook salmon (Chapters 2 and 3) are all listed under the ESA, there has been little targeted data collection for Yelloweye Rockfish compared to very intensive monitoring for Columbia River salmonids. Data collection for ESA vs. MSA also differs in that data collection for MSA requirements is often lethal, whereas data collection for ESA-listed species avoids harming or killing any individuals. This makes data collection significantly harder for many ESA-listed species, as can be seen in the comparison of Chapter 1 (ESA-listed Yelloweye Rockfish) and

Chapter 4 (MSA-managed Sablefish). Chapters 3 and 4 also offer an insightful comparison of data collection for ESA vs. MSA requirements. These chapters each study a similar process (survival/recruitment) but with a different core dataset: the Juvenile Salmon and Ocean Ecosystem Survey (JSOES) for Chapter 3 and the West Coast Groundfish Bottom Trawl Survey (WCGBTS) for Chapter 4. The JSOES, funded by the Bonneville Power Administration as part of its requirements for mitigating the impacts of hydropower on ESA-listed anadromous salmonids, has a distinctly ecological focus on the drivers of salmon marine survival which is reflected by the different types of data collected. In contrast, the WCGBTS is designed to provide the best scientific information available to achieve optimum yield for each individual stock under the MSA. The differing purpose of these surveys, driven by different statutory requirements, likely played a role in the clearer conclusions for Chapter 3 than for Chapter 4. Given all of these differences, an interesting thought experiment is to imagine how different data collection would be if Sablefish were ESA-listed instead of MSA-listed.

The California Current has nine different fisheries research surveys (Gallo et al. 2022), making it one of the most data-rich and well-studied large marine ecosystems in the world. The PIT tagging program in the Columbia River Basin has tagged over 57 million salmonids since 1987 (Tenney et al. 2023). And yet, as this dissertation demonstrates, studying ecological processes using these long-term ecological datasets is a challenging endeavor and often still leads to equivocal conclusions. Given that future expansions of long-term data collection are highly unlikely, it is worth discussing the opportunities and limitations of present long-term monitoring efforts for continued ecological study. Maintaining data collection efforts will increase the statistical power of these datasets and provide data on processes under different conditions, for example in studies of salmon survival or Sablefish recruitment. Furthermore, additional years of data for more recently inaugurated surveys like the California Current Ecosystem Survey will allow coastal pelagic species to be included in efforts like Chapter 3. As more data is collected, data management and processing challenges will also increase. This was evident with the aforementioned California Current Ecosystem Survey, as a change in data processing currently precludes the use of the first ten years of the time series. However, longer time series and increased taxonomic resolution will still not allow us to overcome the inherent limitations of studying ecological processes with these long-term observational datasets. Foremost among these is the ever-present issue of pattern and scale in ecology (Levin 1992). Fisheries research surveys typically collect data once per year throughout the range of a stock. In contrast, ecological processes occur on a multitude of spatial and temporal scales that are not captured by these surveys. As such, the process error (or “noise”) in the system that is not captured by these datasets makes it difficult to parse apart ecological drivers. This is perhaps why efforts (such as Chapter 4) to use coarse survey data to study fisheries recruitment, a highly complex and multidimensional process, continually struggle.

A further limitation of these federally run surveys is the restricted spatial scale of these surveys, which often do not match the spatial scale of the process – especially when that process crosses international borders. With the exception of my second chapter, which was the only chapter to focus solely on fresh water, each of my dissertation chapters also was constrained to U.S. waters despite the fact that the ecology was not. Although interior Columbia River Basin juvenile Chinook salmon migrate from U.S. waters north into the waters off of Vancouver Island within a few months of ocean entry, Chapter 3 was restricted to only the U.S. waters due to the spatial footprint of our surveys. Similarly, while Sablefish from the U.S. West Coast to Alaska are a panmictic population (Jasonowicz et al. 2017), Chapter 4 was restricted to the U.S. West Coast because of the different survey designs. These federally run surveys therefore can only capture part of the spatial footprint of ecological processes due to their focus on the national EEZ.

The role of life history in studying ecological processes was also evident in this dissertation, with two chapters focusing on salmonids and two chapters focusing on groundfish. The anadromous salmonid life history, especially the spatial bottlenecks that occur when juveniles outmigrate to the ocean and adults return to fresh water, make these species considerably easier to study than their marine counterparts. It is perhaps unsurprising that core ecological concepts, such as the portfolio effect (Schindler et al. 2010) or the stock-recruit relationship (Ricker 1954) draw upon evidence from salmon populations. In this dissertation, the strength of the conclusions drawn in Chapters 3 and 4, which can each be viewed as a study of survival/recruitment, was influenced by life history. For PIT-tagged salmon, the fact that all adults return to the same river and must pass by the same PIT tag antennas at Bonneville Dam ensures that there is little measurement error in the response variable (survival). In contrast, age-0 Sablefish are distributed all throughout the California Current, with many outside of the depth or geographic range of the trawl survey, and with only a very small fraction of the population observed in the survey. Therefore, the clearer conclusions with regard to drivers of survival in Chapter 3 relative to Chapter 4 are at least partially driven by this difference in life history and ease of study. Similarly, the study of Steelhead movement in Chapter 2 was facilitated by knowing when and where fish were in the Columbia River Basin through tag detections. These types of monitoring efforts that are facilitated by anadromous life histories allow ecological outcomes to be observed more easily than for the marine groundfish species in Chapters 1 and 4.

Both data-poor species (Chapter 1) and the limitations of long-term monitoring data (Chapters 2-4) suggest that finding new data streams may improve our ability to study ecological processes. One example may be the inclusion of local ecological knowledge, such as that of recreational or commercial fishers. For example, interviews with resource users in Puget Sound, primarily recreational fishers, produced abundance time series for Yelloweye Rockfish (Beaudreau and Levin 2014) that could have been included as an index of abundance in our data-limited assessment model for Chapter 1. Fishery management councils throughout the United States are

also exploring ways to collect and integrate more local ecological knowledge, with initiatives currently being considered at the Pacific Fishery Management Council and with other councils already including these in their annual ecosystem status reports (e.g., the Mid-Atlantic Fishery Management Council; Gaichas et al. 2025). Other emerging technologies for providing quantitative ecological data, such as environmental DNA (Shelton et al. 2023) or acoustic data collected by gliders (Greene et al. 2014), may also be able to provide alternative data streams that cannot be collected by shipboard observations due to cost or weather conditions.

Another theme of this dissertation was the use of recently developed methods and computational ecology. In Chapter 2, high-performance computing enabled the estimation of parameters describing the effect of hydropower and environmental covariates from the individual movement histories of tens of thousands of fish. Correlative species distribution models, which are growing in their use and complexity (Thorson 2019, Anderson et al. 2022), facilitated the analyses in both Chapters 3 and 4. In Chapter 3, species distribution models were used to allow datasets from surveys with different designs to be integrated into one statistical framework, thereby allowing these previously disparate sources to “talk” to each other. In Chapter 4, species distribution models were key to characterizing the spatiotemporal distribution of both spawners and age-0 Sablefish recruits and integrating these distributions with oceanographic modeling outputs.

As the amount and variety of data in ecology continues to increase (Hampton et al. 2013), analytical approaches that can integrate these different data types will become increasingly important. However, the utility of increasingly large datasets for studying ecological processes will still be limited by inherent scale mismatches, difficult to study life histories, and the often-differing driving questions for federal agencies and ecologists. In this dissertation, I addressed ecological questions for U.S. West Coast fishes by integrating numerous data types, including tagging data, fishery-independent survey data, oceanographic modeling outputs, stream gage measurements, and remotely sensed ocean properties. My efforts to integrate these existing data sources also tested the frontiers of what these ongoing monitoring programs can tell us about population dynamics and ecological processes. Overall, this dissertation presents new perspectives on longstanding questions of management interest, including how anadromous fish survive and move through modified rivers, what causes major swings in marine survival in salmon, and drivers of fisheries recruitment.

References

Anderson, S. C., E. J. Ward, P. A. English, and L. A. K. Barnett. 2022. sdmTMB: an R package for fast, flexible, and user-friendly generalized linear mixed effects models with spatial and spatiotemporal random fields. *bioRxiv* 2022.03.24:1–17.

- Báez, J. C., L. Gimeno, and R. Real. 2021. North Atlantic Oscillation and fisheries management during global climate change. *Reviews in Fish Biology and Fisheries* 31:319–336.
- Beaudreau, A. H., and P. S. Levin. 2014. Advancing the use of local ecological knowledge for assessing data-poor species in coastal ecosystems. *Ecological Applications* 24:244–256.
- Beverton, R. J. H., and S. J. Holt. 1957. *On the dynamics of exploited fish populations*. Springer Science & Business Media.
- Costello, C., D. Ovando, R. Hilborn, S. D. Gaines, O. Deschenes, and S. E. Lester. 2012. Status and solutions for the world's unassessed fisheries. *Science* 338:517–520.
- Di Lorenzo, E., N. Schneider, K. M. Cobb, P. J. S. Franks, K. Chhak, A. J. Miller, J. C. McWilliams, S. J. Bograd, H. Arango, E. Curchitser, T. M. Powell, and P. Rivière. 2008. North Pacific Gyre Oscillation links ocean climate and ecosystem change. *Geophysical Research Letters* 35:2–7.
- Gaichas, S., J. Caracappa, A. Beet, B. Beltz, G. DePiper, K. Hyde, S. Large, and S. Weisberg. 2025. *State of the Ecosystem 2025: Mid-Atlantic*.
- Gallo, N. D., N. M. Bowlin, A. R. Thompson, E. V. Satterthwaite, B. Brady, and B. X. Semmens. 2022. Fisheries Surveys Are Essential Ocean Observing Programs in a Time of Global Change: A Synthesis of Oceanographic and Ecological Data From U.S. West Coast Fisheries Surveys. *Frontiers in Marine Science* 9:1–18.
- Greene, C. H., E. L. Meyer-Gutbrod, L. P. McGarry, L. C. Hufnagle Jr, D. Chu, S. McClatchie, A. Packer, J.-B. Jung, T. Acker, and H. Dorn. 2014. A wave glider approach to fisheries acoustics: transforming how we monitor the nation's commercial fisheries in the 21st century. *Oceanography* 27:168–174.
- Hampton, S. E., M. D. Scheuerell, M. J. Church, and J. M. Melack. 2019. Long-term perspectives in aquatic research. *Limnology and Oceanography* 64:S2–S10.
- Hampton, S. E., C. A. Strasser, J. J. Tewksbury, W. K. Gram, A. E. Budden, A. L. Batcheller, C. S. Duke, and J. H. Porter. 2013. Big data and the future of ecology. *Frontiers in Ecology and the Environment* 11:156–162.
- Jasonowicz, A. J., F. W. Goetz, G. W. Goetz, and K. M. Nichols. 2017. Love the one you're with: genomic evidence of panmixia in the sablefish (*Anoplopoma fimbria*). *Canadian Journal of Fisheries and Aquatic Sciences* 74:377–387.
- Keller, A. A., J. R. Wallace, and R. D. Methot. 2017. *The Northwest Fisheries Science Center's West Coast Groundfish Bottom Trawl Survey: History, Design, and Description*. NOAA Technical Memorandum:47.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943–1967.
- Litzow, M. A., L. Ciannelli, P. Puerta, J. J. Wettstein, R. R. Rykaczewski, and M. Opiekun. 2019. Nonstationary environmental and community relationships in the North Pacific Ocean. *Ecology* 100:1–8.
- Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society* 78:1069–1080.

- Myers, R. A. 1998. When do environment-recruitment correlations work? *Reviews in Fish Biology and Fisheries* 8:285–305.
- Ricker, W. E. 1954. Stock and recruitment. *Journal of the Fisheries Board of Canada* 11:559–623.
- Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. *Nature* 465:609–612.
- Shelton, A. O., Z. J. Gold, A. J. Jensen, E. D’Agnese, E. Andruszkiewicz Allan, A. Van Cise, R. Gallego, A. Ramón-Laca, M. Garber-Yonts, K. Parsons, and R. P. Kelly. 2023. Toward quantitative metabarcoding. *Ecology* 104:e3906.
- Tenney, J., N. Tancreto, G. Axel, and S. Livingston. 2023. Columbia Basin PIT Tag Information System, 1/1/2023 - 12/31/2023 Annual Report, 1990-080-00.
- Thorson, J. T. 2019. Guidance for decisions using the Vector Autoregressive Spatio-Temporal (VAST) package in stock, ecosystem, habitat and climate assessments. *Fisheries Research* 210:143–161.

Chapter 1 Appendix

Appendix A. Supplementary Methods

Appendix A.1 Commercial catch reconstruction

Total rockfish catches

In 1921, the Washington state legislature established a Department of Fisheries and Game and passed legislation that required quarterly reporting of catches by licensed fishermen for tax purposes (Nye 1982). While efforts were made to monitor catches prior to 1921, this legislation initiated the collection of the first reliable landings statistics. Reporting of statistics on fish landings relied on tracking the payment of taxes on these landings, with catch data reported as various units dependent on the product being sold (e.g. number of fish, cases of canned salmon, sacks of oysters); these data were later converted in poundage (Nye 1982). While this data has known issues, including unreported data due to reliance on taxation, limited spatial resolution, and the possibility of the inclusion of landings from outside Puget Sound (Nye 1982), this data nonetheless represents the best estimates of rockfish landings from Puget Sound until 1935, when the fish ticket system was introduced. This data is only at the resolution of total rockfish catches from Puget Sound, but does include gear information, which is essential for estimating the proportion of these catches that are ESA-listed species.

In 1935, following a year of transition in 1934, the Washington Department of Fisheries (WDF) overhauled the state’s fisheries statistic system (Nye 1982). Laws enacted by the Director of Fisheries required the submission of individual, daily catch records on fish tickets, which

allowed the Department of Fisheries to collect uniform, specific data using a standardized format, rather than the blank tickets that were previously issued. These new fish tickets represented a vast improvement from the previous system of collecting fisheries statistics, which were based on monthly or quarterly reports of the payment of taxes. This data has critical information on catch area and gear type which was the basis of forming catch estimates for Hood Canal and the rest of Puget Sound separately and prorating total rockfish catch to species.

In 1953, the WDF introduced an interview system, which produced further refined estimates of catch starting in 1955. This system was designed to supplement the information obtained from fish tickets through the stationing of biologists at ports of landing, which interviewed captains of fishing vessels on information such as the species caught, area of catch, and discards (Alverson 1957). This new system generated more confidence in statistics of commercial fish catches.

Coinciding with increased effort and catch of groundfish in Puget Sound, the WDF began publishing reports on groundfish catches for 1970 and onwards (Schmitt et al. 1991). These reports summarize data from Fish Receiving Tickets (FRTs), which document landings in pounds and document gear, vessel, date, port of landing, and Marine Fish-Shellfish Management and Catch Reporting Area. FRTs were required to be submitted to the WDF by processors purchasing fish or shellfish from vessels. Landings of rockfishes were not reported by species on FRTs, but the WDF applied species composition data from field samplings of commercial data to prorate the total rockfish catch to individual species.

Since 2004, the WDFW has been using the Fish Ticket Landing System to record commercial catches. Species are recorded at the time of landing; while Yelloweye Rockfish are a reporting category, Bocaccio are included in the “shelf rockfish” reporting category, along with 12 other rockfish species. However, commercial catches for this time period are very low for both Yelloweye Rockfish and Bocaccio (<100 pounds annually) due to a number of significant regulatory changes in the Puget Sound commercial fishery. These regulatory changes include: the prohibition of bottom trawling south of Admiralty Inlet in 1989 and in Admiralty Inlet, the eastern Strait of Juan de Fuca, and the San Juan Islands in 1994; the ban on bottomfish jig and troll gears in the San Juan Islands in 1984 and east of Sekiu in 1992; and an overall 500 pound vessel trip limit for rockfish for trawl gear and 30 pound limit for set line gear in 1998 (Palsson et al. 2009).

Species composition

Starting in 1955, catch statistics report catch of “red snapper” along with “general rockfish.” These catches of “red snapper” are taken to be Yelloweye Rockfish, as “red snapper” was the common name for *S. ruberrimus* during this time period (Kincaid 1919; Smith 1937). Catch statistics of “red snapper” were thus used as Yelloweye Rockfish statistics for 1955-1969. However, outside of reports of “red snapper,” no reliable species composition data exists for commercial rockfish catches prior to 1970. To estimate catches of Yelloweye Rockfish and Bocaccio prior to 1970 (with the previously mentioned exception of Yelloweye Rockfish catch from “red snapper” for 1955-1969), species composition information from Pedersen and Bargmann (1986) by gear type and region was applied to commercial rockfish catches for 1921-1969. Commercial catches from 1921-1933 were based on tax receipts rather than the fish ticket

system that was introduced in 1935, and therefore lack region-specific information. To apply the region-specific catch compositions from Pedersen and Bargmann (1986), the distribution of catch by region from fish ticket data was applied to divide the 1921-1933 catch into regions.

The WDFW has used species composition data from field samples of commercial catch to prorate “total rockfish” commercial catch into species for the years 1970 to the present. Field samples of catch by gear type and region were reported by Pedersen and Bargmann (1986) and were applied to rockfish catches for 1970-1987 (Schmitt et al. 1991). Subsequent to this report, observations of commercial catches were made for 1989, 1990, 1991, and 1993, when the last observations of commercial rockfish compositions were taken (Palsson et al. 2009). By the mid-1990s, landings from the commercial groundfish fishery in Puget Sound were in steep decline and thus field samples of commercial catches were no longer taken. The catch composition data collected in 1989, 1990, 1991, and 1993 were applied to rockfish catches from 1988-2003.

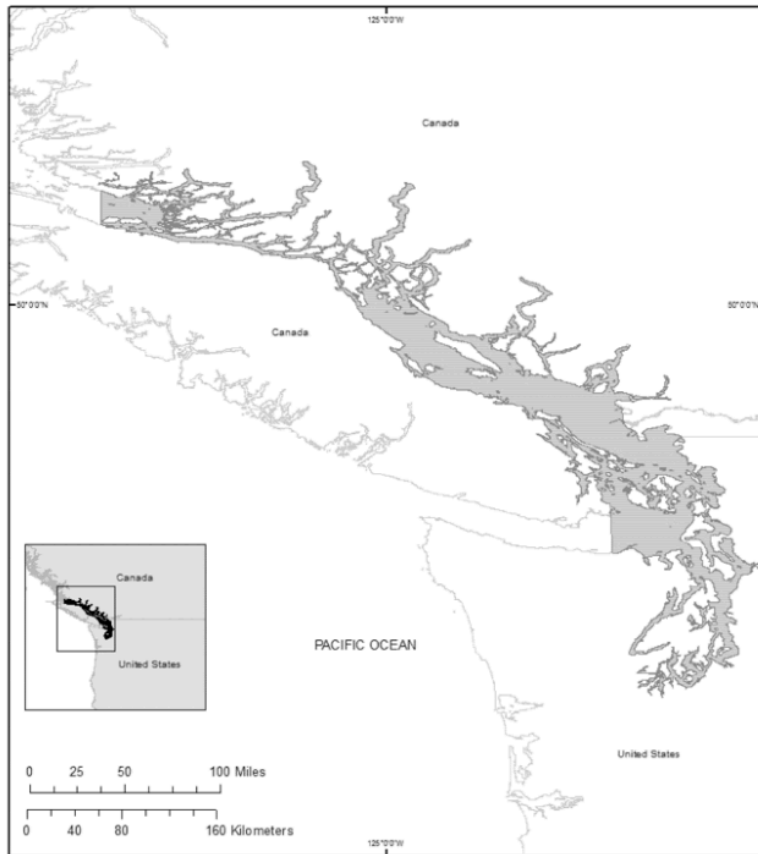
Catch scenarios

1921-1933

For most of the history of removals, a primary source of uncertainty is the mismatch between the DPS boundaries (Fig. 1) and the marine fish management regions by which catch was reported (Fig. 2), with the main area of concern being region 3 (Strait of Juan de Fuca), which is partially inside the DPS. Particularly for Yelloweye Rockfish, this is also an area of high catch. However, because there is no regional catch information for this time period, region 3 cannot be parsed apart for catch scenarios. Therefore, we applied fixed factors to the catch estimates to determine the various catch scenarios:

1. High Catch Scenario: All catch is multiplied by a factor of two.
2. Medium Catch Scenario: Catches are not multiplied by a factor.
3. Low Catch Scenario: Catches are multiplied by a factor of 0.5.

Revised Change to Yelloweye Rockfish DPS Area



DPS Boundary

Yelloweye Rockfish DPS Area

Figure 1. Yelloweye Rockfish DPS boundaries, updated 2017.

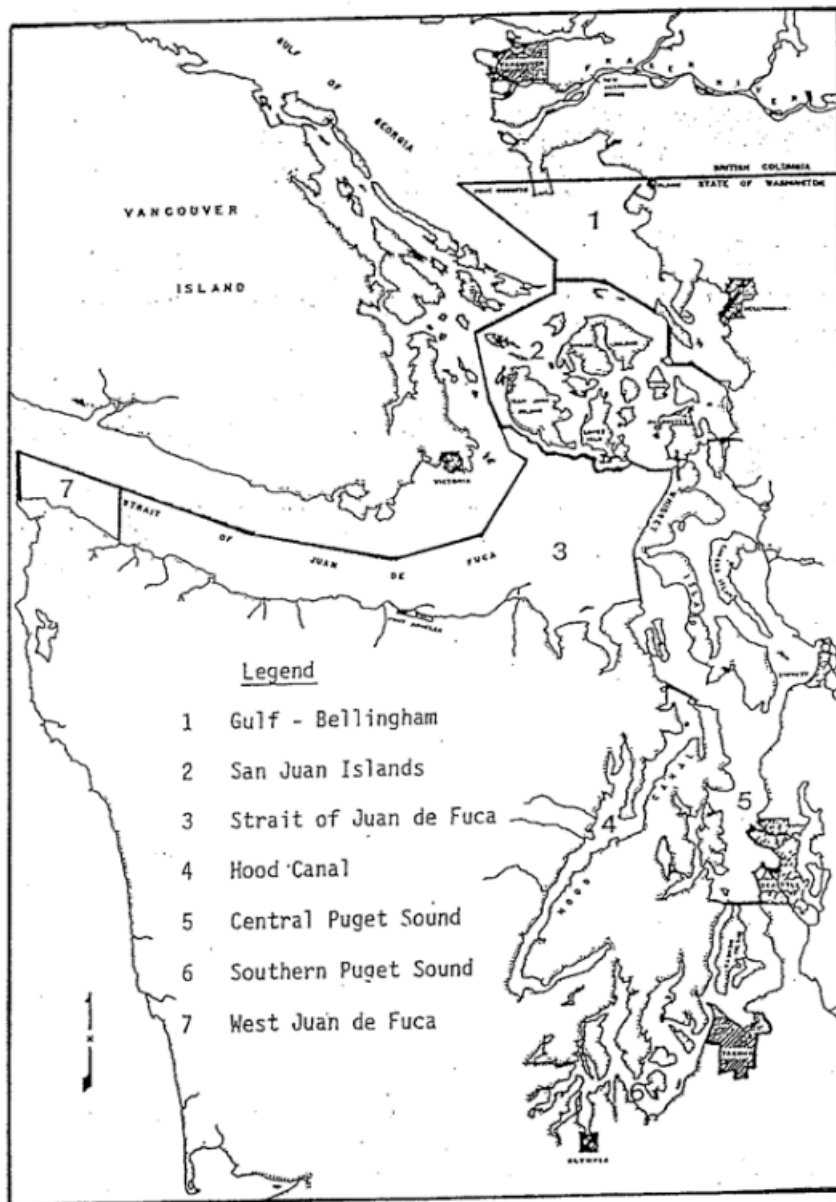


Figure 2. Marine fish management regions of Puget Sound. Map from Schmitt et al. 1991.

1935-1954

Starting in 1935, catch data exists at the level of the marine fish management regions of Puget Sound detailed in Fig. 2. Therefore, for Yelloweye Rockfish and Bocaccio, the catch scenarios for this time period concern the treatment of region 3 (Strait of Juan de Fuca), which is partially inside the DPS. Thus, the catch scenarios for both species for this time period are as follows:

1. **High Catch Scenario:** All catch from the Strait of Juan de Fuca (region 3) is included.
2. **Medium Catch Scenario:** Half of the catch from the Strait of Juan de Fuca (region 3) is included.

3. **Low Catch Scenario:** No catch from the Strait of Juan de Fuca (region 3) is included.

1955-1969

For the catch scenarios for this time period, the source of uncertainty that is addressed is again the mismatch between the DPS boundaries (Fig. 1) and the marine fish management regions by which catch was reported (Fig. 2) with the main area of concern being region 3 (Strait of Juan de Fuca), which is partially inside the DPS. However, because gear types that caught Bocaccio from our catch composition data (Pedersen and Bargmann 1986) were not recorded for this time period in the Strait of Juan de Fuca, there are only catch scenarios for Yelloweye Rockfish, which was reported as “red snapper”:

1. **High Catch Scenario:** All “red snapper” from the Strait of Juan de Fuca (region 3) is included.
2. **Medium Catch Scenario:** Half of the “red snapper” from the Strait of Juan de Fuca (region 3) is included.
3. **Low Catch Scenario:** No “red snapper” from the Strait of Juan de Fuca (region 3) is included.

1970-2003

For the catch scenarios for this time period, the source of uncertainty that is addressed is again the mismatch between the DPS boundaries (Fig. 1) and the marine fish management regions by which catch was reported (Fig. 2) with the main area of concern being region 3 (Strait of Juan de Fuca), which is partially inside the DPS. Thus, the catch scenarios for this time period are as follows:

1. **High Catch Scenario:** All catch from the Strait of Juan de Fuca (region 3) is included.
2. **Medium Catch Scenario:** Half of the catch from the Strait of Juan de Fuca (region 3) is included.
3. **Low Catch Scenario:** No catch from the Strait of Juan de Fuca (region 3) is included.

2004-2020

For Yelloweye Rockfish, there are no catch scenarios for this period, as the WDFW has been tracking commercial landings of this species. However, for Bocaccio, the catch scenarios concern the proportion of the “shelf rockfish” category that is estimated to be Bocaccio. While no catch composition data exists for the “shelf rockfish” category from Puget Sound for this time period, anecdotal evidence suggests that Bocaccio are very rare; experienced field samplers have not encountered them in over 30 years (Greg Bargmann, pers. comm.). Therefore, the catch scenarios are as follows:

1. **High Catch Scenario:** 5% of the “shelf rockfish” catch is Bocaccio.
2. **Medium Catch Scenario:** 0% of the “shelf rockfish” catch is Bocaccio.
3. **Low Catch Scenario:** 0% of the “shelf rockfish” catch is Bocaccio.

Catch scenarios combined

When all of the catch scenarios are combined, the commercial catch data for Yelloweye Rockfish shows two primary periods of catches in the 1940's and 1970's for the Hood canal population (Fig. 3), while catches of the non-Hood Canal population were largest from the mid-1970s to the mid-1990s (Fig. 4). For Bocaccio, the commercial catch is highest in the late 1970s to early 1980s (Fig. 5). For all three species, there is also higher catch that starts during World War II and then tapers off in the 1950s.

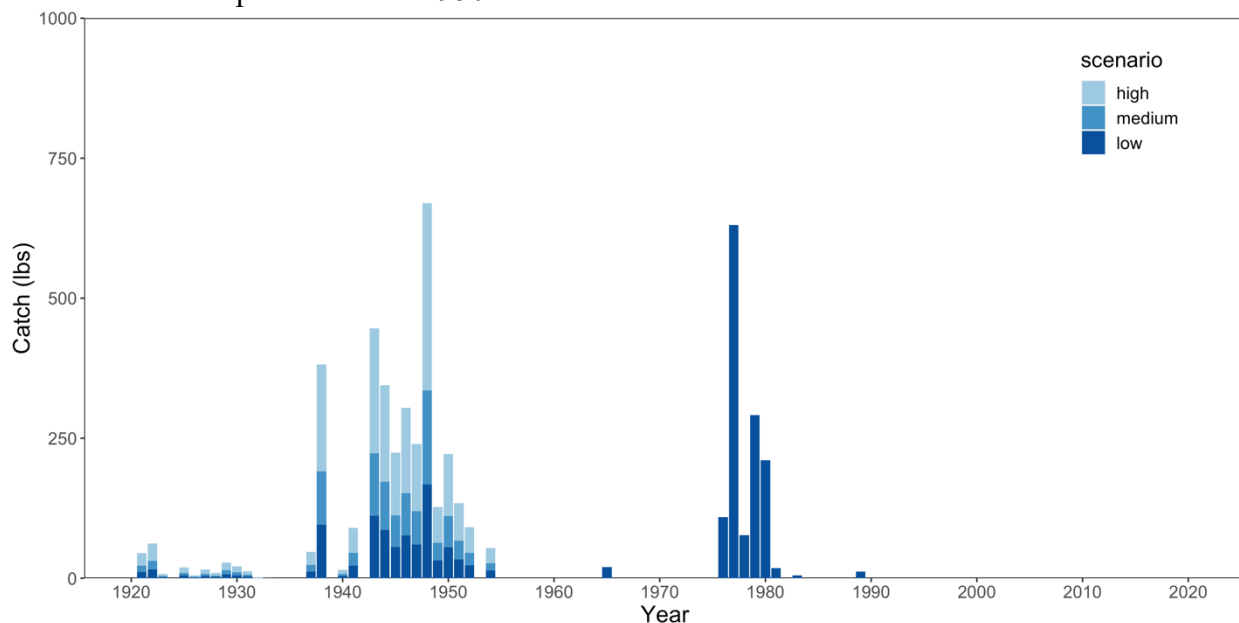


Figure 3. Hood Canal population Yelloweye Rockfish commercial catch. For the catch scenarios, the stacked bars show the differences between the different catch scenarios, such that the high catch scenario is the sum of all three stacked bars.

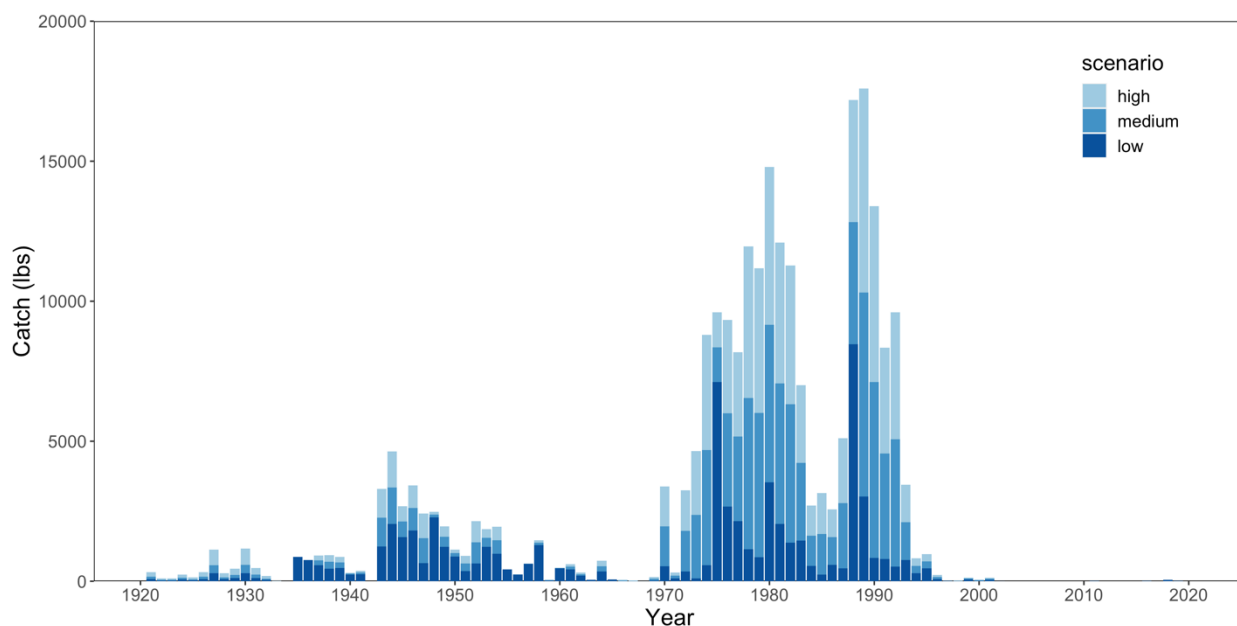


Figure 4. Non-Hood Canal population Yelloweye Rockfish commercial catch for the U.S. portion of the DPS. For the catch scenarios, the stacked bars show the differences between the different catch scenarios, such that the high catch scenario is the sum of all three stacked bars.

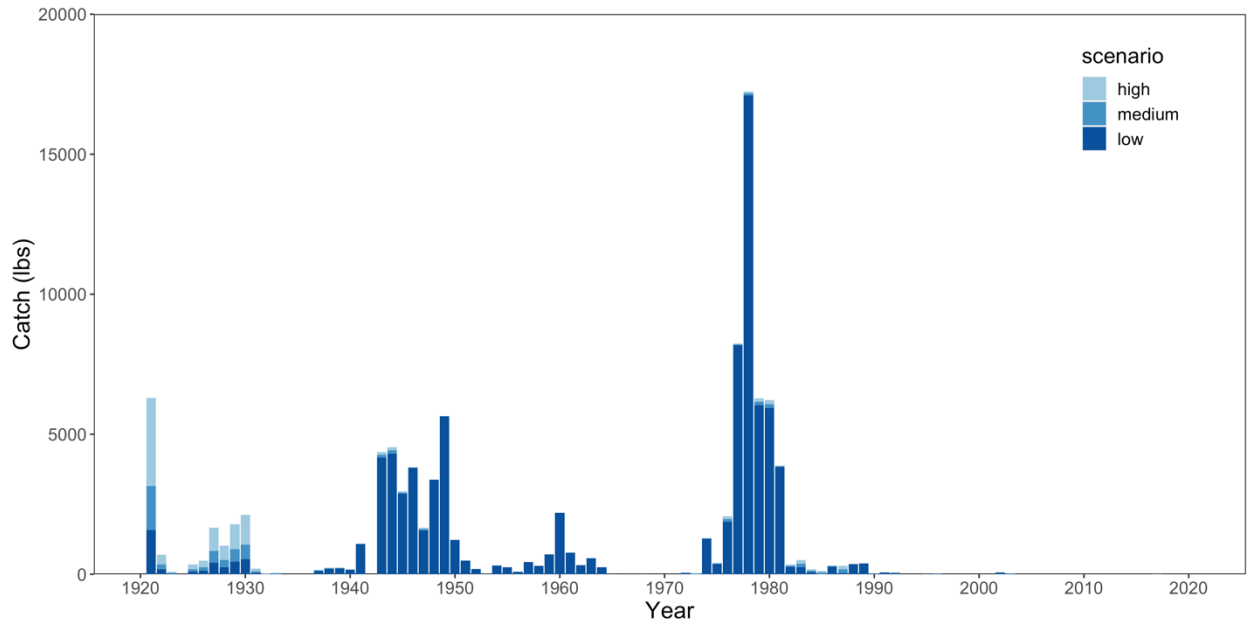


Figure 5. Bocaccio commercial catch for the U.S. portion of the DPS. For the catch scenarios, the stacked bars show the differences between the different catch scenarios, such that the high catch scenario is the sum of all three stacked bars.

Appendix A.2. Recreational catch reconstruction

Estimation of total rockfish catches

As is noted in Palsson et al. 2009, monitoring the recreational bottomfish fishery has been a significant challenge for the WDFW. However, the recreational fishery has also been the dominant source of rockfish landings in the past half century (Palsson et al. 2009), particularly for Yelloweye Rockfish and Bocaccio. This is because these species are strongly associated with untrawlable (hard/rocky bottom with complex structure) habitat, and thus were not a major part of bottom trawl landings, which were the primary gear type by which rockfish were landed (Palsson et al. 2009). While Palsson et al. 2009 estimated recreational rockfish harvest back to 1970, we have expanded these estimates back to 1938, when the WDF first attempted to gather catch statistics on the bottomfish sport fishery.

From 1938 to 1941, the WDF Annual Bulletin included a report on sport fishing statistics, which focused on recreational catch estimates of various salmon species (the primary targets of recreational anglers), but also estimated catches of some bottomfish (e.g. rock cod, lingcod, sole). The sport fishing statistics were obtained through a series of monthly reports from

saltwater boathouses, which rented boats out to recreational anglers. Sport catch report forms were distributed to all boathouses of record by the WDF, with cooperation from the boathouses in filling out and returning these forms being entirely voluntary; this resulted in reporting rates around 50-60% (WDF 1938, 1939, 1940, 1941). In addition to reporting the number of fish caught, the reports also include the number of fisherman days, the number of boathouses reporting, and the total number of boathouses on record. Many limitations of the data are noted in the report:

1. As reporting was voluntary, many boathouses were not accounted for in final catch numbers.
2. Many months are missing from the data, with only the summer months being consistently reported. Additionally, the number of reports submitted for spring or summer months was less than the peak months (May – August).
3. As reports were only submitted by boathouses, private anglers are not accounted for in these statistics.
4. There is no species composition data. In 1940 and 1941, “rock cod” and “red snapper” were included as reporting categories, but in 1938 and 1939 only “rock cod” is a reporting category.
5. The locations of the boathouses are not reported.

In order to address the shortcomings of the data, the following modifications were made to the published reports:

1. To calculate the effort from boathouses that did not report catches, the mean number of fisherman days per boathouse that reported data was first calculated for each month. This value of fisherman days per boathouse was then multiplied by the number of boathouses known to have not reported data and added to the total number of fisherman days from boathouses that reported data to arrive at an estimate of total effort across all boathouses.
2. For the months that were not reported in some years but were reported in other years, the number of rock cod and red snapper caught were estimated by taking the mean of that month across all years where that month was reported. For the months of December and January, which were never reported, the mean catch in November across all years was used, as this was assumed to be most similar to these winter months.
3. To account for private boat ownership, the findings from the 1949 WDF Annual Bulletin (WDF 1949) were applied. 1949 was the first year that private boats were accounted for in the sport landing statistics; this report states that boat counts in the sport fishing areas showed an average of about 30 private craft for every 100 rented boats during the busiest part of the season, and the average in the winter months, from November through February, was about 7 for every 100. To convert this to a ratio of private boats to rented boats, the “busiest part of the season” was assumed to be August, and exponential growth assumed from February to August and exponential decay assumed from August to November. These month-specific ratios were then multiplied by the estimated total effort of all boathouses to arrive at an estimate of total effort across rented boats and private boats. This estimated total effort (fisherman days) was then multiplied by the CPUE (for rock cod and red snapper separately) in terms of fish per fisherman day of the reporting boathouses to arrive at an estimated total catch.

4. Reports of “red snapper” are assumed to be Yelloweye Rockfish, as “red snapper” was the common name for *S. ruberrimus* in the early- to mid-20th century (Kincaid 1919; Smith 1937). However, “red snapper” was only reported in 1940 and 1941, and it is also unknown for years where “red snapper” was reported, what percentage of boathouses actually separated “red snapper” from “rock cod”. There are no estimates of the proportion of Bocaccio from these landing statistics, and thus a fixed value in line with later observed Bocaccio catch proportions were used. The catch composition data is further addressed in the *Species composition* and *Catch scenarios* sections.
5. The total catch is divided into Hood Canal and non-Hood Canal catch, in accordance with the distinct Yelloweye Rockfish populations described in the 2017 Rockfish Recovery Plan (National Marine Fisheries Service 2017). To achieve this, a map of boathouses from 1957 (Fig. 6) was used to determine the relative number of boathouses by regions, which revealed that approximately 16% of all boathouses were in Hood Canal. Thus, 16% of total catch for this period was allocated to Hood Canal, with the other 84% of catch allocated to the rest of Puget Sound.

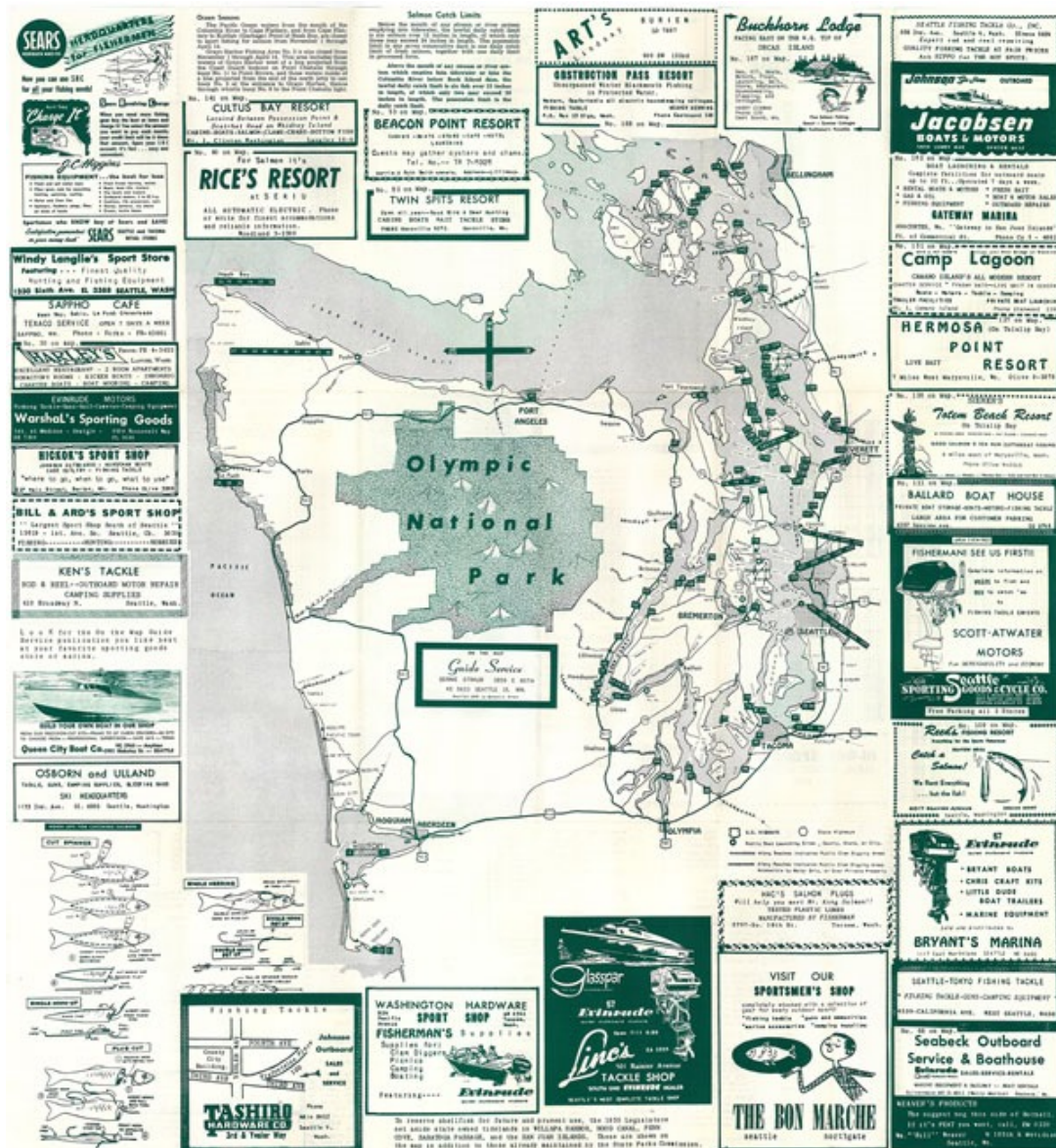


Figure 6. Map of boathouses in Puget Sound (green squares) in 1957. This map was originally part of the Center for Wooden Boat's "Fish On!" exhibit, which documented the recreational salmon fishery in Puget Sound.

Sport fishing statistics were also reported for 1942, but these records were excluded from this analysis because only about 10% of boathouses reported catch statistics, with low returns blamed on the attempt of the WDF to establish a new system of reporting. Following this last, unsuccessful report, catch statistics for bottomfish were abandoned until 1965. To estimate catches for 1942-1965, catch statistics were interpolated using similar methodology to how catch statistics were estimated for 1970-2003, through estimates of effort from the recreational salmon fishery. During this time period, Washington marine anglers were primarily salmon oriented:

“At present, the majority of Washington’s sport anglers consider most bottomfish as “scrap fish” and the ratio of the number retained in the harvest to the number actually caught appears extremely low in all areas. One primary concept responsible for the discarding of bottomfish, and retarding expansion of the fishery, is the conviction among Washington anglers that catches involving anything less than salmon have little prestige.” (Buckley 1967)

However, as evidenced by reports on either side of this 1942-1965 data gap, bottomfish catches by boat anglers were not negligible. The majority of the catch occurred as “incidental catch,” whereby anglers targeting salmon also caught bottomfish. To estimate catches of rockfish during this time period, we first calculated the mean CPUE (rockfish per angler day) across all sport fishing statistical reports from 1938-1941. We then multiplied this CPUE value by estimates of total angler days in Puget Sound published in WDF annual bulletins from 1942-1965. Estimates of total angler days were published for most years; any missing values were imputed using linear interpolation (Fig. 7). Catches were apportioned to Hood Canal and non-Hood Canal using the same proportions as for 1938-1941, with 16% of catches allocated to Hood Canal.

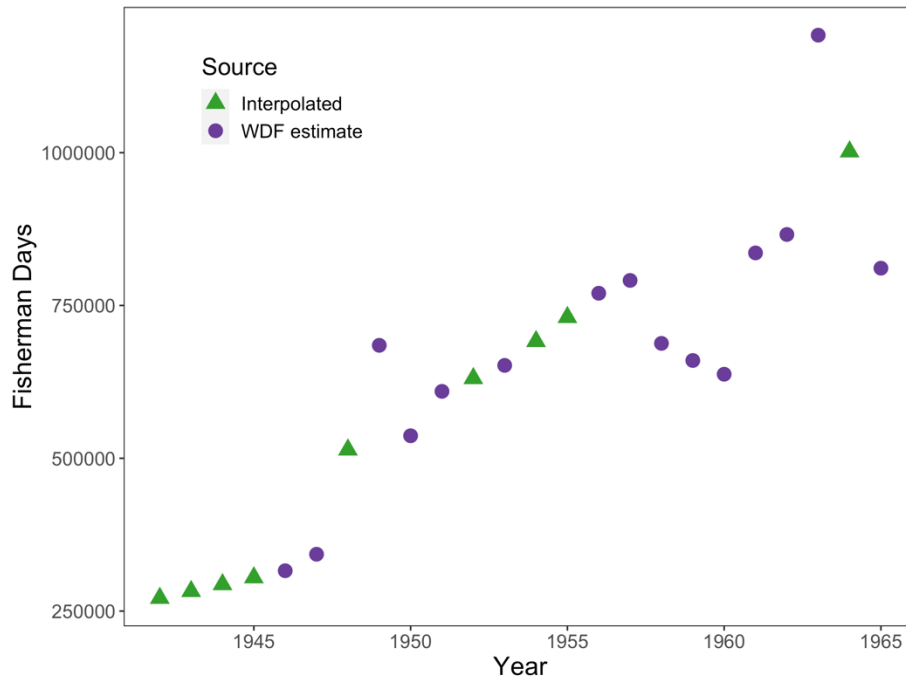


Figure 7. Fisherman days per year in Puget Sound. All years with missing data were imputed using linear interpolation.

Brought about by an increasing interest in monitoring the growing fishery, estimating complete recreational bottomfish catches was first attempted in 1965 by the WDF (Buckley 1967). This initiated a series of reports on the bottomfish sport fishery for 1965-1973 that all used a similar approach (Buckley 1967, 1968; Buckley and Satterthwaite 1970; Bargmann 1977). In short, technicians employed by the WDF who were sampling the salmon sport fishery secondarily recorded data on the bottomfish harvests. Total catch and effort for bottomfish harvests were estimated by extrapolating sampled bottomfish harvests to the total effort from the salmon sport fishery.

These reports from 1965-1973 report rockfish catches at the species level, but species identifications for these reports are questionable. Technicians attempted to identify bottomfish to species, but if this was not possible (due to insufficient time for positive identification or lack of certainty) fish were recorded on the family level. It is also noted that in 1965, several samplers were still learning to identify species on sight (Buckley 1967). After exploring the data and considering the uncertainty in species identification, the decision was made to remove the report on the 1965 bottomfish sport fishery (Buckley 1967). This was because of anomalously high values of Yelloweye Rockfish, with the report estimating that Yelloweye Rockfish comprised 22.7% of all rockfish caught in Hood Canal and 15.4% of all rockfish caught in South Puget Sound. These values are over an order of magnitude higher than later observations taken in the same areas by trained samplers through the Marine Recreational Fisheries Statistical Survey (MRFSS). The most likely explanations for these anomalous values include incorrect species identification or the extrapolation of a small sample size (only 6 technicians covered all of Puget Sound and the Strait of Juan de Fuca) to the total effort from the salmon sport fishery. Thus, rockfish catches for 1965 were estimated using the methods for the 1942-1965 timeframe, while catches from the reports covering 1966-1969 were included. Palsson 1987 recalculated bottomfish sport fishery catches for 1970 onwards with higher confidence species identifications from MRFSS, and thus these values were preferred over the report by Bargmann 1977 covering the years 1970-1973.

From 1970 to 2003, the WDFW estimated catches from the recreational bottomfish fishery through a combination of catch records from salmon anglers and a dockside creel survey of hook-and-line anglers (Palsson et al. 2009). Punch cards were required to be returned by salmon anglers, from which the number of salmon trips were estimated. The creel survey was used to determine the catch per trip of bottomfish, which was then multiplied by the number of trips per month and area to estimate the total number of bottomfish caught (Palsson 1987). However, this reliance on the salmon sport fishery to estimate bottomfish catches proved problematic following large-scale closures in the fishery from 1994 to 2003. Consequently, bottomfish catch and effort estimates were severely underestimated during this time period (Palsson et al. 2009); this limitation is addressed in the *Catch scenarios* section.

Beginning in 2003 and continuing through the present, the WDFW has conducted surveys of the recreational fishery through a telephone survey of licensed fishers to estimate fishing effort and the dockside WDFW creel survey that estimates catch rates of specific species. This new system removed the reliance on open salmon fisheries for bottomfish catch estimates. Importantly, this reporting system also collects information on released rockfish, which was previously not estimated.

Species compositions

The composition of recreational catches, particularly the identification of rockfishes, has been highly problematic throughout the monitoring of the recreational fishery. However, to estimate catches of ESA-listed Yelloweye Rockfish and Bocaccio, the proportion of the recreational catch that are the two species of interest must be estimated. Species composition data at a resolution finer than “North Puget Sound” and “South Puget Sound,” as was reported in Palsson et al. 2009,

was necessary for this analysis for two reasons. First, because the Rockfish Recovery Plan (National Marine Fisheries Service 2017) states that the Hood Canal Yelloweye Rockfish population is genetically distinct from the rest of the Puget Sound/Georgia Basin DPS, this population must be treated separately. Second, because Yelloweye Rockfish and Bocaccio are not evenly distributed throughout the DPS, different species composition data for each area were necessary to apply to the region-specific estimates of total rockfish catch. For this second reason, species compositions for areas 6-13 shown in Fig. 8 were calculated; areas 1-5 are outside the DPS boundary (Fig. 1) and thus were not of interest for this analysis.

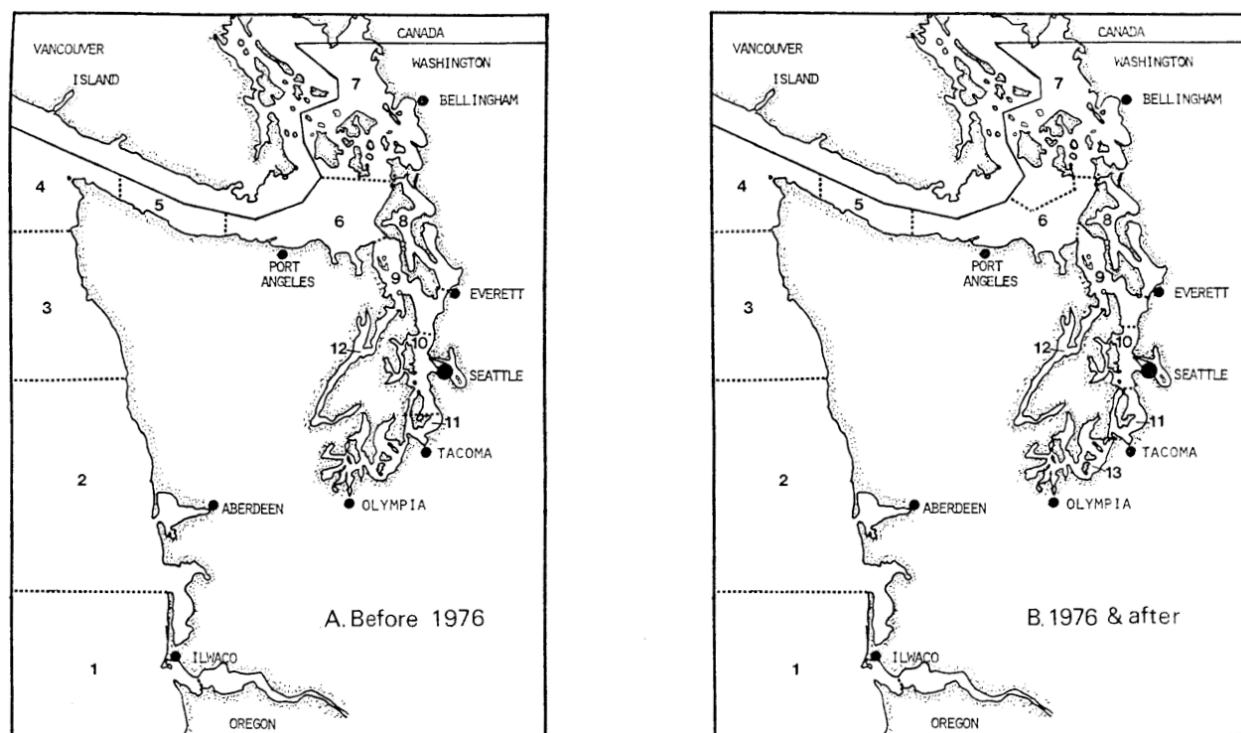


Figure 8. Washington Department of Fisheries Punch Card Areas. A.) Boundaries before 1976; B.) Boundaries 1976 and after.

Prior to 2003, when WDFW samplers were first trained to identify rockfish, the most accurate species identification came through the MRFSS program, which sampled recreational catch in Puget Sound in 1980-1986, 1989, and 1996-2003. MRFSS was a federal survey which employed personnel trained in rockfish identification to both interview bottomfish anglers and identify catch. These observations through the MRFSS program were the primary source of species composition data that was used to estimate the number of Yelloweye Rockfish and Bocaccio in the “total rockfish” category. A secondary source of species composition data were the catch compositions from the reports on the bottomfish sport fishery in 1965-1967 (Buckley 1967, 1968; Buckley and Satterthwaite 1970). Proportions of Yelloweye Rockfish and Bocaccio in the reports from 1965-1967 and the MRFSS species composition data from 1980-2003 are summarized in Tables 1 and 2. Because the sample sizes were relatively small (see Tables 1 and 2), the MRFSS observations were summarized across all years of the survey. These appear to

show a decrease in both Yelloweye Rockfish and Bocaccio as a proportion of total rockfish catch compared to the reports from 1965-1967, but there is considerably less confidence in the species composition data from 1965-1967. Additionally, for Yelloweye Rockfish, reports of “red snapper” in the recreational catch from 1938-1941 were interpreted as being Yelloweye Rockfish and used to inform the proportion of total rockfish catch that were Yelloweye Rockfish, as sources from around this time period indicate that “red snapper” referred to *S. ruberrimus* (Kincaid 1919; Smith 1937). Dividing the number of “red snapper” by the total number of rockfish (“rock cod” + “red snapper”) yielded an estimated percentage of 0.83% of rockfish being Yelloweye Rockfish across all boathouses. However, this is almost certainly an underestimate, as it is highly likely that some boathouses were not separating “red snapper” from “rock cod.” This uncertainty is addressed in *Catch scenarios*.

Table 1. Yelloweye proportions from reports by Buckley (1967, 1968) and Buckley and Satterthwaite (1970), for the years 1965-1967, and MRFSS (1980-2003). For the MRFSS data, the number of Yelloweye Rockfish and the total rockfish sample size are shown in parentheses (number of Yelloweye Rockfish/number of rockfish); this data is not available for the reports covering the years 1965-1967. The punch card areas (PCA) are those shown in Fig. 8; note that area 13 (South Puget Sound) was part of area 11 prior to 1976 and therefore is absent from the species composition data for 1965-1967.

PCA	Buckley/Buckley and Satterthwaite (1965-1967)	MRFSS (1980-2003)
6	2.6%	1.8% (13/737)
7	2.3%	1.5% (61/3951)
8	0%	0.5% (4/838)
9	0.6%	0.7% (8/1076)
10	1.6%	0.5% (9/1747)
11	7.3%	0.5% (11/2432)
12	4.2%	1.3% (8/624)
13	NA	0% (0/2437)

Table 2. Bocaccio proportions from reports by Buckley (1967, 1968) and Buckley and Satterthwaite (1970), for the years 1965-1967, and MRFSS (1980-2003). For the MRFSS data, the number of Bocaccio and the total rockfish sample size are shown in parentheses (number of Bocaccio/number of rockfish); this data is not available for the reports covering the years 1965-1967. The punch card areas (PCA) are those shown in Fig. 8; note that area 13 (South Puget Sound) was part of area 11 prior to 1976 and therefore is absent from the species composition data for 1965-1967.

PCA	Buckley/Buckley and Satterthwaite (1965-1967)	MRFSS (1980-2003)
6	0%	0.4% (3/737)
7	0%	0% (0/3951)
8	0%	0.2% (2/838)
9	0.8%	0% (0/1076)
10	0%	0.2% (3/1747)

11	2.6%	0.2% (6/2432)
12	0%	0% (0/624)
13	NA	0.3% (8/2437)

Catch scenarios

For each time period, which for the purposes of this report are defined by the data sources and methods used to estimate the catch of ESA-listed species, catch scenarios were developed to attempt to capture the range of plausible removals. For each time period, different scenarios were applied, based on sources of uncertainty specific to the data sources or the methodology used to estimate catches. However, for data sources where catches were reported in a summarized format, the options for developing catch scenarios were more limited.

2003-2019

The WDFW creel survey, which is the primary source of catch data for this time period, includes estimates of both rockfish catches and releases, as well as the variance in these estimates. The catch scenarios for this time period are derived from the variance in these estimates, as well as from applying different mortality rates to the released catches. Because of the ban on Yelloweye Rockfish retention in 2002, the majority of the uncertainty for this time period concerns the treatment of the released catches. A study of Yelloweye Rockfish caught at a depth of 18-72 m found that 99% of individuals released at depth survived, whereas only about 22% of Yelloweye Rockfish released at the surface were able to re-submerge, with the percentage of individuals re-submerging representing a maximum survival estimate (Hochhalter and Reed 2011). Therefore, the depth of release is the most important factor in released Yelloweye Rockfish survival.

Interviews of anglers conducted in 2011 revealed that only 3% of boat-based anglers reported using a descending device (Sawchuk 2012). In response to this, Puget Sound Anglers began outreach in 2012 to local anglers to better identify rockfish and use rapid-submergence techniques to reduce the effects of barotrauma. Additionally, in recent years, thousands of descending devices have been distributed to local anglers by NMFS, the WDFW, Puget Sound Anglers, and PSMFC to aid in these efforts. The effects of these efforts on the proportion of anglers using descending devices is unknown, but it is likely that most anglers still do not use descending devices when releasing rockfishes. Thus, the catch scenarios for this time period concern the use of descending devices and the variance in the estimates of catches and releases:

- 1. High Catch Scenario:** One standard deviation is added to the creel survey estimates of both catches and releases of Yelloweye Rockfish and Bocaccio. The 3% descending device use is assumed constant over the entire time period, meaning that 97% of rockfishes are released at the surface, and of the rockfishes released at the surface, 22% survive.
- 2. Medium Catch Scenario:** The creel survey estimates of both catches and releases of Yelloweye Rockfish and Bocaccio are used. Descending device usage is assumed to have increased over time, leading to a mean usage of 10% over the entire time period.

Therefore, 90% of rockfishes are released at the surface, and of the rockfishes released at the surface, 22% survive.

3. **Low Catch Scenario:** One standard deviation is subtracted from the creel survey estimates of both catches and releases of Yelloweye Rockfish and Bocaccio. Descending device usage is assumed to have increased significantly over time, leading to a mean usage of 25% over the entire time period. Therefore, 75% of rockfishes are released at the surface, and of the rockfishes released at the surface, 22% survive.

1970-2002

Estimates of bottomfish sport catch published by the WDFW are the basis for this time period. Palsson (1987) estimated bottomfish catches from 1970-1985, and prorated most of the total rockfish catch to species using species composition data from MRFSS; some catch was still classified as “unidentified.” However, for data from 1986-2002, which used the same catch estimation methods as for 1970-1985, catch had not been previously prorated to species. Therefore, we applied region-specific species composition data from MRFSS from 1980-2003 (Tables 1 and 2) for this time period (as well as to the “unidentified” rockfish from 1970-1985) to estimate the catches of Yelloweye Rockfish and Bocaccio.

For the catch scenarios for this time period, the source of uncertainty that is addressed is the mismatch between the punch card areas (PCA) by which catch was reported (Fig. 8) and the DPS boundaries (Fig. 1), with the main area of concern being PCA 6 (East Strait of Juan de Fuca), which is partially inside the DPS. Particularly for Yelloweye Rockfish, this is also an area of high catch. Thus, the catch scenarios for this time period are as follows:

4. **High Catch Scenario:** All catch from the East Strait of Juan de Fuca (PCA 6) is included.
5. **Medium Catch Scenario:** Half of the catch from the East Strait of Juan de Fuca (PCA 6) is included.
6. **Low Catch Scenario:** No catch from the East Strait of Juan de Fuca (PCA 6) is included.

1994-2002

The period of 1994-2002 must be treated differently than the catch estimates from 1970-1993 because of severe closures in the recreational salmon fishery that began in 1994. Because of the reliance on effort from the salmon sport fishery, this resulted in incomplete bottomfish catch estimates until 2003, when the creel survey began. While the estimates of bottomfish catch can be treated as minimum estimates for this time period, these estimates are multiplied by a factor in an attempt to estimate true removals. Therefore, the catch scenarios from the previous time period are adjusted as follows:

1. **High Catch Scenario:** All catch from the East Strait of Juan de Fuca (PCA 6) is included. Catch of Yelloweye Rockfish and Bocaccio are multiplied by a factor of 3.
2. **Medium Catch Scenario:** Half of the catch from the East Strait of Juan de Fuca (PCA 6) is included. Catch of Yelloweye Rockfish and Bocaccio are multiplied by a factor of 2.

3. **Low Catch Scenario:** No catch from the East Strait of Juan de Fuca (PCA 6) is included. Catch of Yelloweye Rockfish and Bocaccio are not multiplied by a factor.

1966-1969

For the catch scenarios for this time period, the source of uncertainty that is addressed is the same as the one for the data from 1970-2002: the mismatch between the punch card areas (PCA) by which catch was reported (Fig. 8) and the DPS boundaries (Fig. 1). Thus, the catch scenarios for this time period are as follows:

4. **High Catch Scenario:** All catch from the East Strait of Juan de Fuca (PCA 6) is included.
5. **Medium Catch Scenario:** Half of the catch from the East Strait of Juan de Fuca (PCA 6) is included.
6. **Low Catch Scenario:** No catch from the East Strait of Juan de Fuca (PCA 6) is included.

1942-1965

The primary source of uncertainty addressed by the catch scenarios for this time period is the species composition data. The closest estimate in time, the estimates from Buckley (1967, 1968) and Buckley and Satterthwaite (1970) that cover the years 1965-1967, have some anomalously high values for Yelloweye Rockfish, which may have been due to issues with the sampling design, but may also represent changes in species composition over time. The other species composition data, from MRFSS, is more reliable but also covers a time period that is much later (1980-2003). Therefore, we use these two sources of catch composition data (Tables 1 and 2) to examine the sensitivity of our catch estimates when these different species compositions are applied. The MRFSS catch compositions generally have lower proportions of ESA-listed species, particularly Yelloweye Rockfish, than the data from 1965-1967; therefore, the MRFSS data is treated as the lower catch scenario and the 1965-1967 data as the higher catch scenario. The catch scenarios are as follows:

1. **High Catch Scenario:** The catch composition data for the years 1965-1967 from Buckley (1967, 1968) and Buckley and Satterthwaite (1970) are applied.
2. **Medium Catch Scenario:** The catch composition data for the years 1965-1967 from Buckley (1967, 1968) and Buckley and Satterthwaite (1970) and for the years 1980-2003 from MRFSS are averaged and applied.
3. **Low Catch Scenario:** The catch composition data for the years 1980-2003 from MRFSS are applied.

1938-1941

For this time period, the largest source of uncertainty is once again the species composition data and is addressed in the catch scenarios. In particular, while Yelloweye Rockfish is reported (as “red snapper”) in 1940 and 1941, because of the lack of standardization in reporting, it is likely that not all boathouses were reporting “red snapper” and some were including them in the “rock cod” category. Additionally, because “red snapper” was not a reporting category in 1938 and

1939, these years again must be treated different from 1940 and 1941, where “red snapper” was reported. Therefore, for Yelloweye Rockfish, the following catch scenarios are applied:

1. **High catch scenario:** In years where "red snapper" is listed, all of the other rockfish catch is prorated to red snapper, based on the mean proportion of total rockfishes that are "red snapper" from the years 1940-1941, and is added to the "red snapper" catch. In years where no red snapper is listed (1938 and 1939), catch was prorated based on mean proportion of total rockfishes that are "red snapper" from the years 1940-41 * 2.
2. **Medium catch scenario:** In years where "red snapper" is listed, half of the rockfish catch is prorated to red snapper, based on the mean proportion of total rockfishes that are "red snapper" from the years 1940-1941, and is added to the "red snapper" catch. In years where no red snapper is listed (1938 and 1939), catch was prorated based on mean proportion of total rockfishes that are "red snapper" from the years 1940-41.
3. **Low catch scenario:** In years where "red snapper" is listed, it is the only yelloweye catch. In years where no red snapper is listed (1938 and 1939), catch was prorated based on mean proportion of total rockfishes that are "red snapper" from the years 1940-41 * 0.5.

For Bocaccio, there is no reporting of this species for this time period. Therefore, the proportion of catch that is Bocaccio is the main source of uncertainty that is addressed in the catch scenarios. Proportions are chosen that are in line with proportions from MRFSS (Table 2):

1. **High catch scenario:** 0.5% of the “rock cod” catch is Bocaccio.
2. **Medium catch scenario:** 0.25% of the “rock cod” catch is Bocaccio.
3. **Low catch scenario:** 0% of the “rock cod” catch is Bocaccio.

Catch scenarios combined

When all of the catch scenarios are combined, the recreational catch shows a pronounced peak during the 1980s (Figs. 9, 10, 11). For Bocaccio, the recreational catch appears to have one peak period, whereas the Yelloweye Rockfish catch occurs over a broader period of time.

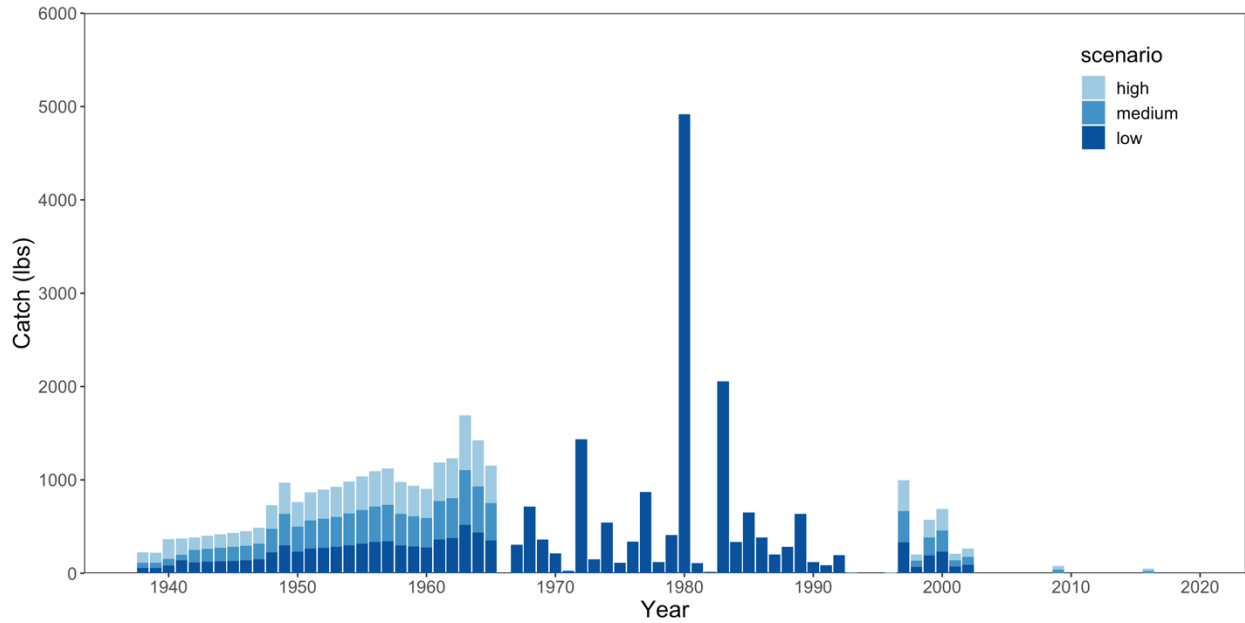


Figure 9. Hood Canal population Yelloweye Rockfish recreational catch. For the catch scenarios, the stacked bars show the differences between the different catch scenarios, such that the high catch scenario is the sum of all three stacked bars.

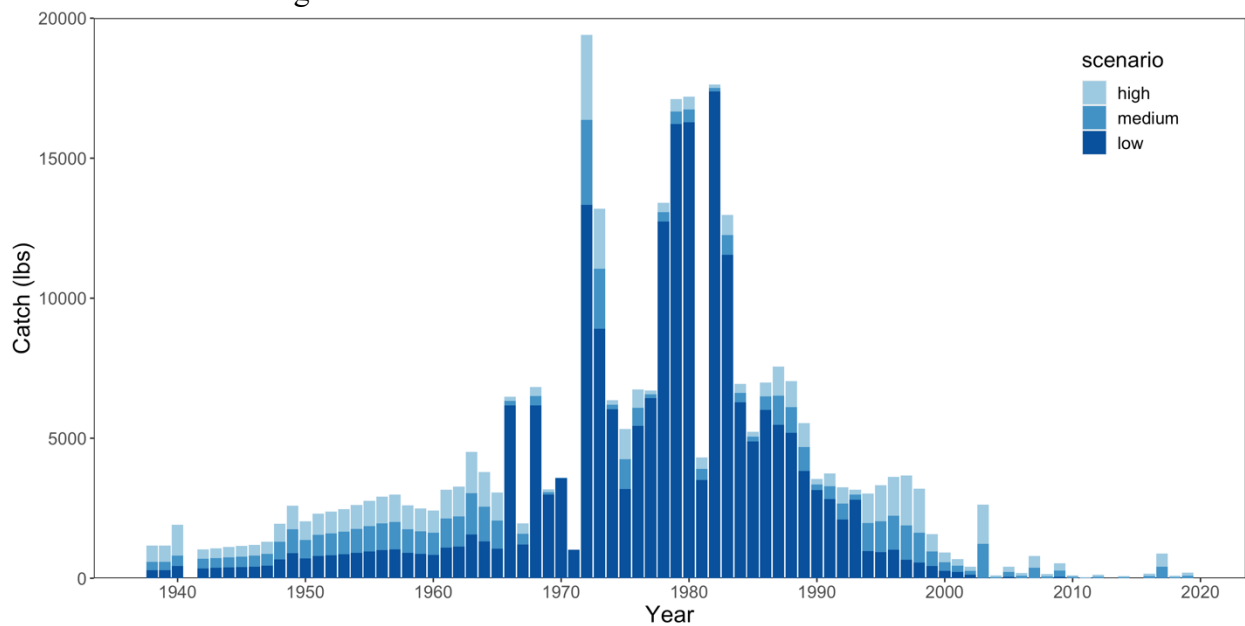


Figure 10. Non-Hood Canal population Yelloweye Rockfish recreational catch for the U.S. portion of the DPS. For the catch scenarios, the stacked bars show the differences between the different catch scenarios, such that the high catch scenario is the sum of all three stacked bars.

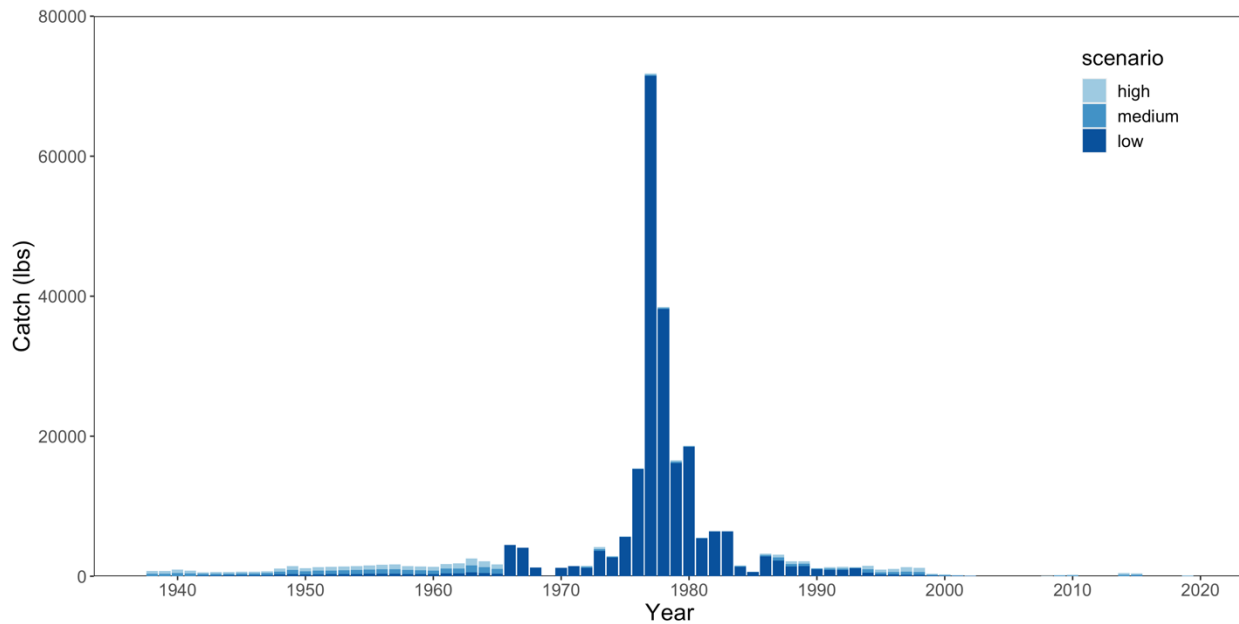


Figure 11. Bocaccio recreational catch for the U.S. portion of the DPS. For the catch scenarios, the stacked bars show the differences between the different catch scenarios, such that the high catch scenario is the sum of all three stacked bars.

Chapter 2 Appendix

Appendix A. Tributary detection efficiency

Detection efficiency at the in-stream PIT tag array closest to the mouth of the tributary (the confluence of the tributary with the mainstem Columbia or Snake River) was estimated for each tributary state. However, detection efficiency was not modeled for three tributaries of the Snake River (the Salmon River, the Grande Ronde River, and the Clearwater River), as these tributaries did not have a detection site on the mainstem of the tributary within 100 km of the confluence. The data used to estimate detection efficiency at the river mouth sites was detections at the river mouth site and detections anywhere upstream of the river mouth site. In this analysis, we only included fish that were detected at a site upstream of the river mouth site, and then used a binary indicator to record if those fish were also detected at the river mouth site.

We modeled detection efficiency in tributaries using logistic regression based on two predictors: 1) changes in antenna configurations over time, and 2) the discharge in the tributary. Changes in antenna configurations were identified from the operational history of the site, based on antennas being installed, decommissioned, upgraded, or moved. Changes in antenna configurations are identified in Table S1. Discharge was included as a predictor based on our hypothesis that river stage would influence the antenna coverage of the river channel. Discharge data were queried from USGS by finding the station on the interactive USGS dashboard closest the river mouth array and navigating to the data page for the specific site. Discharge data were available for all tributaries except Fifteenmile Creek and the Imnaha River; detection efficiency in these

tributaries was therefore only modeled as a function of antenna configurations. We processed discharge data for inclusion in the model by taking the mean discharge across the run year.

Table 1: Tributary PIT tag antenna configurations used in detection efficiency estimation. Years refer to the Steelhead run years in which the site was active in a specific configuration. Site refers to the PIT tag detection site chosen for the detection efficiency estimation, based on its proximity to the mouth of the tributary. Configuration refers to the configuration of antennas at the site, where Initial is the name given to the antenna configuration at the site at the start of the time series, and any subsequent changes from the initial configuration at the site are noted in this column.

Tributary	Years	Site	Configuration
Hood River	12/13-23/24	Hood River Mouth (HRM)	Initial
Fifteenmile Creek	11/12-18/19	Fifteenmile Ck at Eighmile Ck (158)	Initial
Deschutes River	13/14-18/19	Deschutes River Mouth (DRM)	Initial
John Day River	12/13-23/24	John Day River, McDonald Ferry (JD1)	Initial
Umatilla River	06/07-13/14	Three Mile Falls Dam (TMF)	Initial
Umatilla River	14/15-23/24	Three Mile Falls Dam (TMF)	Antenna installation at entrance to adult ladder
Walla Walla River	05/06-11/12	Oasis Road Bridge (ORB)	Initial
Walla Walla River	12/13-14/15	Oasis Road Bridge (ORB) and Walla Walla R at Pierce RV Pk (PRV)	Initial configuration where two mouth sites were operational simultaneously and their joint detection efficiency was estimated
Walla Walla River	15/16-18/19	Walla Walla R at Pierce RV Pk (PRV)	Initial
Walla Walla River	19/20-23/24	Walla Walla River Barge Array (WWB)	Initial
Yakima River	05/06-23/24	Prosser Diversion Dam (PRO)	Initial
Wenatchee River	10/11-23/24	Lower Wenatchee River (LWE)	Initial
Entiat River	07/08-23/24	Lower Entiat River (ENL)	Initial
Methow River	09/10-16/17	Lower Methow River at Pateros (LMR)	Initial
Methow River	17/18-23/24	Lower Methow River at Pateros (LMR)	Site was moved 5 km upstream and transceivers replaced
Okanogan River	13/14-23/24	Lower Okanogan Instream Array (OKL)	Initial
Tucannon River	10/11-19/20	Lower Tucannon River (LTR)	Initial

Tributary	Years	Site	Configuration
Tucannon River	20/21-23/24	Lower Tucannon River (LTR)	All antennas replaced, additional antenna installed
Asotin Creek	11/12-17/18	Asotin Creek Mouth (ACM)	Initial
Asotin Creek	18/19-23/24	Asotin Creek Mouth (ACM)	All components replaced and upgraded
Imnaha River	10/11-23/24	Lower Imnaha River ISA @ km 7 (IR1)	Initial

For our model of detection efficiency, the data included all fish that were detected at a site upstream of the river mouth. We then denote z_i as the detection of fish i at the river mouth site, $p_{det,i}$ as the probability of detection for fish i , $\alpha_{j,k}$ as the antenna configuration for tributary j under configuration k , β_j as the slope for the effect of discharge, and $x_{j,t}$ as the mean discharge for tributary j in run year t . The model for detection efficiency was as follows:

$$z_i \sim \text{Bernoulli}(p_{det,i})$$

$$\text{logit}(p_{det,i}) = \alpha_{j,k} + \beta_j x_{j,t}$$

The above model was implemented in Stan (Carpenter et al., 2017), with 3 chains run for 5,000 warmup and 5,000 sampling iterations each. Discharge values were Z-scored prior to the model being fit. The posteriors from this model for each of the α (site configuration intercepts) and β (effect of discharge) terms were used as priors in the primary Stan model that was used to estimate movement. The resulting detection efficiency correction for each run year can be found in Appendix F.

Appendix B. Covariate data processing

Temperature data

Due to the noise and gaps inherent to the temperature data, a series of steps were performed to clean this data. First, plots of temperature were manually inspected and sequential runs of temperature points that were outside of the range of possible values for that time of year were removed. Next, a filtering algorithm was applied to remove any temperature values that were more than four degrees outside of the interannual average temperature value for that day of the year, as well as any values that were more than two degrees outside of the 7-day moving average. To address the incomplete temporal resolution for temperature at each dam in our modeling framework, a state-space model was fit using the MARSS package (Holmes et al. 2012). The inputs for this model were the cleaned temperature data at the forebay and tailrace for the eight dams (a total of 16 temperature time series). The model was structured with only a single process (the basin-scale temperature) and 16 observations of that process. Each dam had a different offset/bias term (8 total). Model-estimated temperatures on each day for each dam were then exported by using the estimate of the basin-scale temperature plus the dam-specific offset.

To estimate the temperatures experienced by fish, the median residence time in each state in our model was first calculated. To do so, we calculated the difference between the date on which a fish was observed exiting a state and the date on which a fish was observed entering a state, and

then computed the state-specific median across all fish. However, for the two furthest upstream states (upstream of Lower Granite Dam and upstream of Wells Dam), above which there are no more dams with fish passage, residence times were significantly longer and were found to be bimodal. These furthest upstream states are also observed to have more variability in median residence times because of their position in the PIT tag array network (see plots below). Based on our hypothesis that movement decisions are made soon after a fish enters a state, we fit a two-component mixture model using the *mixtools* package in R (Benaglia et al. 2010) to residence times in these states and used the median residence time for fish in the first mode. The mean temperature experienced by each fish while in a state was estimated as the mean temperature across a window of time defined as the date the fish was observed entering a state plus the median residence time for all fish in that state.

Spill data

Daily average spill (in thousands of cubic feet per second) was queried from the Columbia Basin Conditions portal from the DART page for the eight dams that were modeled as the boundaries of states (Bonneville, McNary, Priest Rapids, Rock Island, Rocky Reach, Wells, Ice Harbor, and Lower Granite). Spill data were processed in two different ways to facilitate the inclusion of two hypothesized relationships between spill and fish fallback over dams. For en-route fallback, spill volume was processed in the same way as temperature: by taking the mean volume of spill across the residence time window. For post-overshoot fallback, spill volume was converted into days of winter spill, by counting the number of days that had nonzero spill in the months of January, February, and March for each year.

Residence time visualization

Residence time was calculated across all fish and all years. Variability in residence time by year (visualized below as the median residence time by year with the error bars showing the 95% interquartile range) was generally not significant. Furthermore, dividing up the dataset by year would have led to small sample sizes in some years, leading to an unrepresentative residence time.

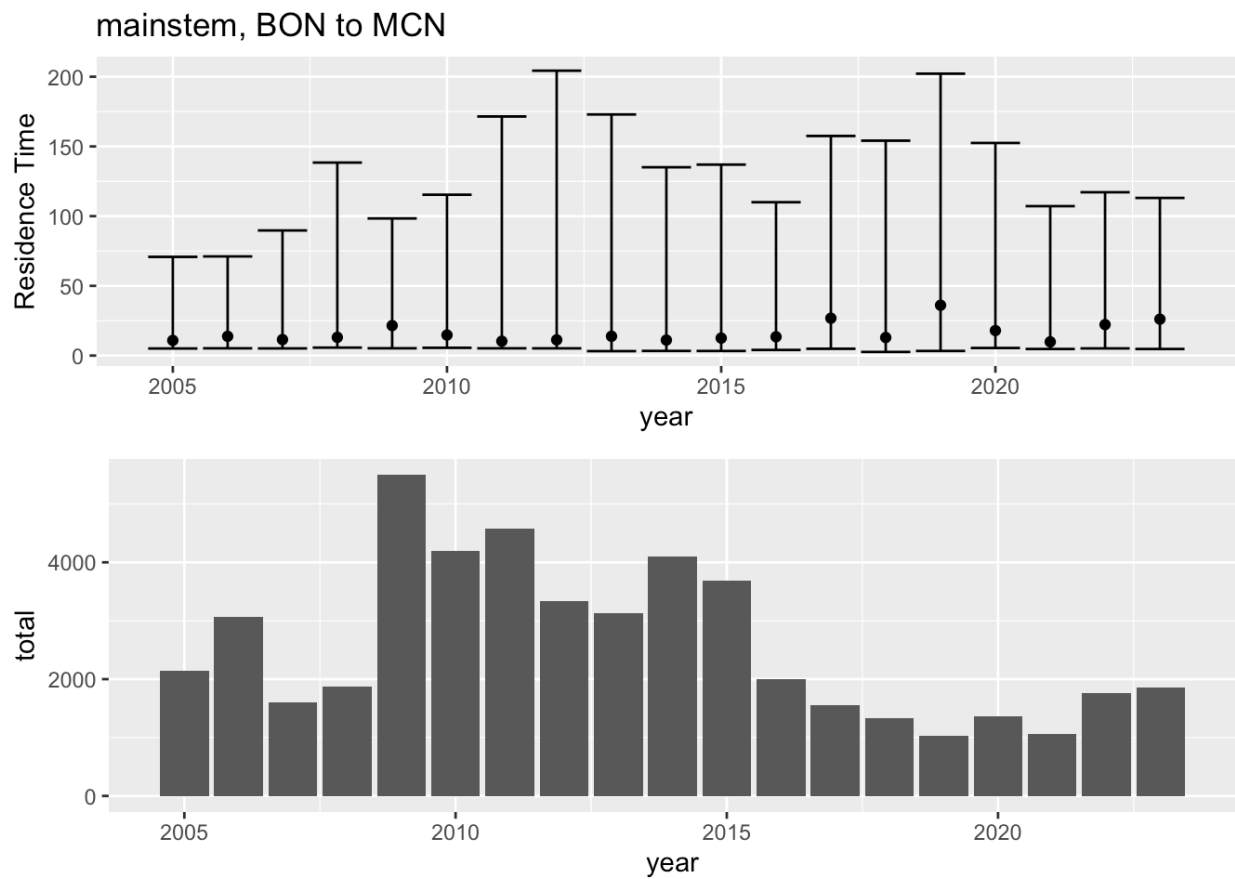


Figure 1. Residence time for fish in the state between Bonneville and McNary Dams.

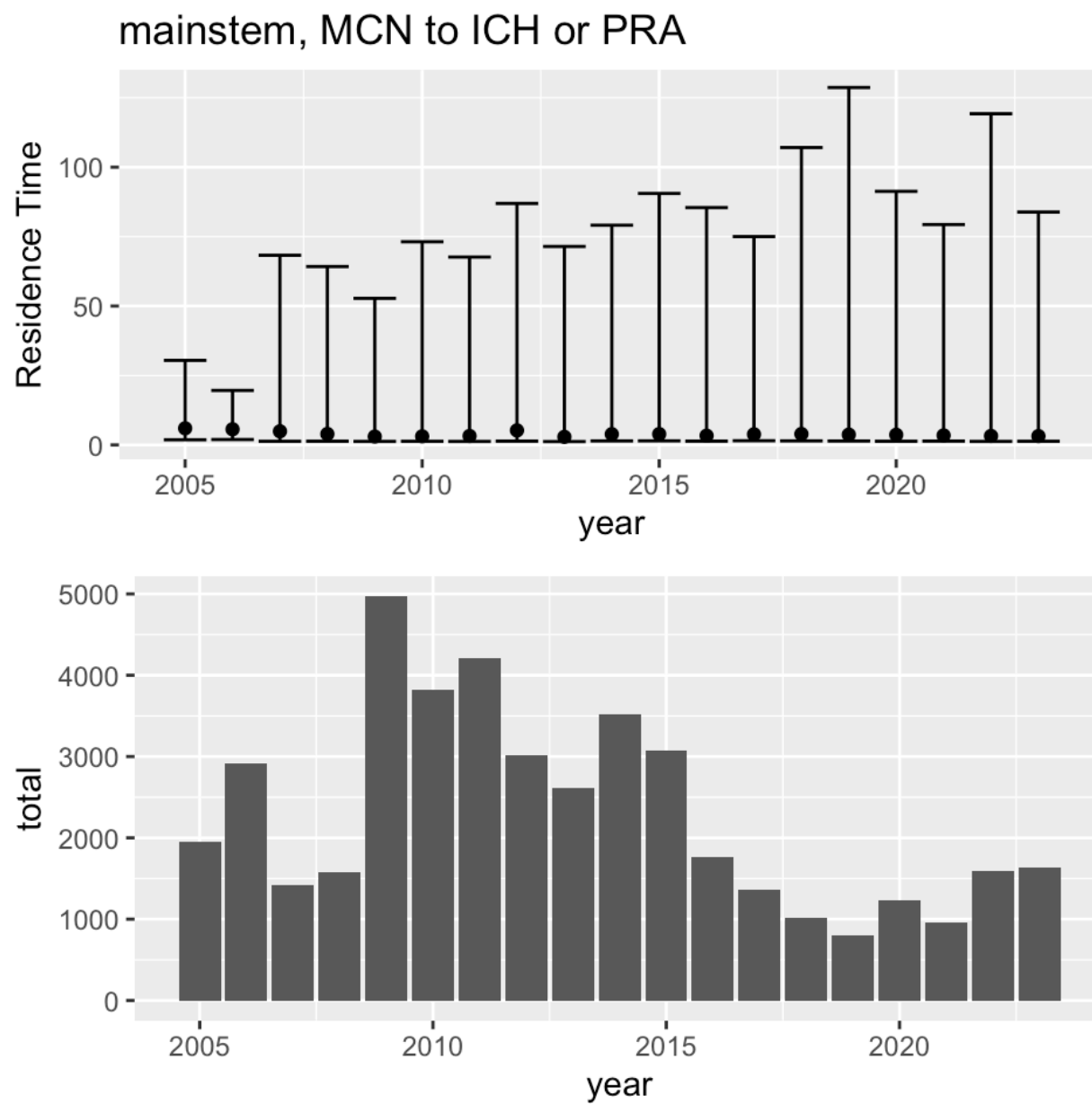


Figure 2. Residence time for fish in the state between McNary and Ice Harbor/Priest Rapids Dams.

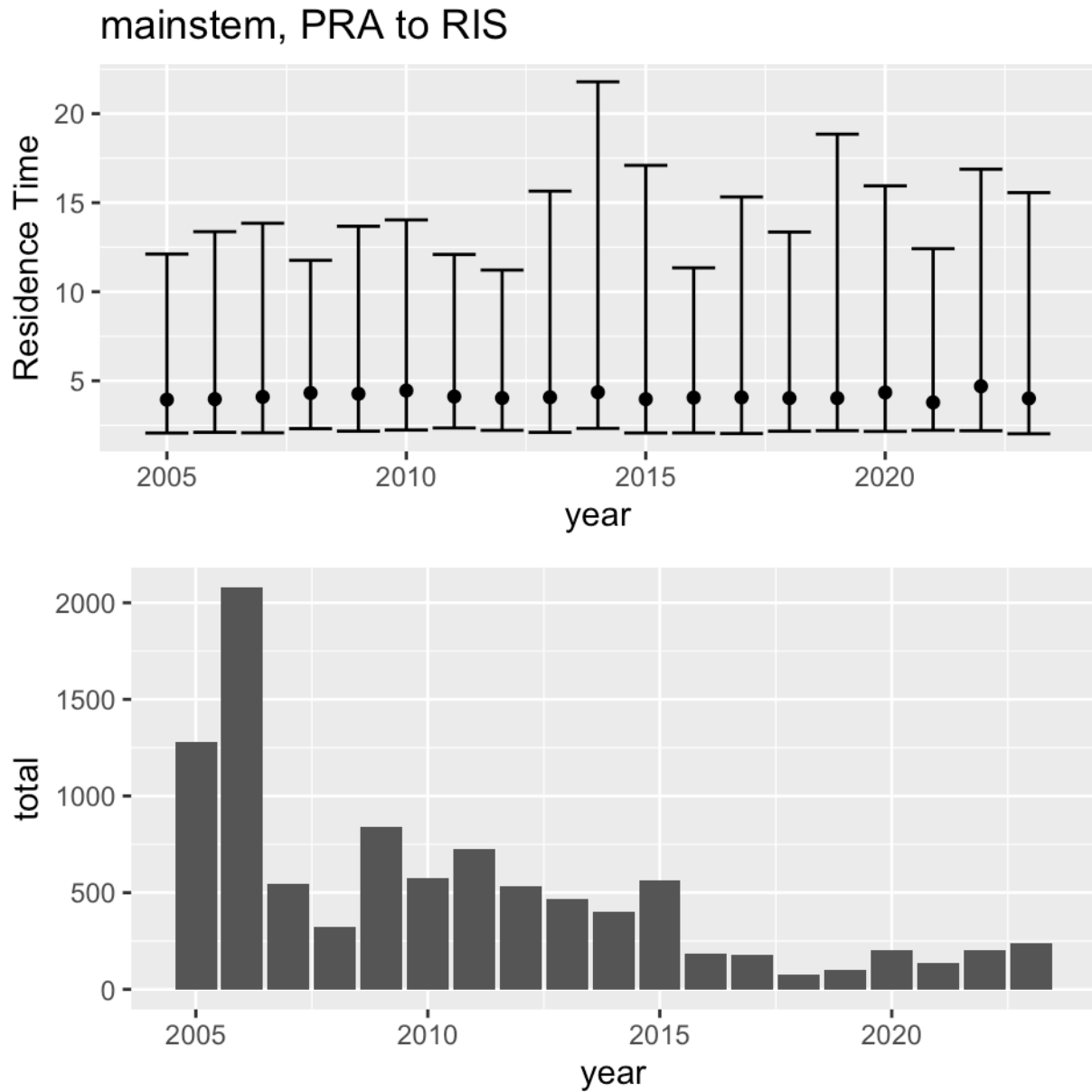


Figure 3. Residence time for fish in the state between Priest Rapids and Rock Island Dams.

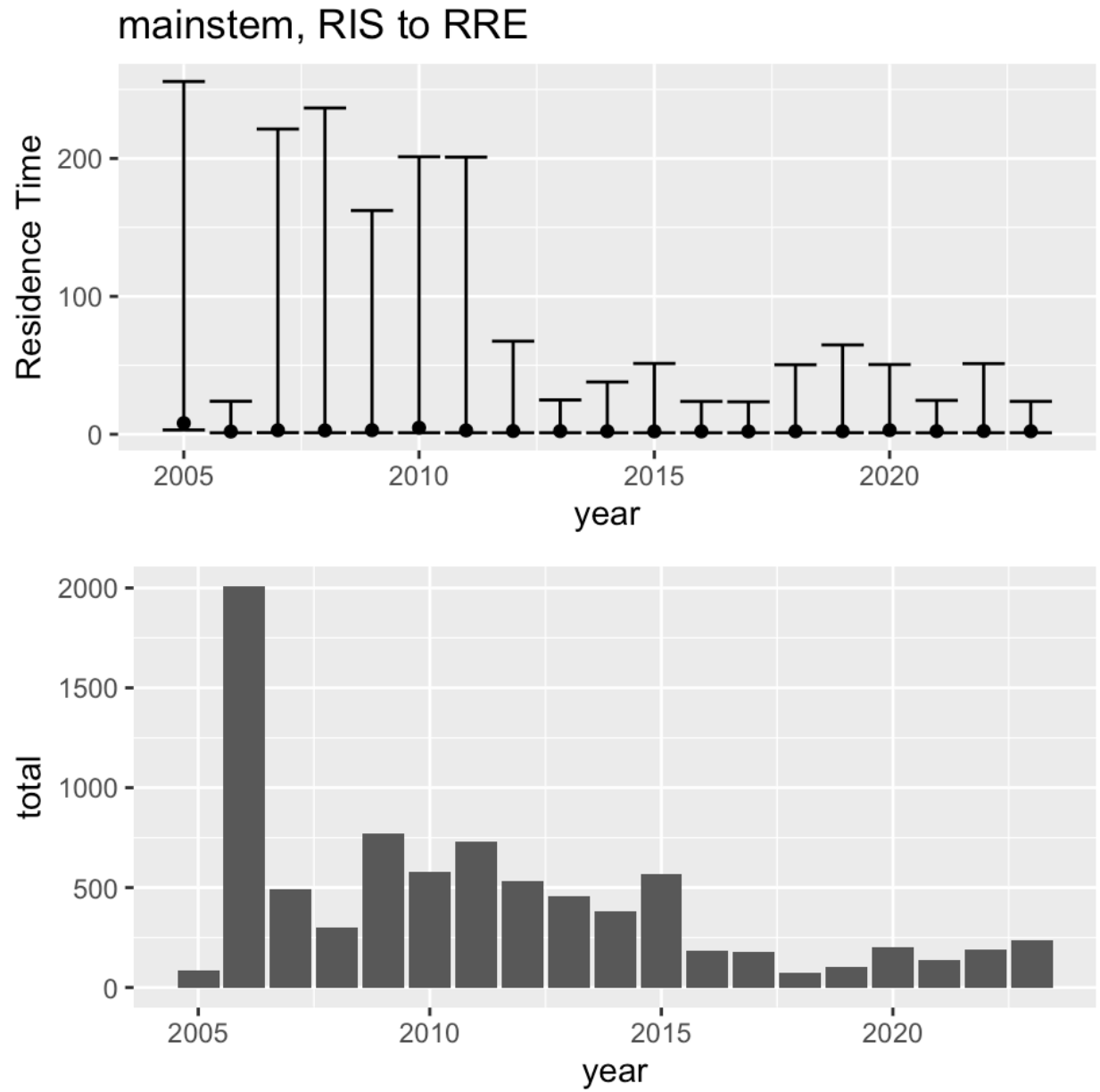


Figure 4. Residence time for fish in the state between Rock Island and Rocky Reach Dams.

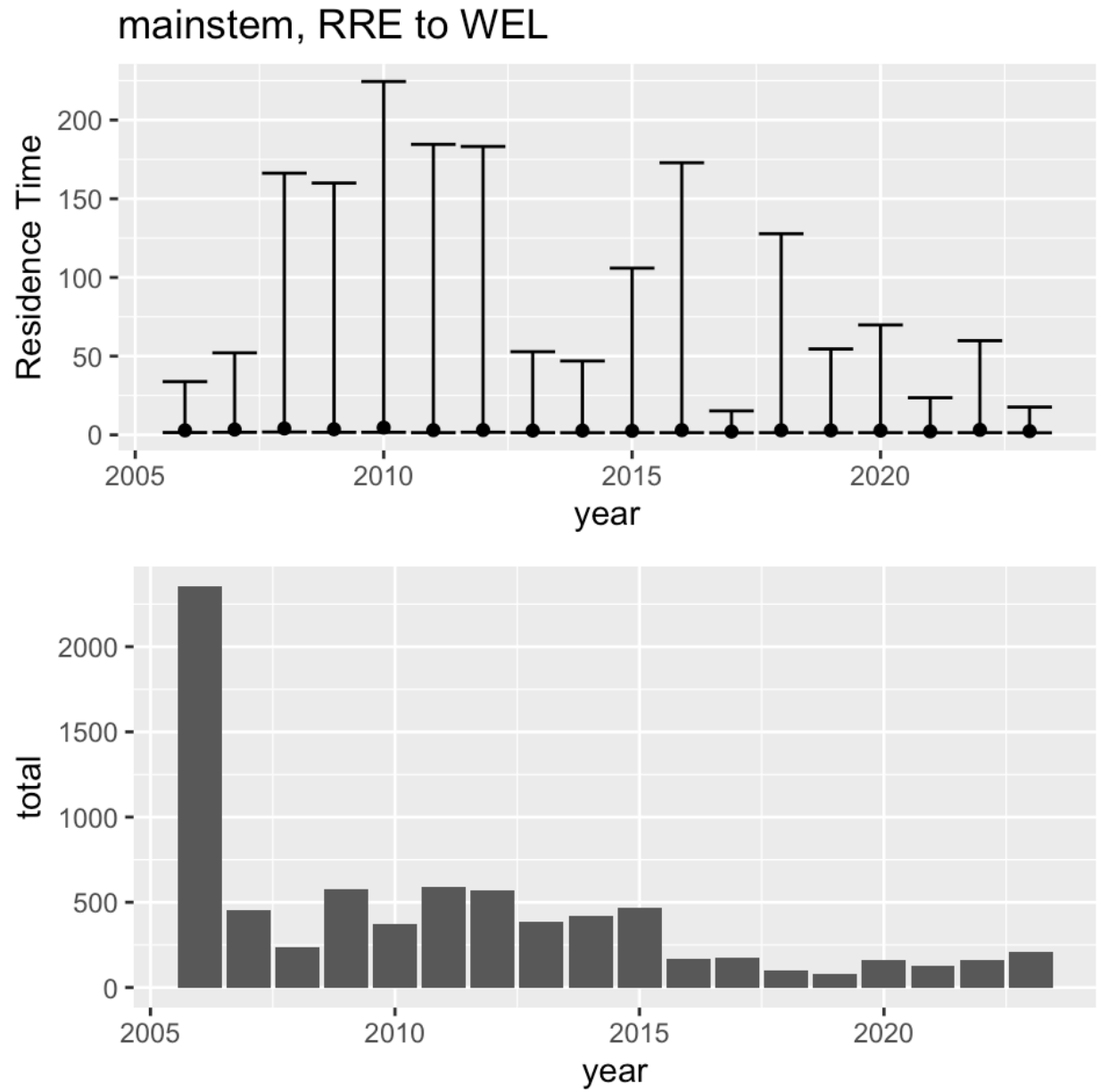


Figure 5. Residence time for fish in the state between Rocky Reach and Wells Dams.

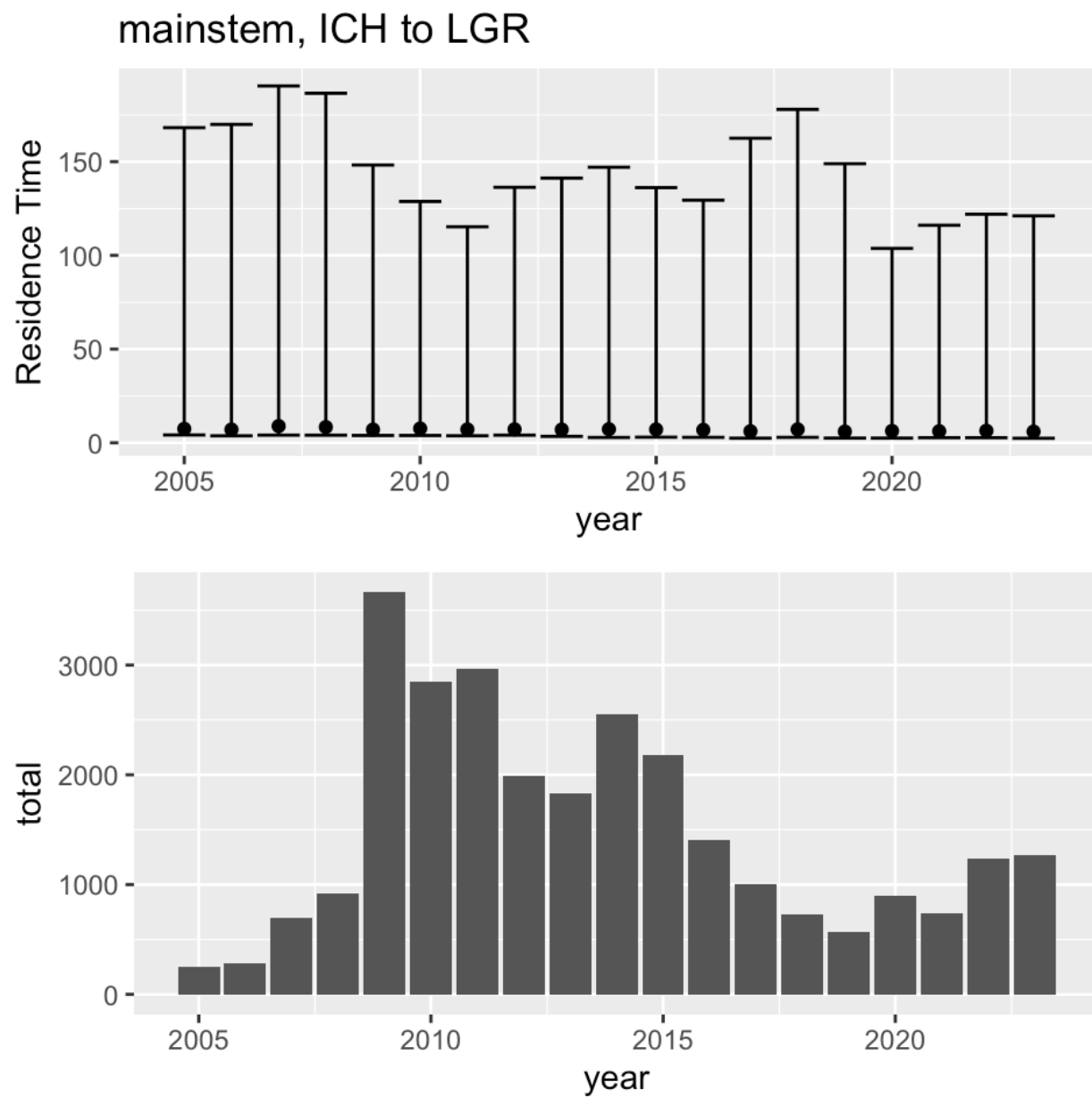


Figure 6. Residence time for fish in the state between Ice Harbor and Lower Granite Dams.

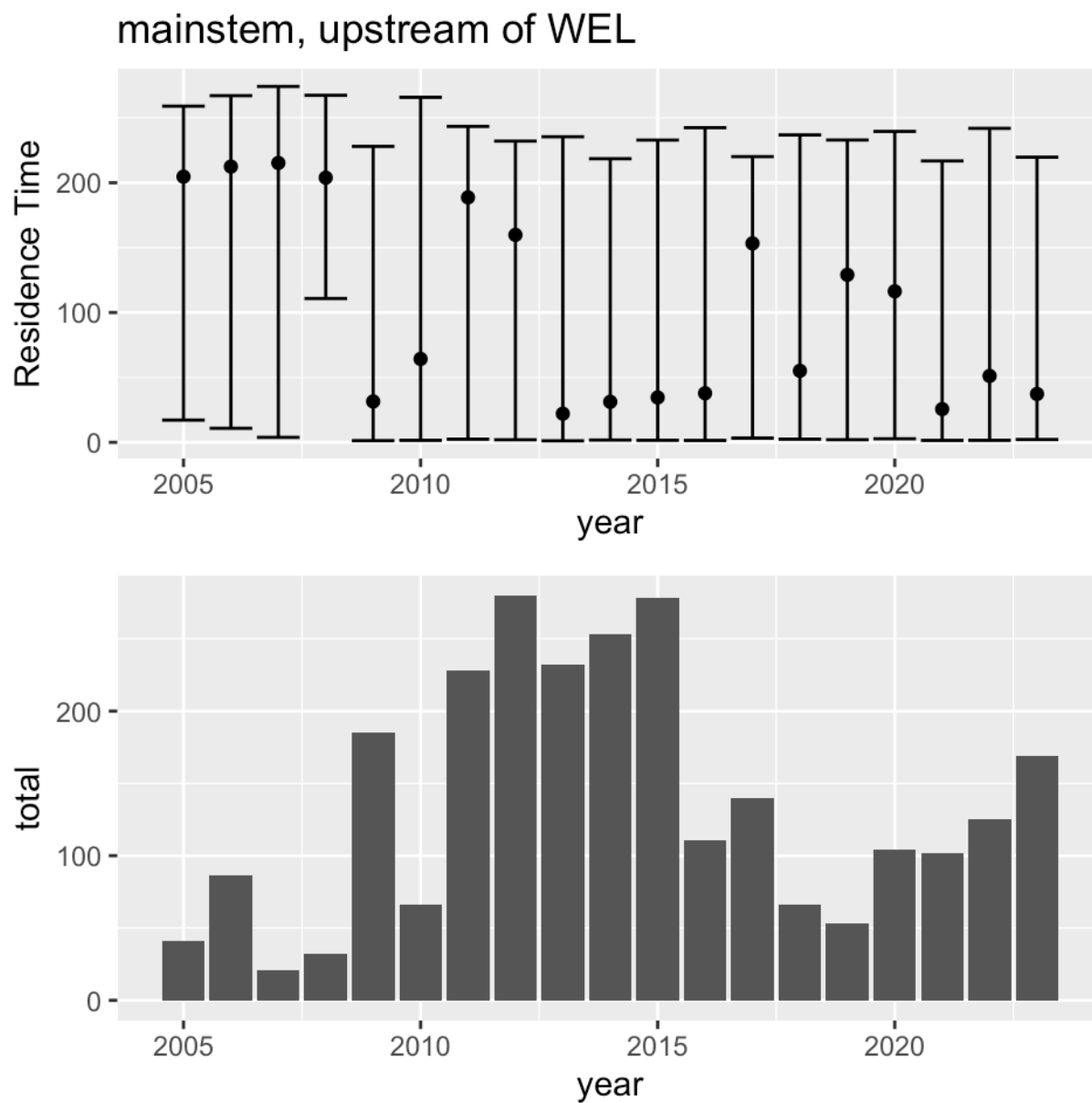


Figure 7. Residence time for fish in the state upstream of Wells Dam.

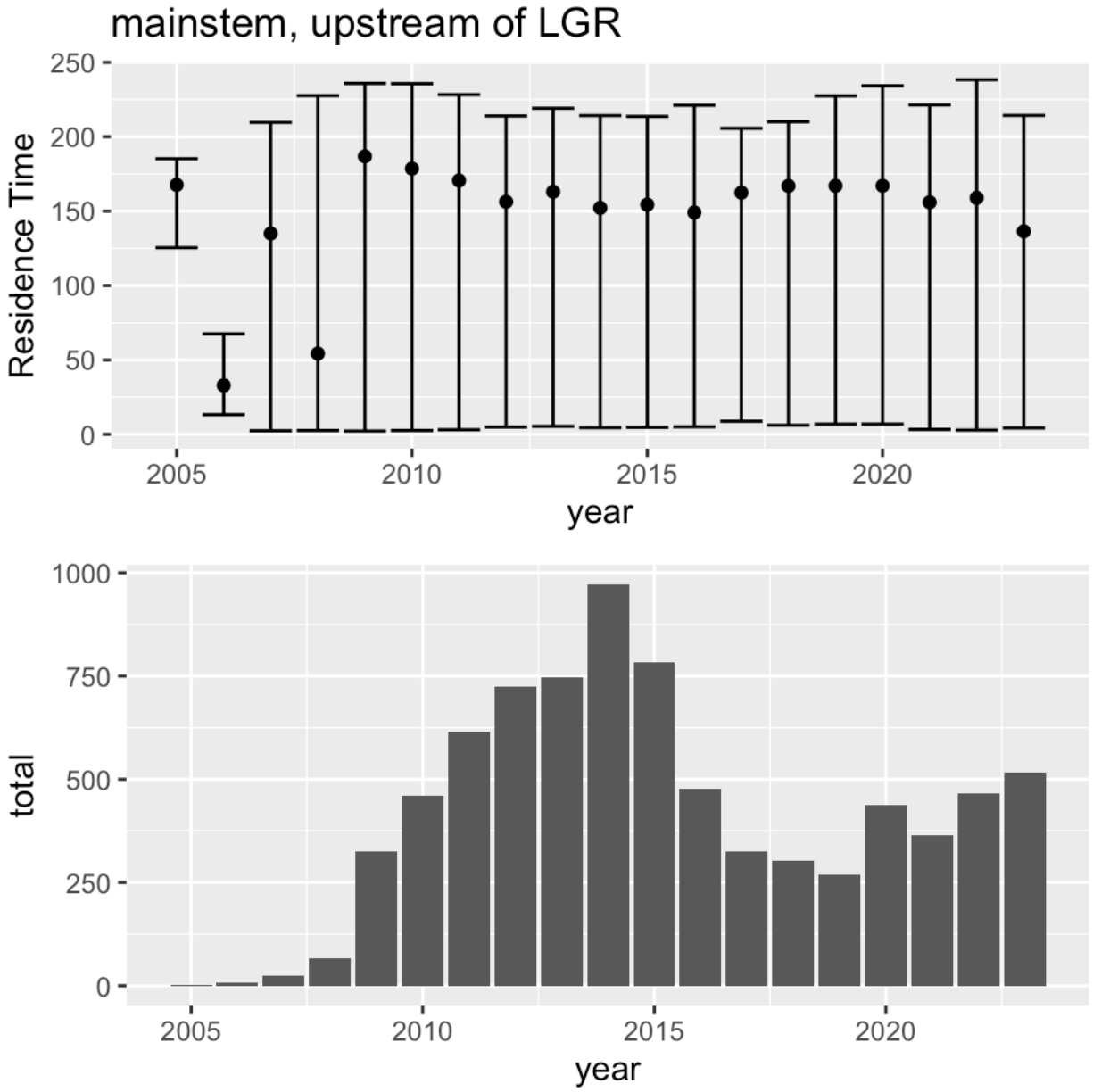


Figure 8. Residence time for fish in the state upstream of Lower Granite Dam.

Appendix C. Sample sizes.

Table 1. The number of fish per run year from each combination of natal tributary, rearing type (natural or hatchery origin), and juvenile pathway (transported or in-river migrants).

Popula tion	05/ 06	06/ 07	07/ 08	08/ 09	09/ 10	10/ 11	11/ 12	12/ 13	13/ 14	14/ 15	15/ 16	16/ 17	17/ 18	18/ 19	19/ 20	20/ 21	21/ 22	22/ 23	23/ 24	Tot al
Fifteen mile Creek (N, in- river)	0	0	0	11	47	89	95	33	32	37	24	10	18	43	39	6	1	0	5	490
Deschu tes River (N, in- river)	0	0	38	68	11 7	11 3	10 9	81	18 0	97	49	40	28	39	45	27	0	3	0	103 4
John Day River (N, in- river)	68	11 9	11 4	24 7	34 7	27 9	28 7	15 1	26 1	24 3	21 7	88	80	67	11 3	72	50	68	11 3	298 4

Table 1. The number of fish per run year from each combination of natal tributary, rearing type (natural or hatchery origin), and juvenile pathway (transported or in-river migrants).

Popula tion	05/ 06	06/ 07	07/ 08	08/ 09	09/ 10	10/ 11	11/ 12	12/ 13	13/ 14	14/ 15	15/ 16	16/ 17	17/ 18	18/ 19	19/ 20	20/ 21	21/ 22	22/ 23	23/ 24	Tot al
Umatilla River (H, in- river)	9	12	59	80	115	77	64	24	13	36	42	29	16	1	1	6	7	36	86	713
Umatilla River (N, in- river)	2	10	17	21	14	13	81	65	68	171	278	145	117	62	58	34	53	113	88	1410
Walla Walla River (H, in- river)	33	32	25	301	415	222	261	120	111	163	114	112	119	97	58	41	48	111	65	2448
Walla Walla River	11	11	10	8	61	95	115	90	57	75	72	19	27	19	23	15	23	39	27	797

Table 1. The number of fish per run year from each combination of natal tributary, rearing type (natural or hatchery origin), and juvenile pathway (transported or in-river migrants).

Popula tion	05/ 06	06/ 07	07/ 08	08/ 09	09/ 10	10/ 11	11/ 12	12/ 13	13/ 14	14/ 15	15/ 16	16/ 17	17/ 18	18/ 19	19/ 20	20/ 21	21/ 22	22/ 23	23/ 24	Tot al
(N, in- river)																				
Yakima River (N, in- river)	15	12	18	16	33	23	40	18	45	78	93	38	42	46	60	50	44	40	66	777
Wenatchee River (H, in- river)	39 9	40 0	35 0	45 0	81 8	52 3	42 7	38 0	18 3	18 9	17 3	25	38	27	20	69	3	31	28	453 3
Wenatchee River (N, in- river)	0	0	2	8	71	73	53	32	31	39	44	9	7	3	15	14	8	7	6	422

Table 1. The number of fish per run year from each combination of natal tributary, rearing type (natural or hatchery origin), and juvenile pathway (transported or in-river migrants).

Popula tion	05/ 06	06/ 07	07/ 08	08/ 09	09/ 10	10/ 11	11/ 12	12/ 13	13/ 14	14/ 15	15/ 16	16/ 17	17/ 18	18/ 19	19/ 20	20/ 21	21/ 22	22/ 23	23/ 24	Tot al
Entiat River (N, in- river)	0	3	8	7	75	74	55	26	43	66	56	34	8	15	17	12	4	5	5	513
Metho w River (H, in- river)	18 66	30 88	47 8	35	12 8	58	31 9	32 4	29 2	28 6	28 9	10 8	12 6	50	31	86	92	11 3	13 9	790 8
Metho w River (N, in- river)	0	0	6	13	42	24	33	18	43	44	51	22	13	7	25	17	19	20	17	414
Okano gan River	17 2	36	8	17	9	9	11 7	13 4	10 0	14 1	11 5	56	78	42	18	50	20	39	76	123 7

Table 1. The number of fish per run year from each combination of natal tributary, rearing type (natural or hatchery origin), and juvenile pathway (transported or in-river migrants).

Popula tion	05/ 06	06/ 07	07/ 08	08/ 09	09/ 10	10/ 11	11/ 12	12/ 13	13/ 14	14/ 15	15/ 16	16/ 17	17/ 18	18/ 19	19/ 20	20/ 21	21/ 22	22/ 23	23/ 24	Tot al
(H, in- river)																				
Tucann on River (H, in- river)	56	40	38 2	32 2	57 6	23 1	16 2	78	96	11 2	95	57	46	38	22	14	39	95	82	254 3
Tucann on River (H, transpo rted)	2	43	16 7	10 1	63	28	4	5	25	29	38	19	23	13	13	6	3	5	7	594
Tucann on River	33	14	22	8	50	43	50	54	45	59	58	9	22	9	20	20	13	25	26	580

Table 1. The number of fish per run year from each combination of natal tributary, rearing type (natural or hatchery origin), and juvenile pathway (transported or in-river migrants).

Popula tion	05/ 06	06/ 07	07/ 08	08/ 09	09/ 10	10/ 11	11/ 12	12/ 13	13/ 14	14/ 15	15/ 16	16/ 17	17/ 18	18/ 19	19/ 20	20/ 21	21/ 22	22/ 23	23/ 24	Tot al
(N, in- river)																				
Tucann on River (N, transpo rted)	2	10	18	7	0	1	0	1	0	0	1	0	3	4	2	10	1	2	1	63
Clearw ater River (H, in- river)	13	30	46	16 3	75	46 9	59 2	49 2	24 1	32 2	26 6	46 7	15 5	23 4	70	20 8	12 8	50 8	36 5	484 4
Clearw ater River (H,	23	4	2	13	20	21 0	12 9	15 8	74	46	51	10 4	5	21	3	10 9	41	44	29	108 6

Table 1. The number of fish per run year from each combination of natal tributary, rearing type (natural or hatchery origin), and juvenile pathway (transported or in-river migrants).

Popula tion	05/ 06	06/ 07	07/ 08	08/ 09	09/ 10	10/ 11	11/ 12	12/ 13	13/ 14	14/ 15	15/ 16	16/ 17	17/ 18	18/ 19	19/ 20	20/ 21	21/ 22	22/ 23	23/ 24	Tot al
transpo rted)																				
Clearw ater River (N, in- river)	13	6	20	51	87	12 8	10 5	63	69	23 4	84	32	20	15	22	44	16	43	23	107 5
Clearw ater River (N, transpo rted)	24	23	30	28	51	72	35	48	19	51	93	50	7	8	23	67	8	10	10	657
Asotin Creek (N,	0	1	11	19	19	18	23	27	18	43	37	13	4	9	7	10	8	7	1	275

Table 1. The number of fish per run year from each combination of natal tributary, rearing type (natural or hatchery origin), and juvenile pathway (transported or in-river migrants).

Popula tion	05/ 06	06/ 07	07/ 08	08/ 09	09/ 10	10/ 11	11/ 12	12/ 13	13/ 14	14/ 15	15/ 16	16/ 17	17/ 18	18/ 19	19/ 20	20/ 21	21/ 22	22/ 23	23/ 24	Tot al
transpo rted)																				
Asotin Creek (N, in- river)	0	0	1	4	11	9	19	18	61	64	20	15	14	6	10	22	11	30	17	332
Grande Ronde River (H, in- river)	18	10	61	75	68 0	38 7	46 9	29 0	30 9	42 7	40 1	28 1	30 5	18 7	93	99	11 8	20 6	24 0	465 6
Grande Ronde River (H, transpo rted)	1	92	10 2	74	45 5	23 2	18 5	12 4	73	14 4	14 8	86	40	38	54	82	28	32	39	202 9

Table 1. The number of fish per run year from each combination of natal tributary, rearing type (natural or hatchery origin), and juvenile pathway (transported or in-river migrants).

Popula tion	05/ 06	06/ 07	07/ 08	08/ 09	09/ 10	10/ 11	11/ 12	12/ 13	13/ 14	14/ 15	15/ 16	16/ 17	17/ 18	18/ 19	19/ 20	20/ 21	21/ 22	22/ 23	23/ 24	Tot al
Grande Ronde River (N, in- river)	8	2	19	21	50	70	65	49	54	53	47	19	13	9	19	10	6	15	8	537
Grande Ronde River (N, transpo rted)	27	13	16	16	15	13	21	15	9	9	21	17	6	10	9	14	3	0	5	239
Salmon River (H, in- river)	14	18	63	71	10 03	74 0	10 17	58 6	69 9	75 3	43 3	26 2	20 8	14 9	11 6	14 3	16 2	19 2	24 1	687 0
Salmon River (H,	22	2	4	7	64 7	49 3	45 4	36 3	26 6	38 4	27 7	16 5	88	68	68	15 4	57	37	49	360 5

Table 1. The number of fish per run year from each combination of natal tributary, rearing type (natural or hatchery origin), and juvenile pathway (transported or in-river migrants).

Popula tion	05/ 06	06/ 07	07/ 08	08/ 09	09/ 10	10/ 11	11/ 12	12/ 13	13/ 14	14/ 15	15/ 16	16/ 17	17/ 18	18/ 19	19/ 20	20/ 21	21/ 22	22/ 23	23/ 24	Tot al
transpo rted)																				
Salmon River (N, in- river)	10	4	8	36	11 7	80	87	45	99	13 5	62	25	16	17	20	23	21	41	27	873
Salmon River (N, transpo rted)	7	17	11	13	41	24	39	25	17	13	28	7	2	4	11	25	6	9	14	313
Imnaha River (H, in- river)	25	31	28	31	35 6	23 3	26 2	91	24 2	24 2	22 5	84	11 4	68	49	54	10 8	16 8	16 3	257 4

Table 1. The number of fish per run year from each combination of natal tributary, rearing type (natural or hatchery origin), and juvenile pathway (transported or in-river migrants).

Popula tion	05/ 06	06/ 07	07/ 08	08/ 09	09/ 10	10/ 11	11/ 12	12/ 13	13/ 14	14/ 15	15/ 16	16/ 17	17/ 18	18/ 19	19/ 20	20/ 21	21/ 22	22/ 23	23/ 24	Tot al
Imnaha River (H, transpo rted)	6	5	5	2	37 8	20 9	13 0	70	95	16 6	18 2	72	50	35	24	41	13	13	29	152 5
Imnaha River (N, in- river)	19	5	11	45	96	77	79	42	63	79	84	34	21	16	21	30	31	42	52	847
Imnaha River (N, transpo rted)	19	9	24	79	55	47	64	28	30	50	78	24	16	8	19	23	11	5	15	604
Total	29 17	41 02	21 84	24 68	71 37	54 86	60 47	41 68	40 63	50 80	43 46	25 77	18 95	14 84	12 18	17 07	12 04	21 54	21 64	624 01

Appendix D. Covariate data summaries

In this section, we present summaries of the three basin condition covariates incorporated in this model: temperature, spill volume, and number of winter spill days. We first present summary tables that show the differences in these covariates by run year and by dam, and then present figures that show the fine-scale details in these trends by dam and across year.

Table 1. Mean temperature (degrees Celsius) by run year across the dams in this study. Dam abbreviations are the ones listed in Table 1 of the main text.

Run Year	BON	MCN	PRA	RIS	RRE	WEL	ICH	LGR
05/06	12.60	11.81	10.93	10.55	10.54	10.36	11.90	11.01
06/07	12.70	11.91	11.03	10.66	10.64	10.46	12.00	11.11
07/08	12.34	11.55	10.67	10.29	10.28	10.10	11.64	10.75
08/09	12.14	11.35	10.47	10.10	10.09	9.90	11.44	10.55
09/10	12.80	12.01	11.13	10.75	10.74	10.56	12.10	11.21
10/11	12.36	11.58	10.70	10.32	10.31	10.13	11.67	10.78

Table 1. Mean temperature (degrees Celsius) by run year across the dams in this study. Dam abbreviations are the ones listed in Table 1 of the main text.

Run Year	BON	MCN	PRA	RIS	RRE	WEL	ICH	LGR
11/12	12.18	11.39	10.52	10.14	10.13	9.94	11.49	10.59
12/13	12.81	12.02	11.14	10.77	10.75	10.57	12.11	11.22
13/14	12.92	12.13	11.26	10.88	10.87	10.68	12.23	11.33
14/15	13.72	12.93	12.06	11.68	11.67	11.49	13.03	12.13
15/16	14.02	13.23	12.35	11.98	11.96	11.78	13.32	12.43
16/17	13.08	12.30	11.42	11.04	11.03	10.85	12.39	11.50
17/18	13.29	12.50	11.62	11.25	11.23	11.05	12.59	11.70
18/19	13.24	12.45	11.57	11.19	11.18	11.00	12.54	11.65

Table 1. Mean temperature (degrees Celsius) by run year across the dams in this study. Dam abbreviations are the ones listed in Table 1 of the main text.

Run Year	BON	MCN	PRA	RIS	RRE	WEL	ICH	LGR
19/20	13.25	12.46	11.59	11.21	11.20	11.01	12.56	11.66
20/21	13.15	12.36	11.49	11.11	11.10	10.91	12.46	11.56
21/22	13.18	12.39	11.52	11.14	11.13	10.94	12.49	11.59
22/23	12.88	12.09	11.21	10.83	10.82	10.64	12.18	11.29
23/24	13.90	13.11	12.23	11.86	11.85	11.66	13.20	12.31

Table 2. Mean spill volume (kcfs) by run year across the dams in this study. Dam abbreviations are the ones listed in Table 1 of the main text.

Run Year	BON	MCN	PRA	RIS	RRE	WEL	ICH	LGR
05/06	41.81	48.98	22.65	9.17	5.45	6.93	16.50	12.10

Table 2. Mean spill volume (kcfs) by run year across the dams in this study. Dam abbreviations are the ones listed in Table 1 of the main text.

Run Year	BON	MCN	PRA	RIS	RRE	WEL	ICH	LGR
06/07	41.00	44.03	13.77	8.11	5.14	9.49	13.98	8.91
07/08	42.10	37.95	8.24	8.01	3.82	4.60	13.54	9.87
08/09	43.57	45.81	10.91	7.92	4.99	6.90	20.56	12.31
09/10	36.58	32.68	8.55	5.91	2.01	2.86	14.49	8.67
10/11	51.84	65.60	22.67	11.34	7.73	8.77	22.48	14.32
11/12	65.71	82.03	43.37	18.61	18.67	21.32	27.35	15.30
12/13	47.16	64.59	41.49	16.55	18.44	17.36	16.08	9.08
13/14	43.32	51.86	21.70	15.52	6.61	7.12	15.22	8.78

Table 2. Mean spill volume (kcfs) by run year across the dams in this study. Dam abbreviations are the ones listed in Table 1 of the main text.

Run Year	BON	MCN	PRA	RIS	RRE	WEL	ICH	LGR
14/15	42.42	46.22	19.42	13.09	5.14	4.86	13.89	7.98
15/16	39.32	35.75	14.26	7.67	3.48	4.63	12.97	6.92
16/17	71.28	74.21	35.89	20.11	19.61	12.14	29.43	19.21
17/18	59.17	69.46	35.61	24.07	18.67	17.40	27.93	14.83
18/19	42.83	49.98	14.60	8.49	5.45	6.87	23.44	12.87
19/20	43.00	49.63	13.27	9.74	6.19	5.36	16.00	13.87
20/21	43.06	49.52	19.19	14.76	10.09	10.14	14.71	13.45
21/22	42.98	47.77	15.57	9.05	3.11	6.65	12.65	10.96

Table 2. Mean spill volume (kcfs) by run year across the dams in this study. Dam abbreviations are the ones listed in Table 1 of the main text.

Run Year	BON	MCN	PRA	RIS	RRE	WEL	ICH	LGR
22/23	51.71	65.12	30.36	20.68	11.20	14.26	21.91	16.43
23/24	43.82	38.14	10.31	5.97	1.58	2.68	16.60	17.13

Table 3. Number of winter (January - March) spill days by run year across the dams in this study. Dam abbreviations are the ones listed in Table 1 of the main text. Please note that Bonneville Dam is not included in this plot because it is not an overshoot dam for any populations in our study.

Run Year	MCN	PRA	RIS	RRE	WEL	ICH	LGR
05/06	7	3	0	2	9	13	0
06/07	20	10	2	15	25	8	7
07/08	2	6	0	4	9	1	2
08/09	1	14	1	17	13	2	1

Table 3. Number of winter (January - March) spill days by run year across the dams in this study. Dam abbreviations are the ones listed in Table 1 of the main text. Please note that Bonneville Dam is not included in this plot because it is not an overshoot dam for any populations in our study.

Run Year	MCN	PRA	RIS	RRE	WEL	ICH	LGR
09/10	0	0	1	5	1	2	4
10/11	71	29	27	19	21	17	3
11/12	20	11	6	17	14	15	9
12/13	17	17	4	18	18	10	1
13/14	27	27	29	31	23	16	9
14/15	74	52	6	42	36	6	2
15/16	11	6	36	8	3	6	2
16/17	49	43	23	49	19	48	36

Table 3. Number of winter (January - March) spill days by run year across the dams in this study. Dam abbreviations are the ones listed in Table 1 of the main text. Please note that Bonneville Dam is not included in this plot because it is not an overshoot dam for any populations in our study.

Run Year	MCN	PRA	RIS	RRE	WEL	ICH	LGR
17/18	33	41	52	29	65	59	8
18/19	0	8	5	13	20	15	2
19/20	29	20	33	50	10	4	2
20/21	21	35	41	39	24	14	14
21/22	59	46	34	10	42	15	13
22/23	14	28	12	6	13	14	25
23/24	31	25	20	10	6	31	52

In the panels below, plots of temperature, spill volume, and number of winter spill days are shown for each of the mainstem dams in this study. Please note that because the temperature visualized here (and incorporated into the model) is an output from a MARSS model that estimated a single temperature state for the entire Columbia River Basin, all dams have the same trends in temperature, but with different overall magnitudes. The choice to model the entire basin as a single temperature trend was necessitated by significant gaps in data at some dams.

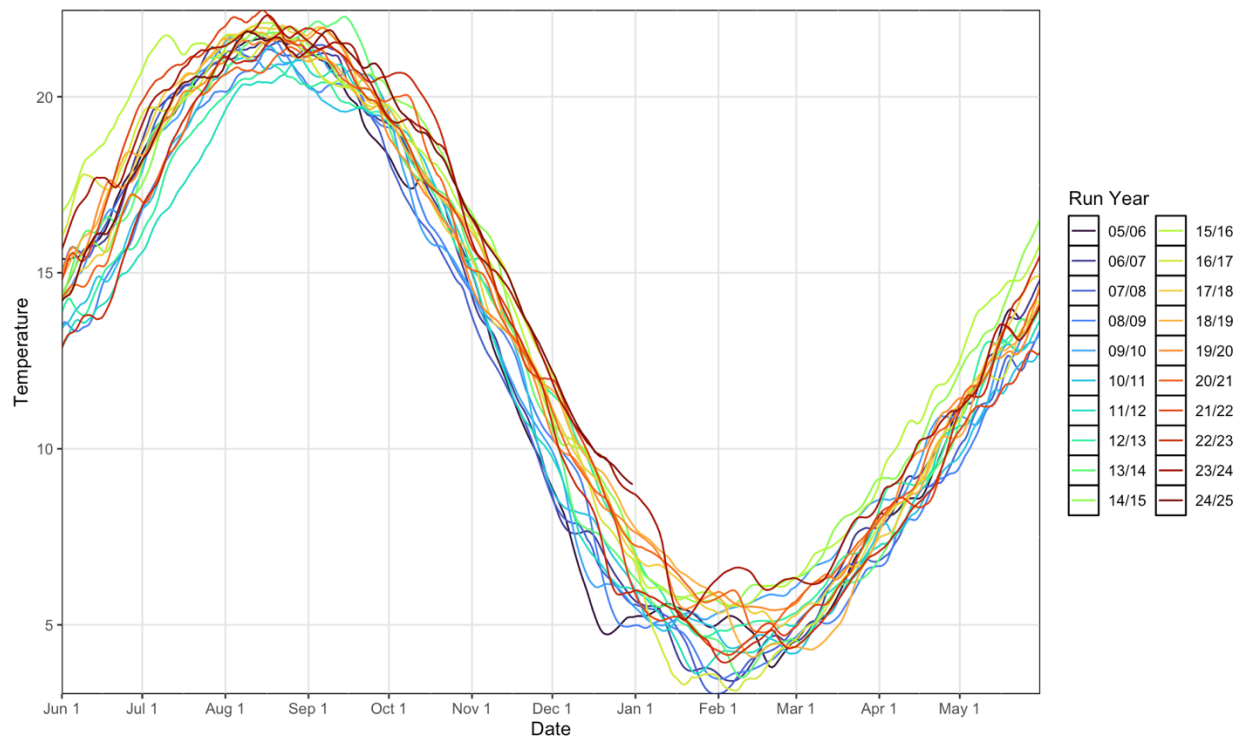


Figure 1. Temperature at Bonneville Dam.

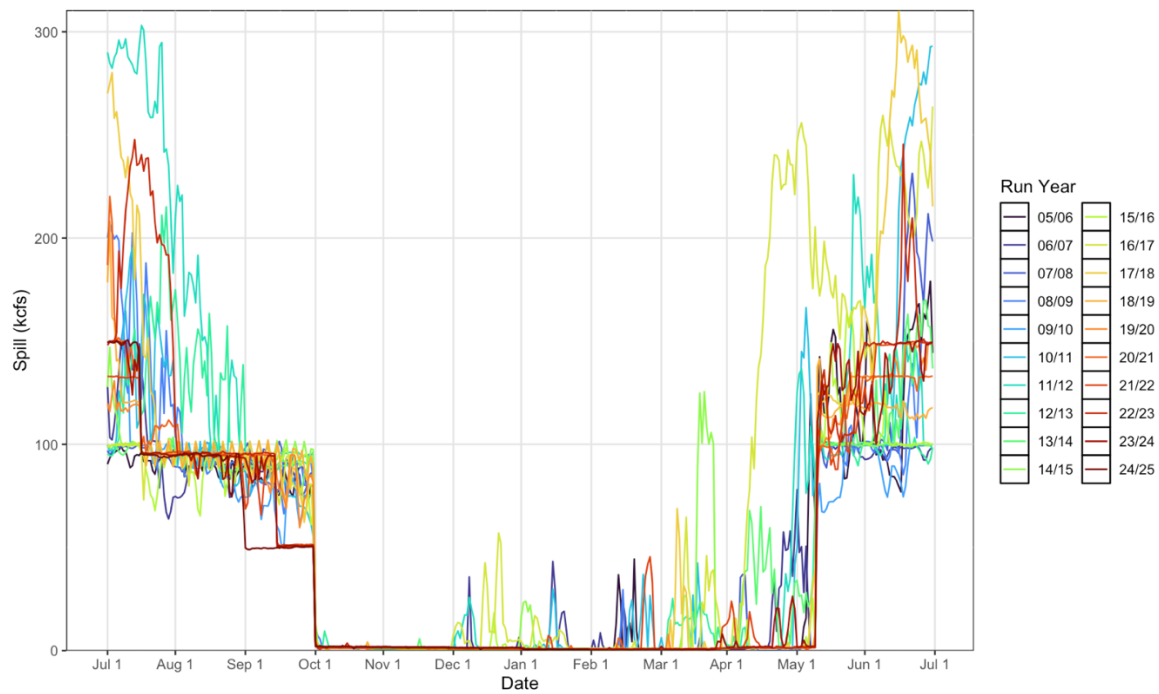


Figure 2. Spill at Bonneville Dam.

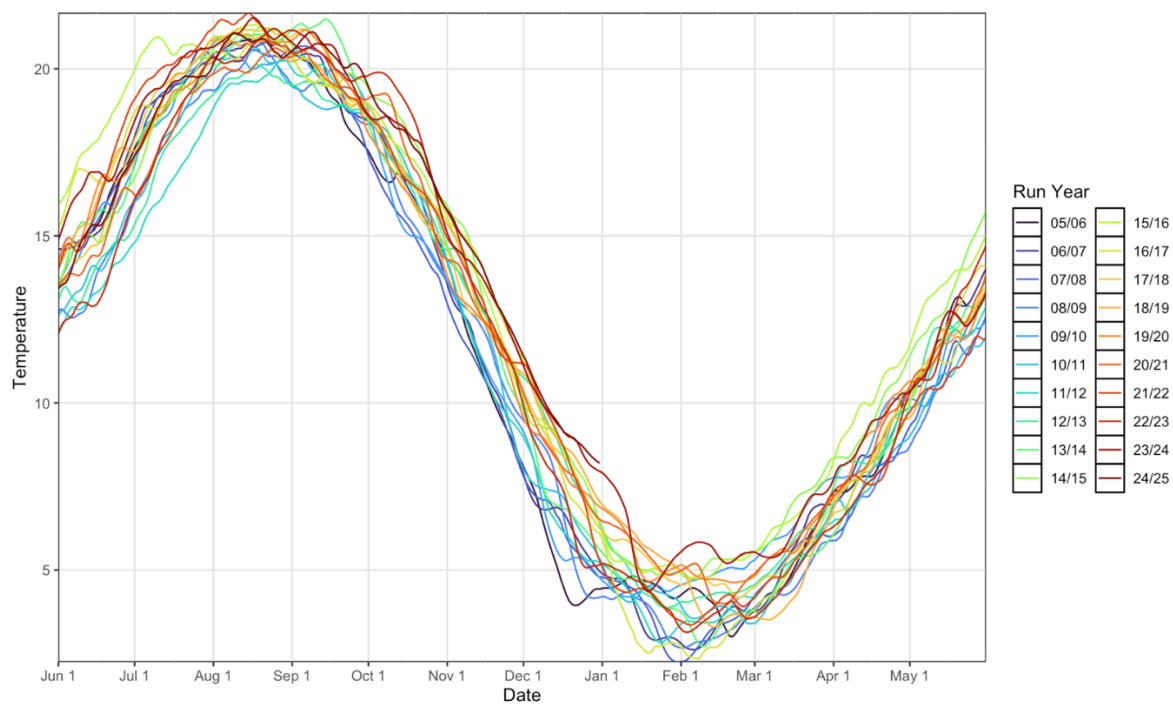


Figure 3. Temperature at McNary Dam.

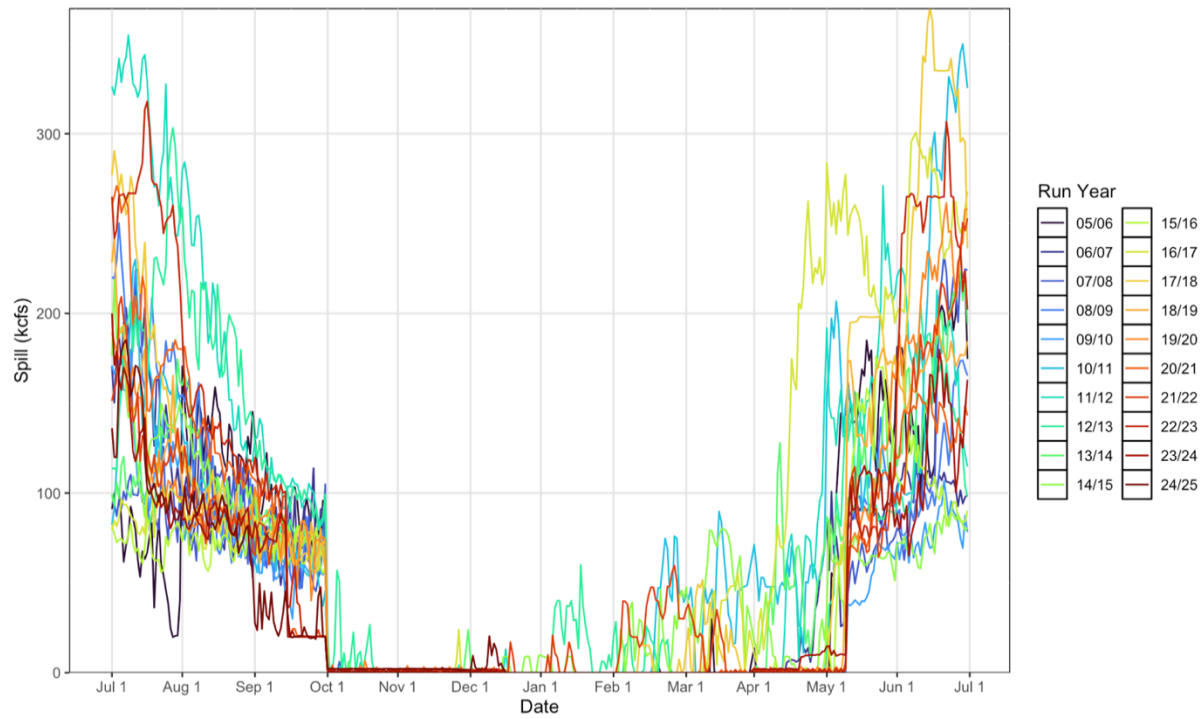


Figure 4. Spill at McNary Dam.

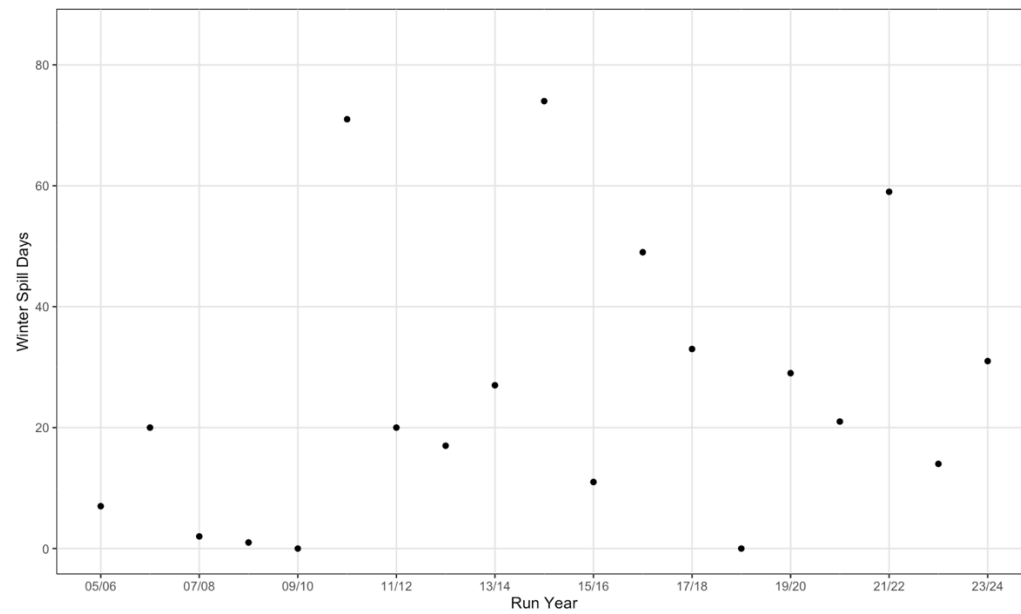


Figure 5. Days of winter spill at McNary Dam.

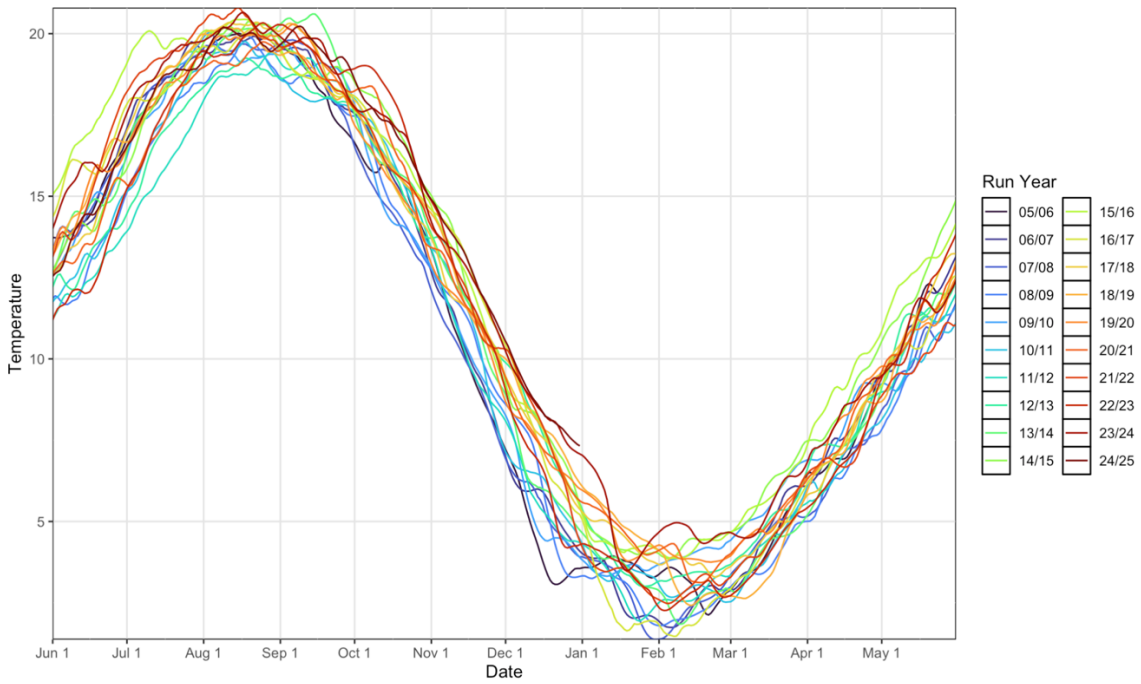


Figure 6. Temperature at Priest Rapids Dam.

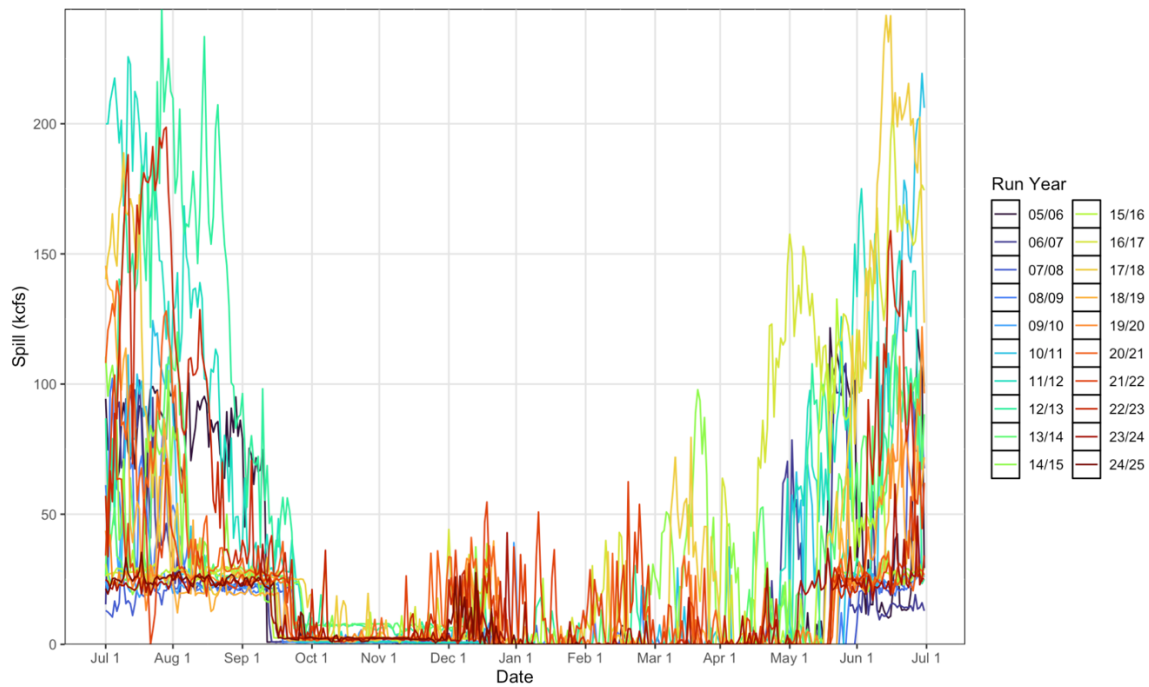


Figure 7. Spill at Priest Rapids Dam.

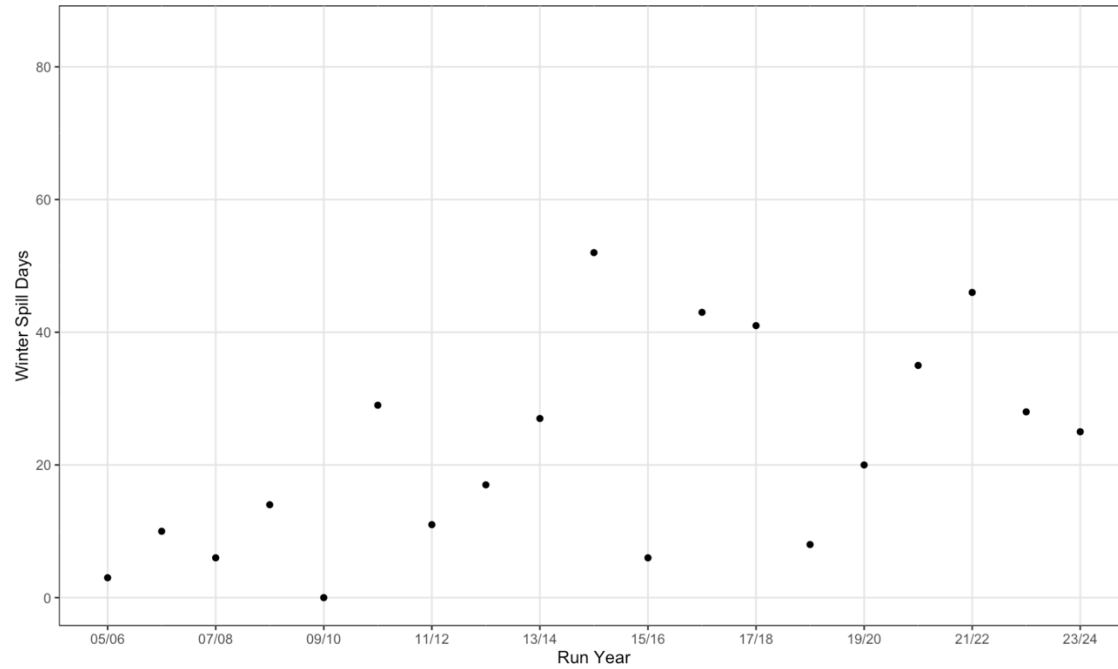


Figure 8. Days of winter spill at Priest Rapids Dam.

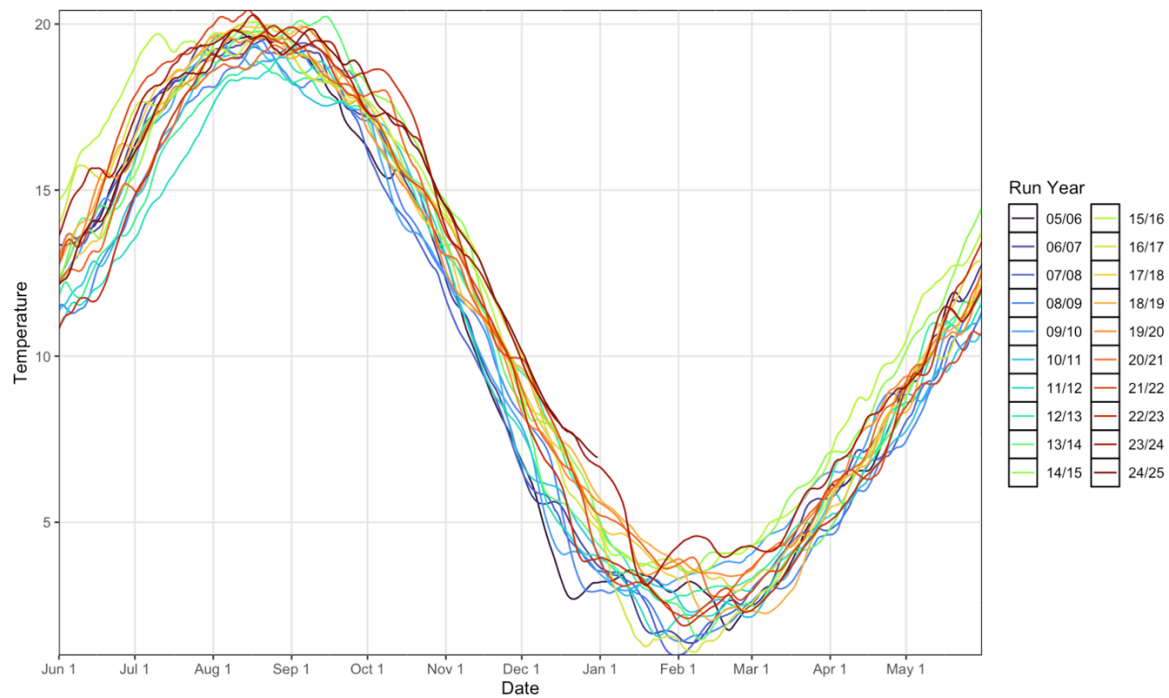


Figure 9. Temperature at Rock Island Dam.

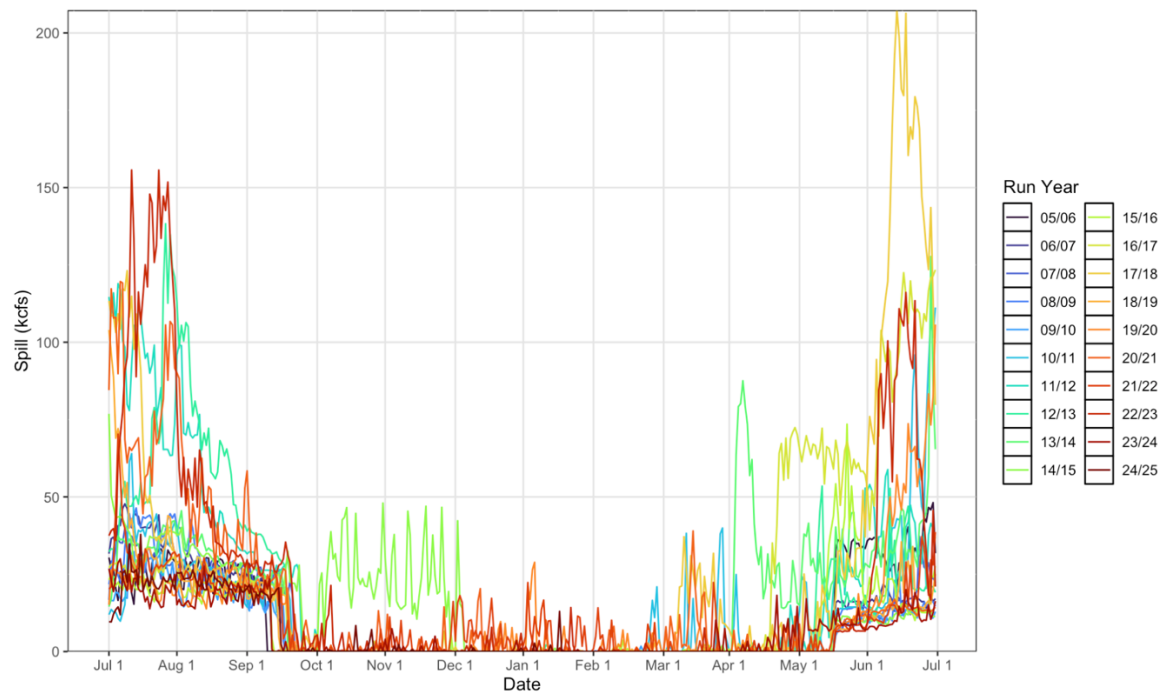


Figure 10. Spill at Rock Island Dam.

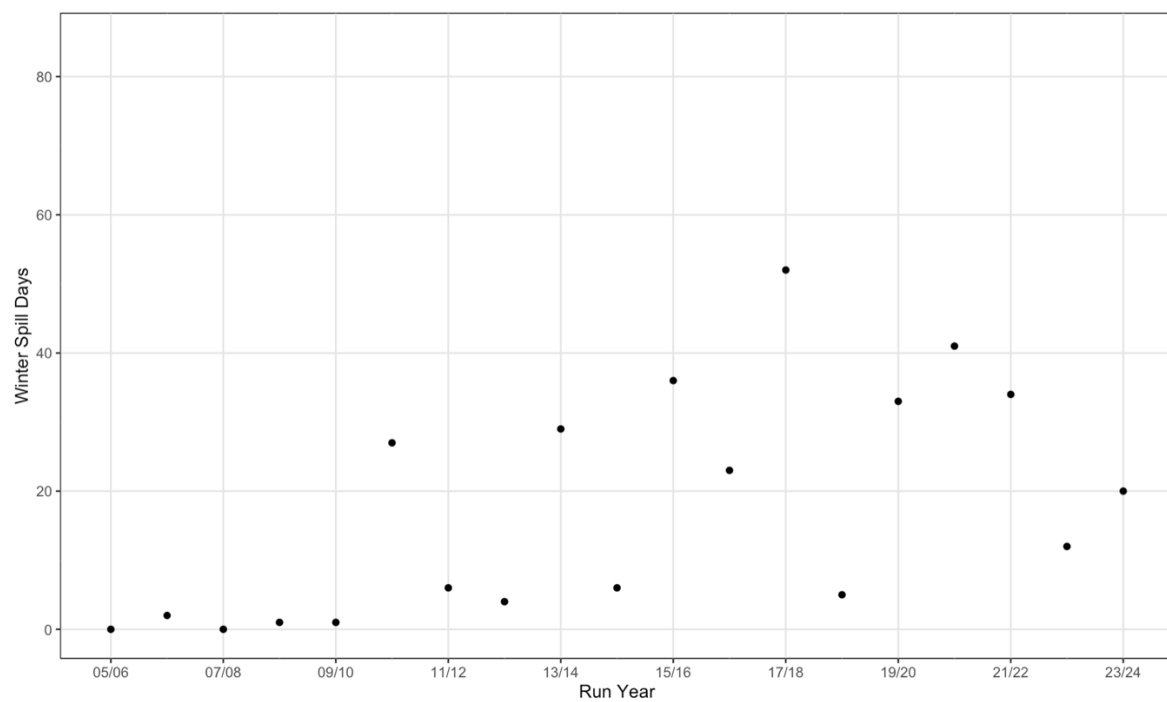


Figure 11. Days of winter spill at Rock Island Dam.

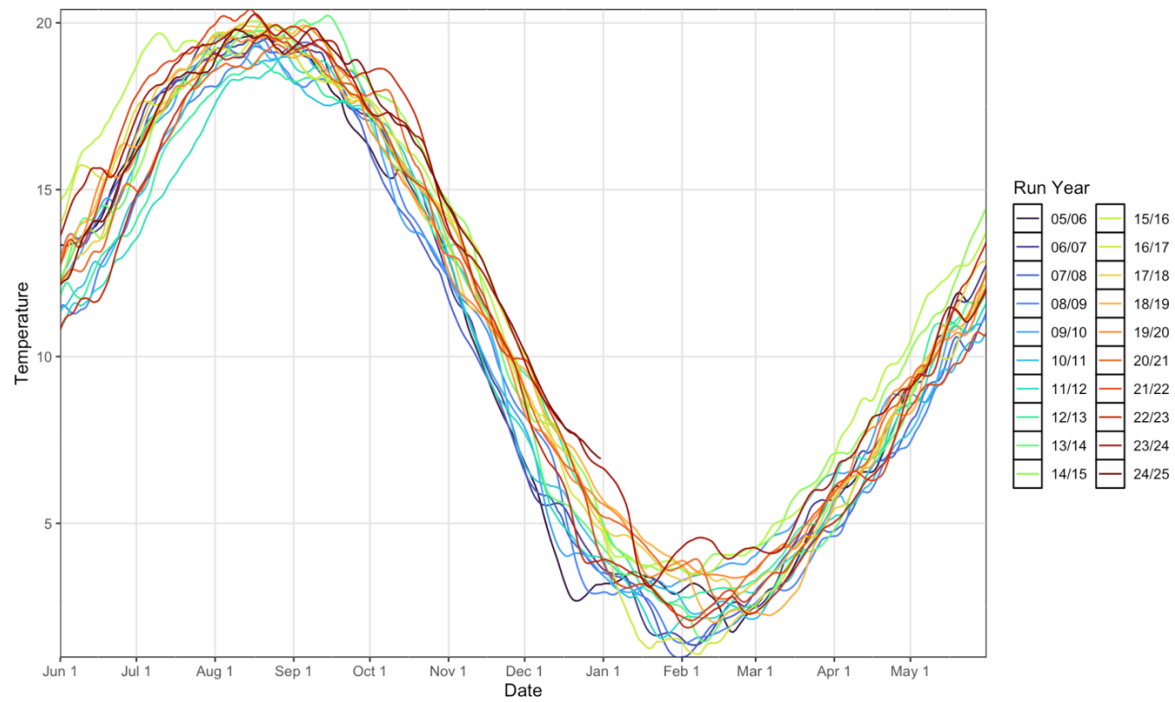


Figure 12. Temperature at Rocky Reach Dam.

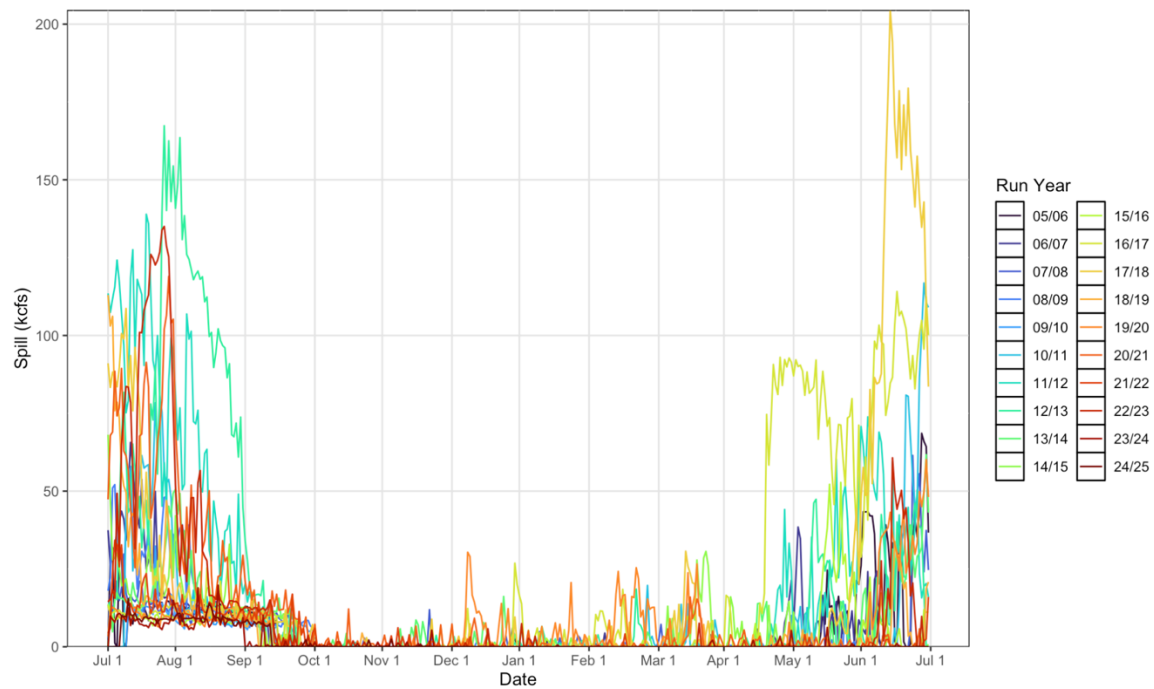


Figure 13. Spill at Rocky Reach Dam.

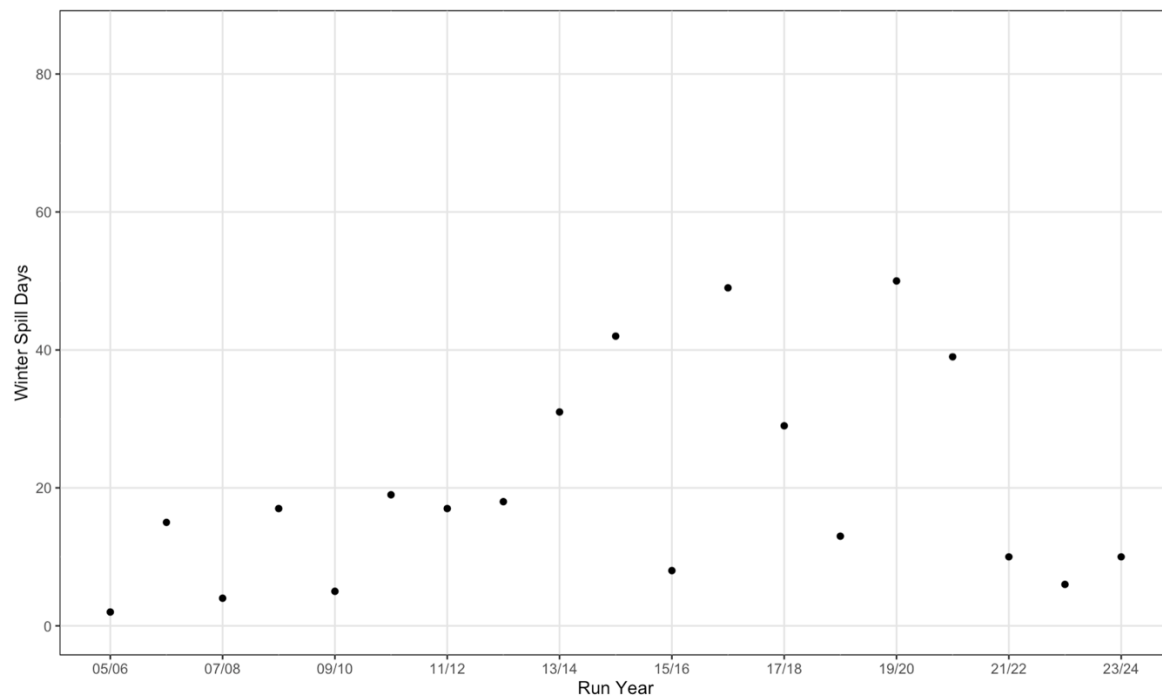


Figure 14. Days of winter spill at Rocky Reach Dam.

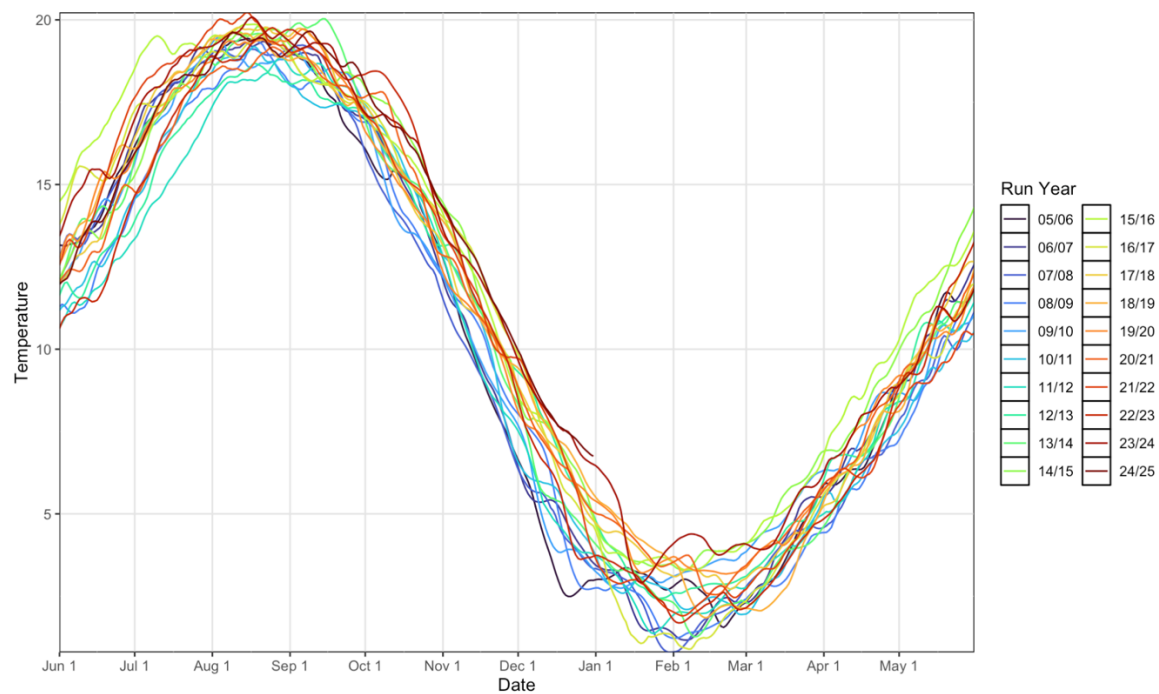


Figure 15. Temperature at Wells Dam.

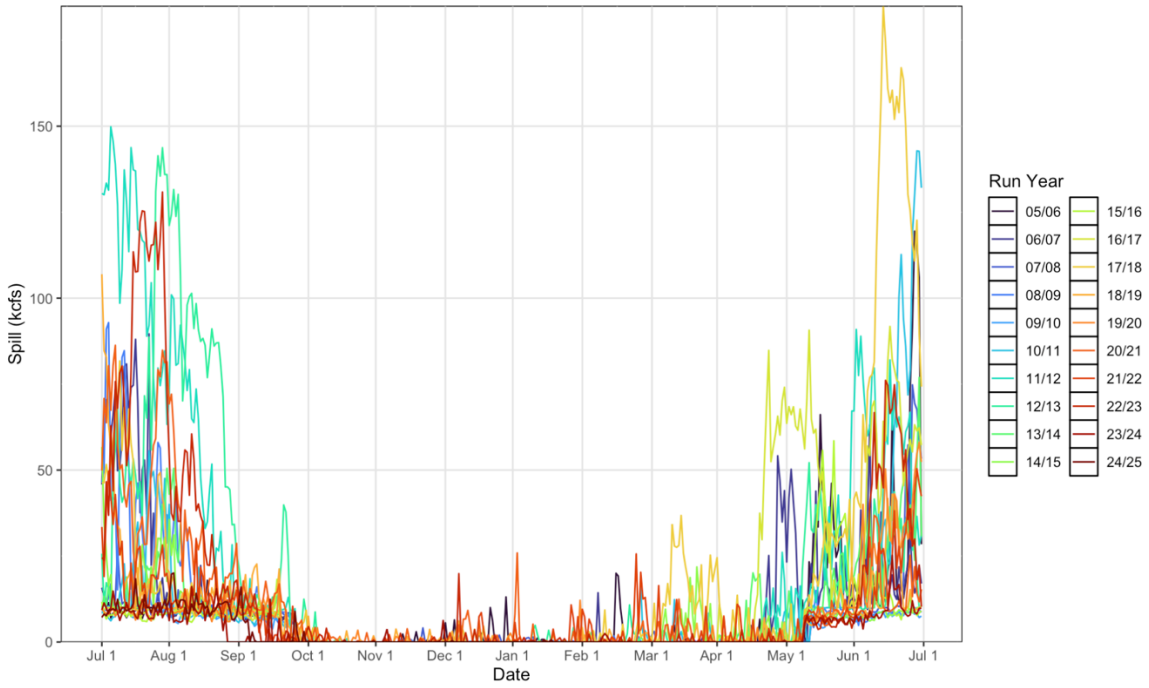


Figure 16. Spill at Wells Dam.

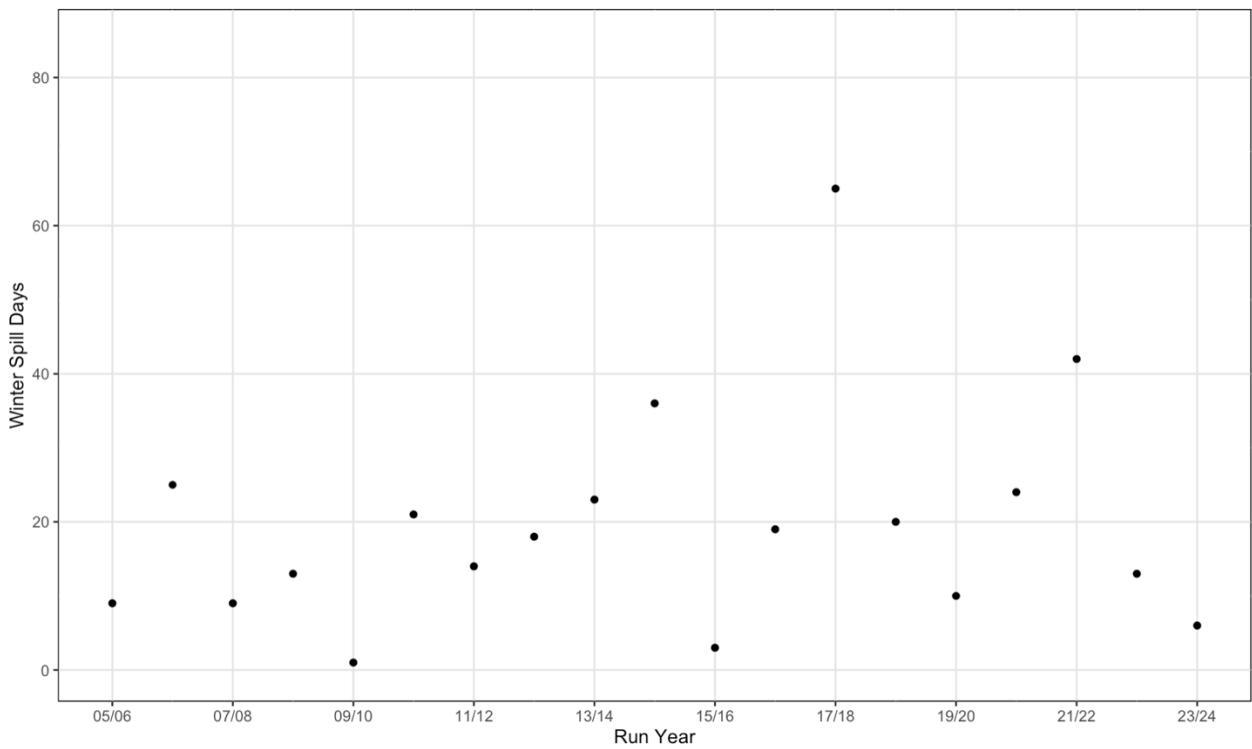


Figure 17. Days of winter spill at Wells Dam.

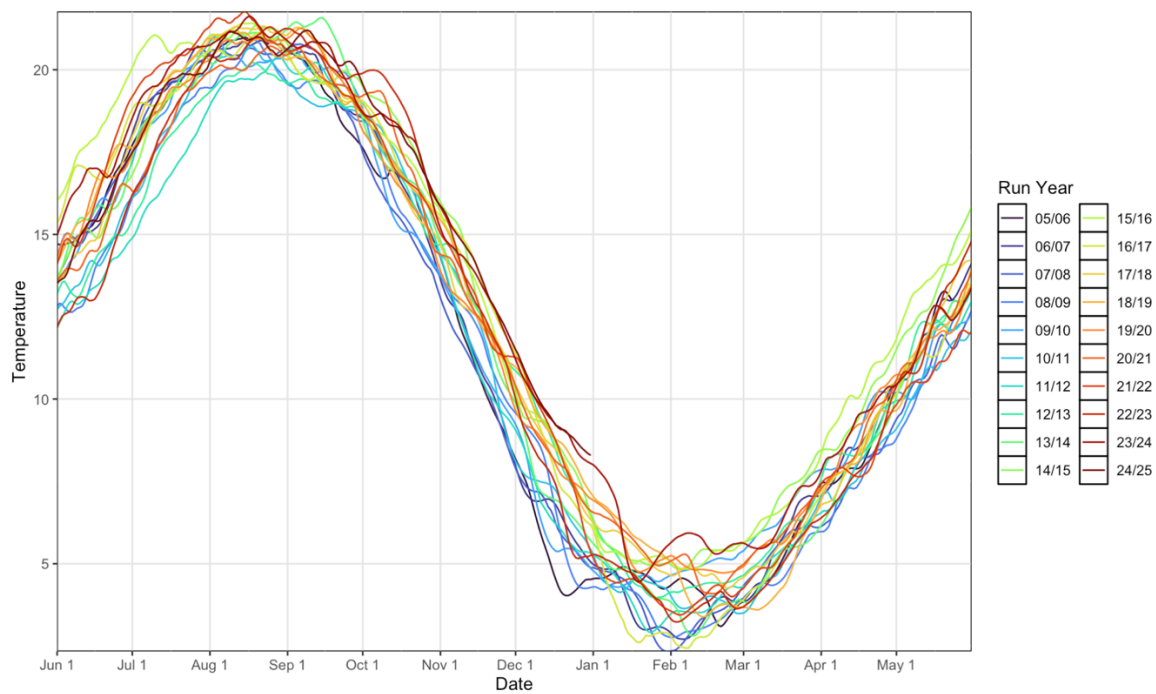


Figure 18. Temperature at Ice Harbor Dam.

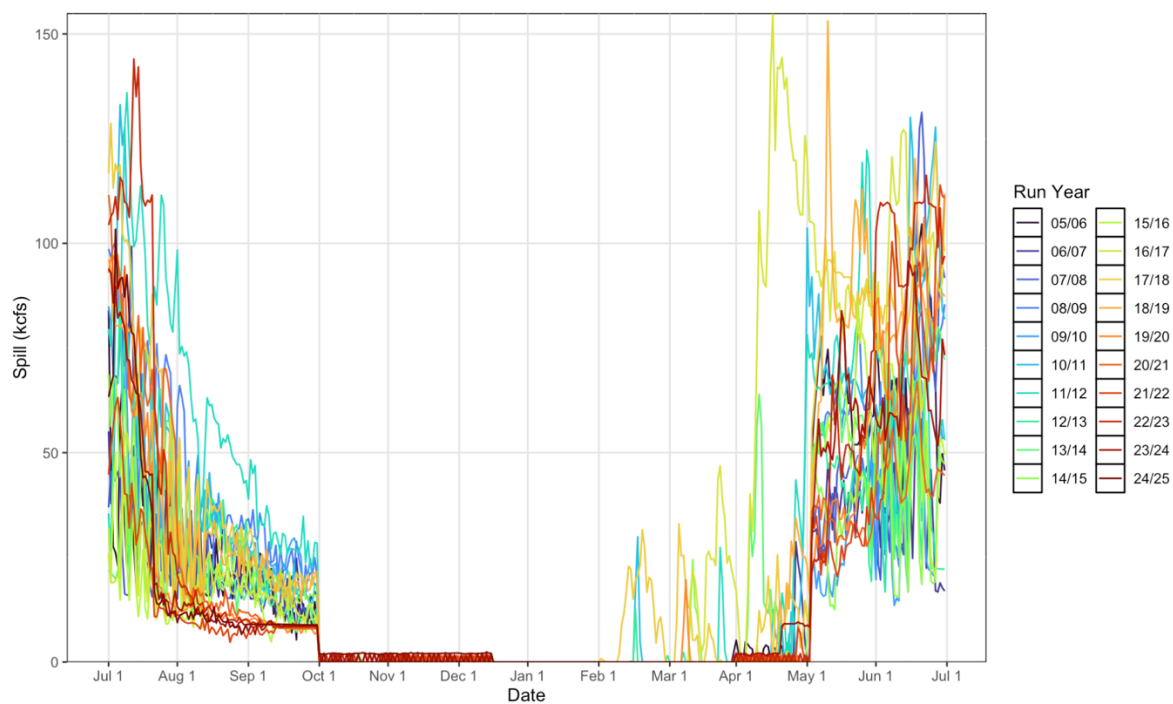


Figure 19. Spill at Ice Harbor Dam.

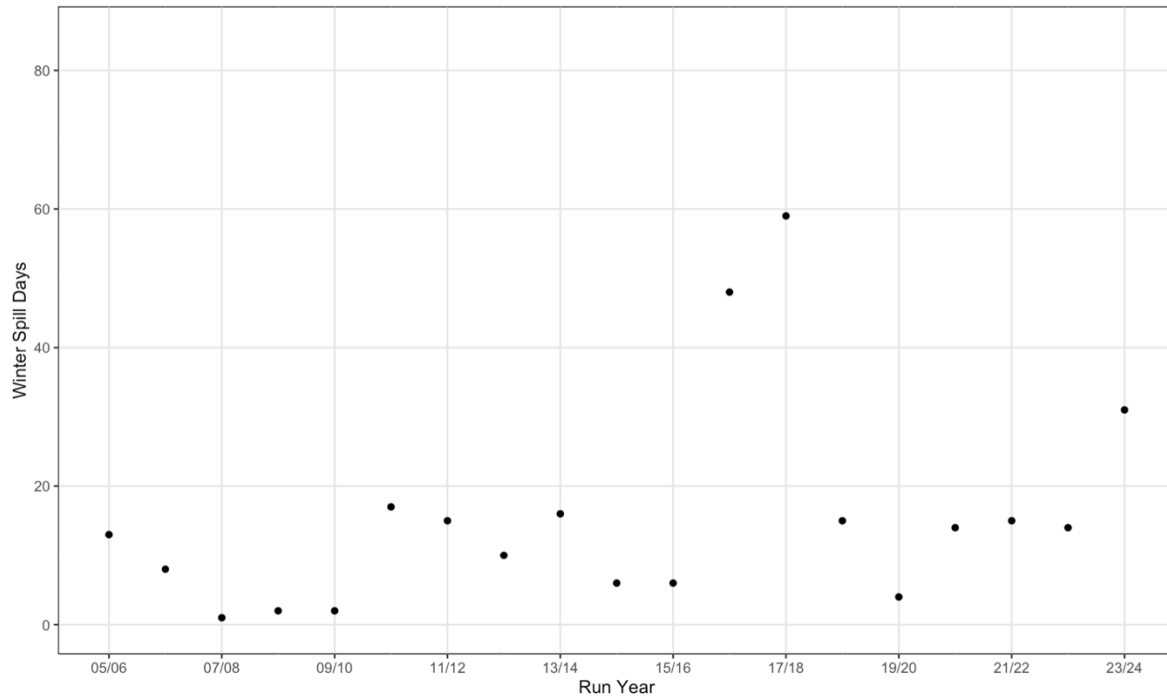


Figure 20. Days of winter spill at Ice Harbor Dam.

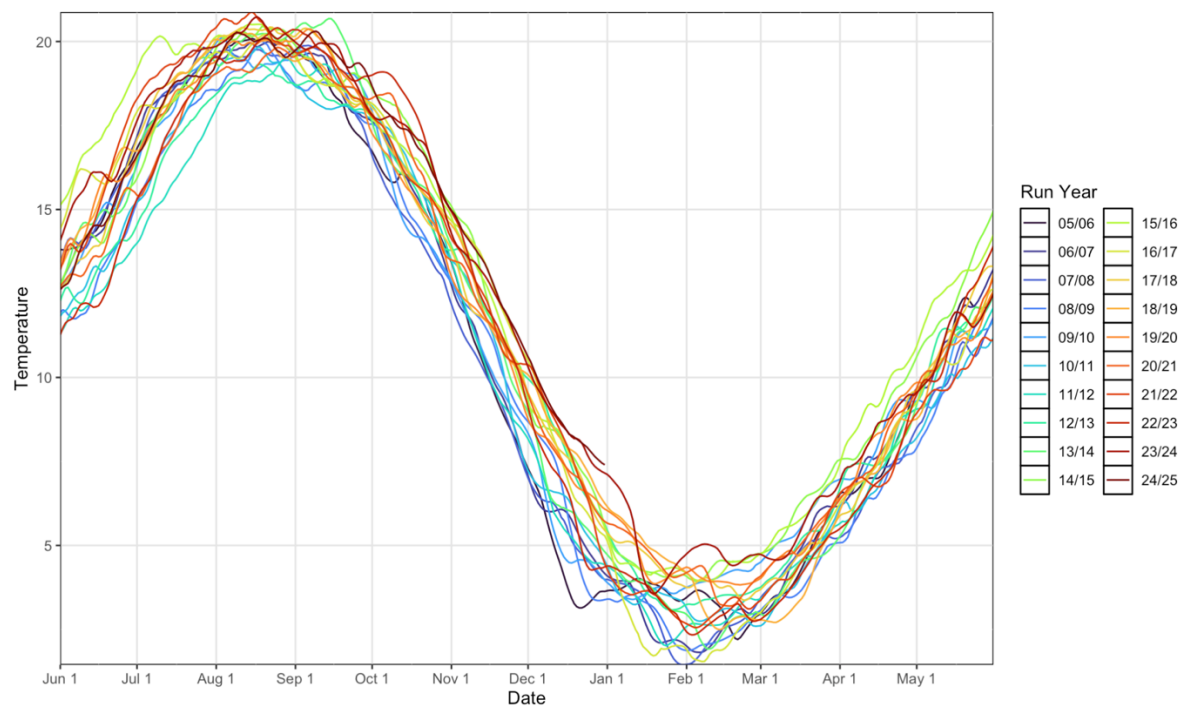


Figure 21. Temperature at Lower Granite Dam.

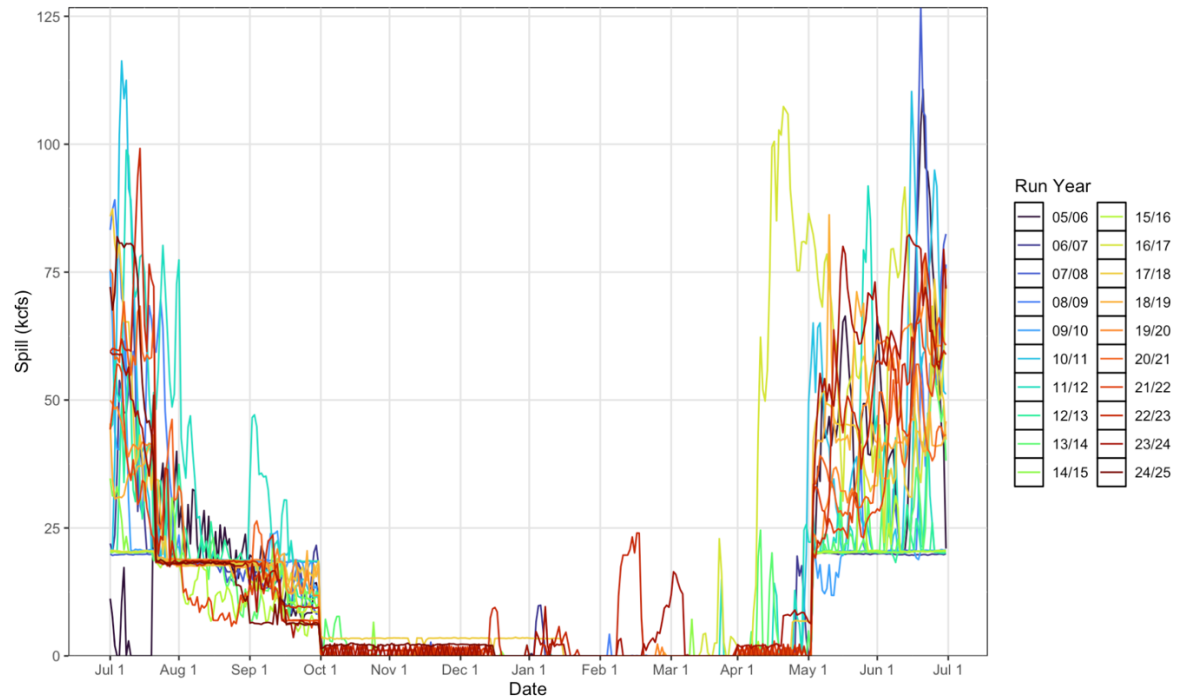


Figure 22. Spill at Lower Granite Dam.

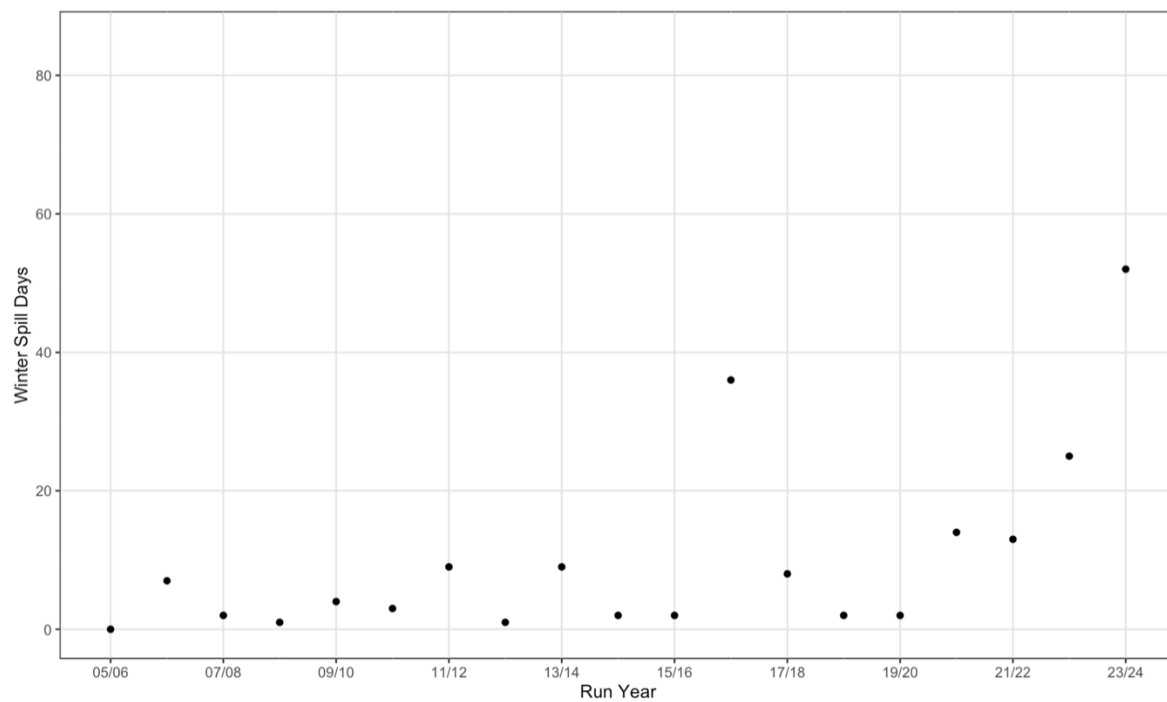


Figure 23. Days of winter spill at Lower Granite Dam.

Appendix E. Post-overshoot fallback timing

Because PIT-tag arrays are largely incapable of directly detecting fallback (most dams do not have PIT antennas in the spillway), we were not able to observe post-overshoot fallback directly. As such, we sought to characterize spillway passage availability during the time of potential fallback as informed by subsequent detections. The figure below shows the next detection after a post-overshoot fallback movement, showing the overall pattern of post-overshoot fallback timing.

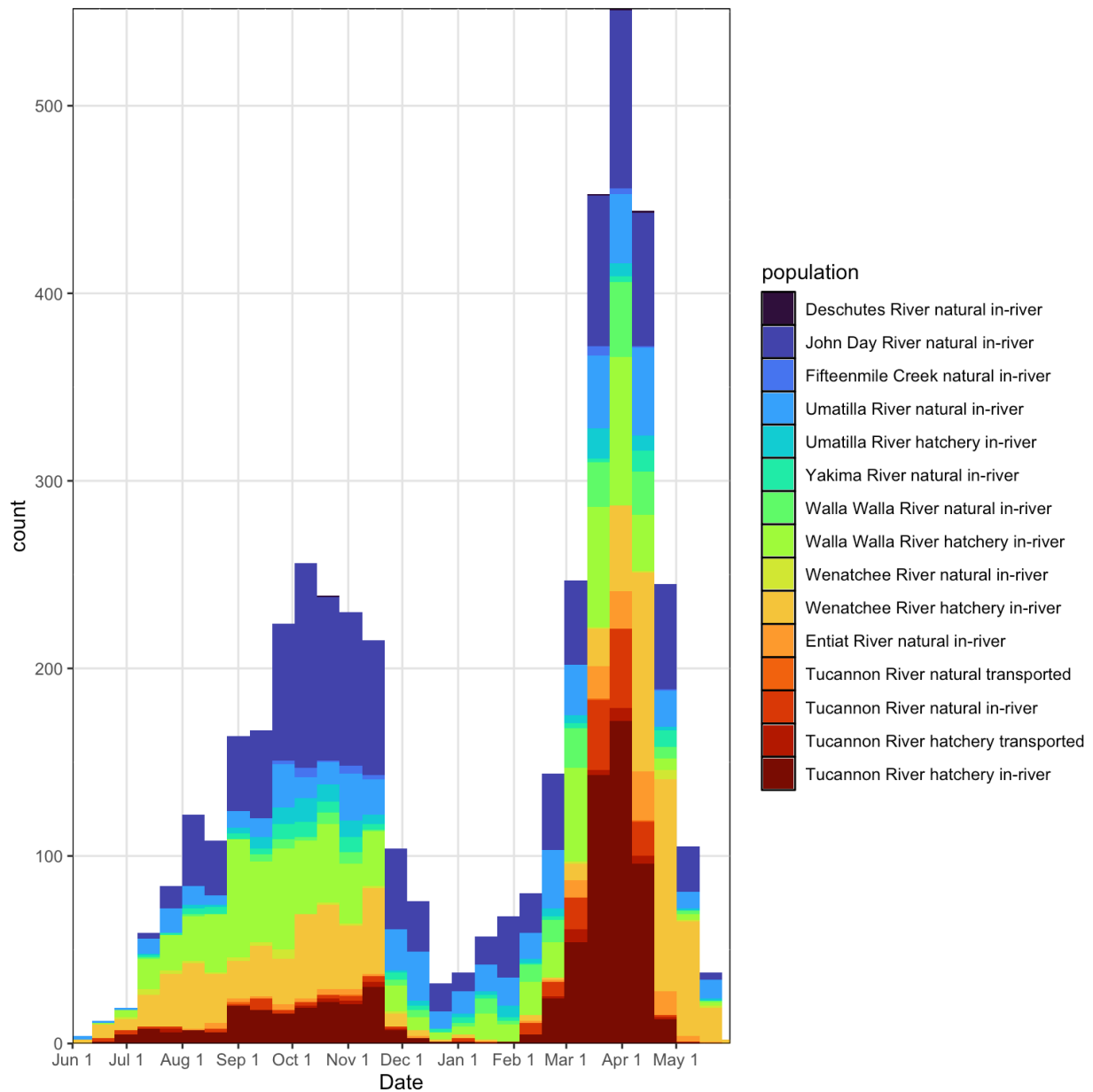


Figure 1. Timing of detections directly following a post-overshoot fallback movement.

The table below shows the proportion of fish from each population that received the January-March spill days covariate, based on their fallback timing.

Table 1. Proportion of overshoot state visits that received the January-March spill days covariate. In Window refers to the number of fish that may have fallen back during the window of time between January 1 and March 31, and therefore received the January-March spill days covariate. Total is the total number of fish that overshoot, and proportion is the proportion of the total fish that may have fallen back in the January-March window.

population	In Window	total	proportion
Deschutes River natural in-river	6	11	0.55
John Day River natural in-river	1328	2703	0.49
Fifteenmile Creek natural in-river	31	55	0.56
Umatilla River natural in-river	482	951	0.51
Umatilla River hatchery in-river	236	366	0.64
Yakima River natural in-river	71	215	0.33
Walla Walla River natural in-river	272	464	0.59
Walla Walla River hatchery in-river	1335	2478	0.54
Entiat River natural in-river	134	197	0.68
Wenatchee River natural in-river	19	73	0.26
Wenatchee River hatchery in-river	1820	4042	0.45

Table 1. Proportion of overshoot state visits that received the January-March spill days covariate. In Window refers to the number of fish that may have fallen back during the window of time between January 1 and March 31, and therefore received the January-March spill days covariate. Total is the total number of fish that overshoot, and proportion is the proportion of the total fish that may have fallen back in the January-March window.

population	In Window	total	proportion
Tucannon River natural in-river	288	373	0.77
Tucannon River natural transported	14	17	0.82
Tucannon River hatchery in-river	1236	1601	0.77
Tucannon River hatchery transported	95	114	0.83

Appendix F. Detection efficiency estimation

The figures below show the estimated relationship between discharge and detection efficiency at the river mouth sites for different tributaries in different site configurations. As mentioned in Appendix A, our a priori hypothesis was that detection efficiency would generally decrease as discharge increases, as increased flow would increase the area that is outside the detection range of the PIT tag arrays. However, as seen below, for some tributaries we estimated a positive relationship between discharge and detection efficiency. This estimated relationship may be the result of spurious correlations, or may be a true positive relationship. Spurious correlations may be due to changes to the PIT-tag antenna configurations or operations that were not captured in our site configuration covariate in the detection level efficiency estimation. While we attempted to capture major changes, an inspection of the operational history and event log summary at each site on the PTAGIS Interrogation Site Metadata reveals numerous events (e.g., battery failures, flood damage, equipment failures and repairs) that may have affected the detection efficiency and confounded the relationship with discharge. However, there may have also been a true positive relationship between discharge and detections efficiency, as there are reasons that higher discharge may actually be favorable for detection efficiency. For example, PIT tag arrays are known to perform poorly in cases where two or more fish pass over the antenna at the same time (Greenberg and Ciller 2000), which may be more likely when flows are low. Furthermore, fish behavior can change with changing stream conditions, and the ability of PIT tag interrogation systems to detect fish can change with conditions that are affected by flow, including water temperature, conductivity, and air temperature (Connolly et al. 2008).

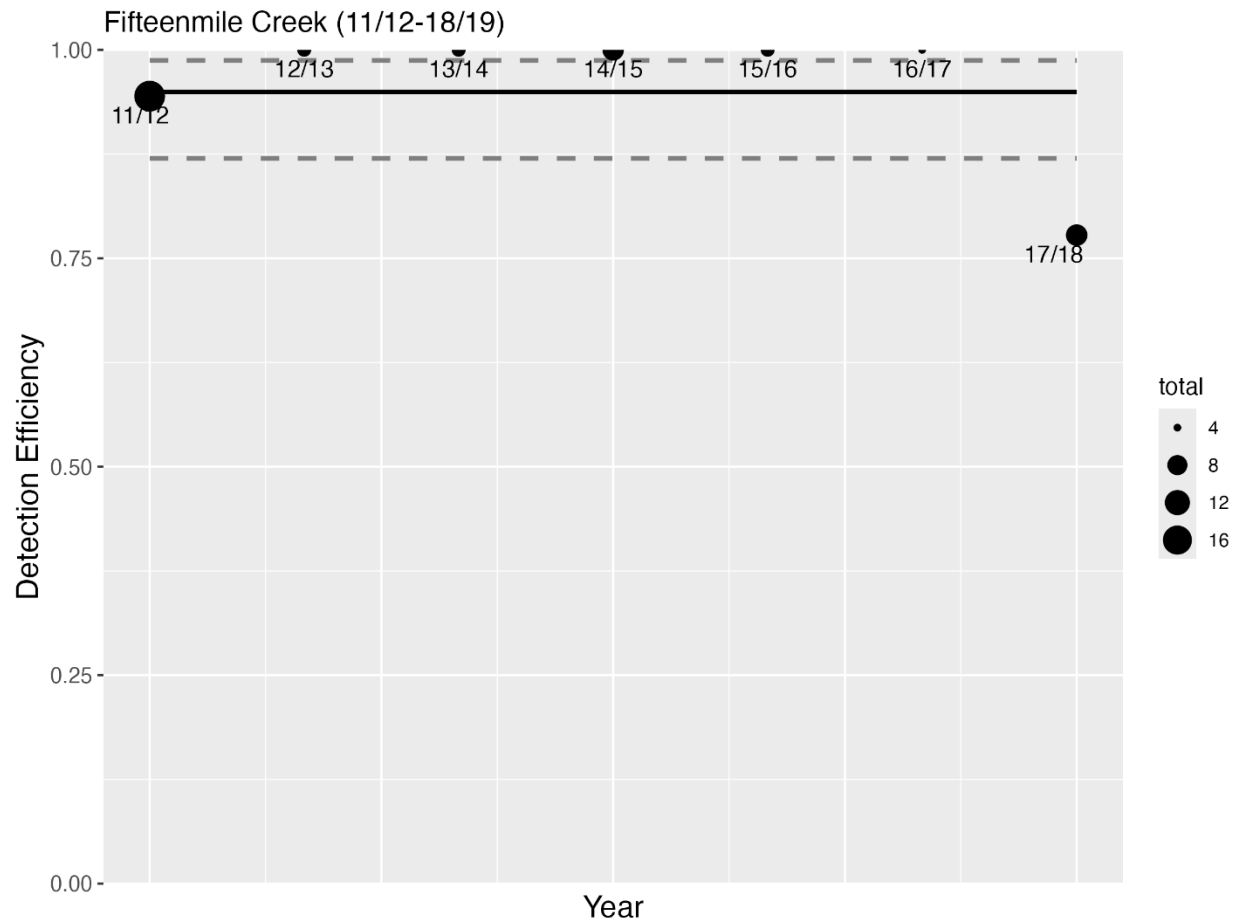


Figure 1. Fifteenmile Creek, estimated detection efficiency.

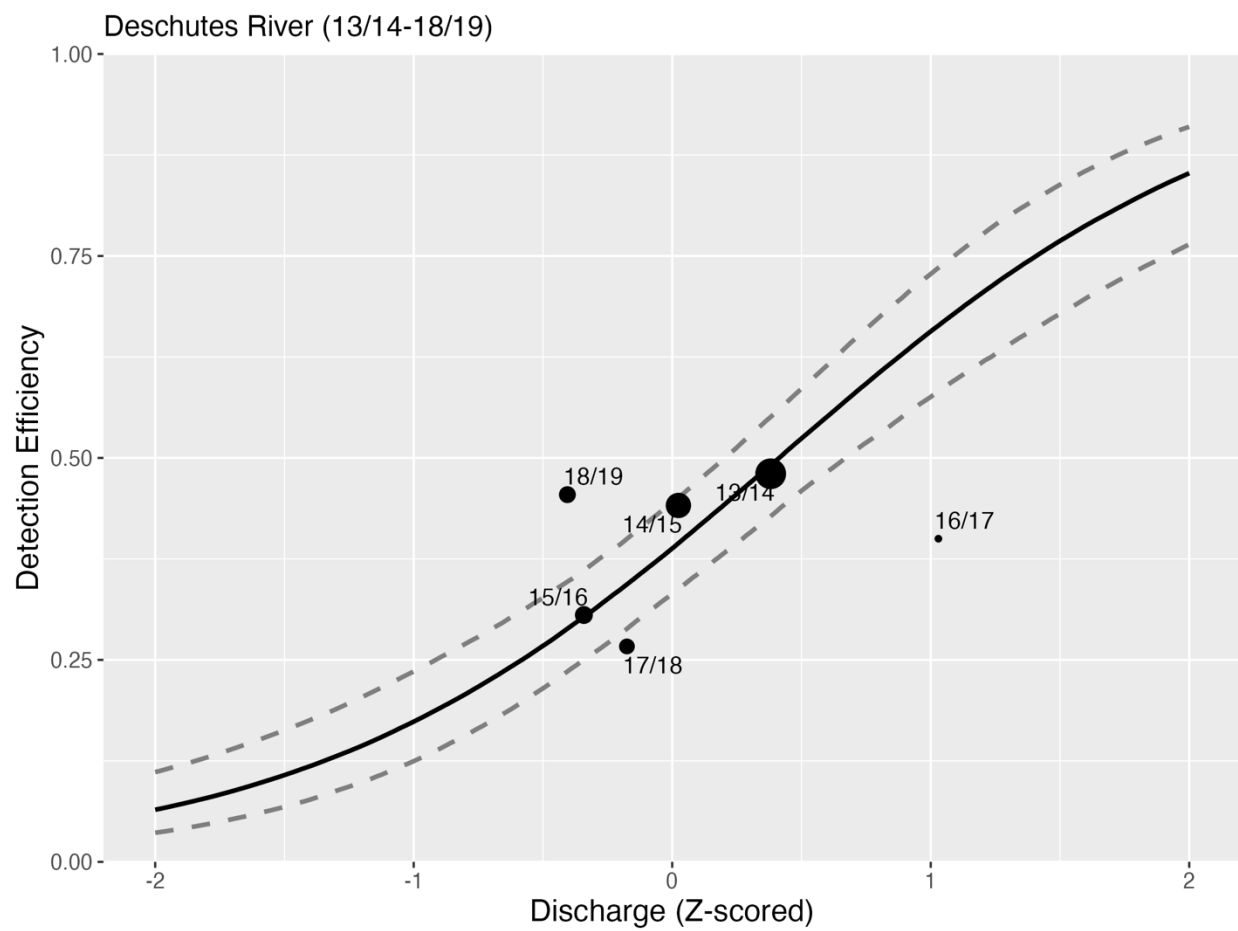


Figure 2. Deschutes River, estimated detection efficiency.

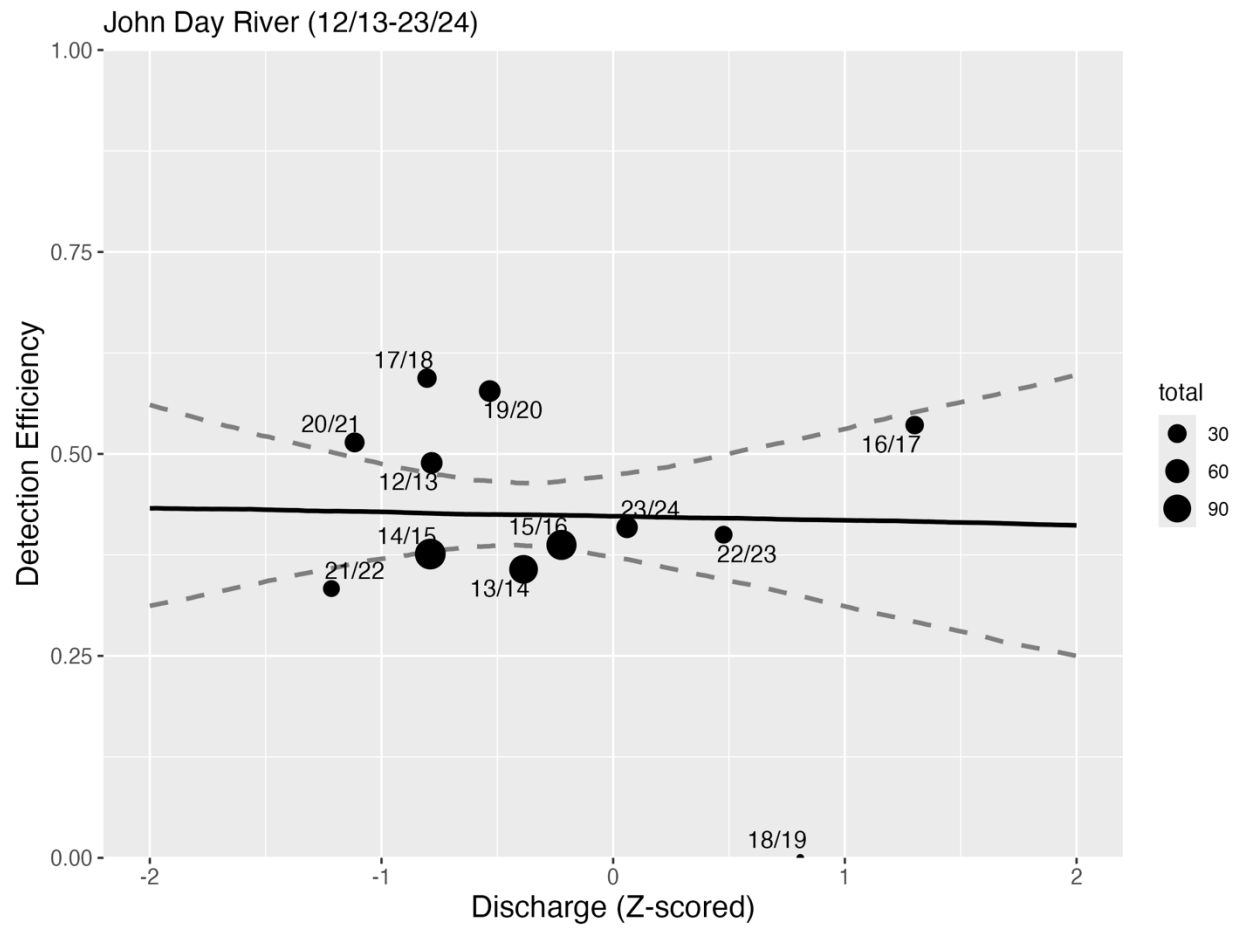


Figure 3. John Day River, estimated detection efficiency.

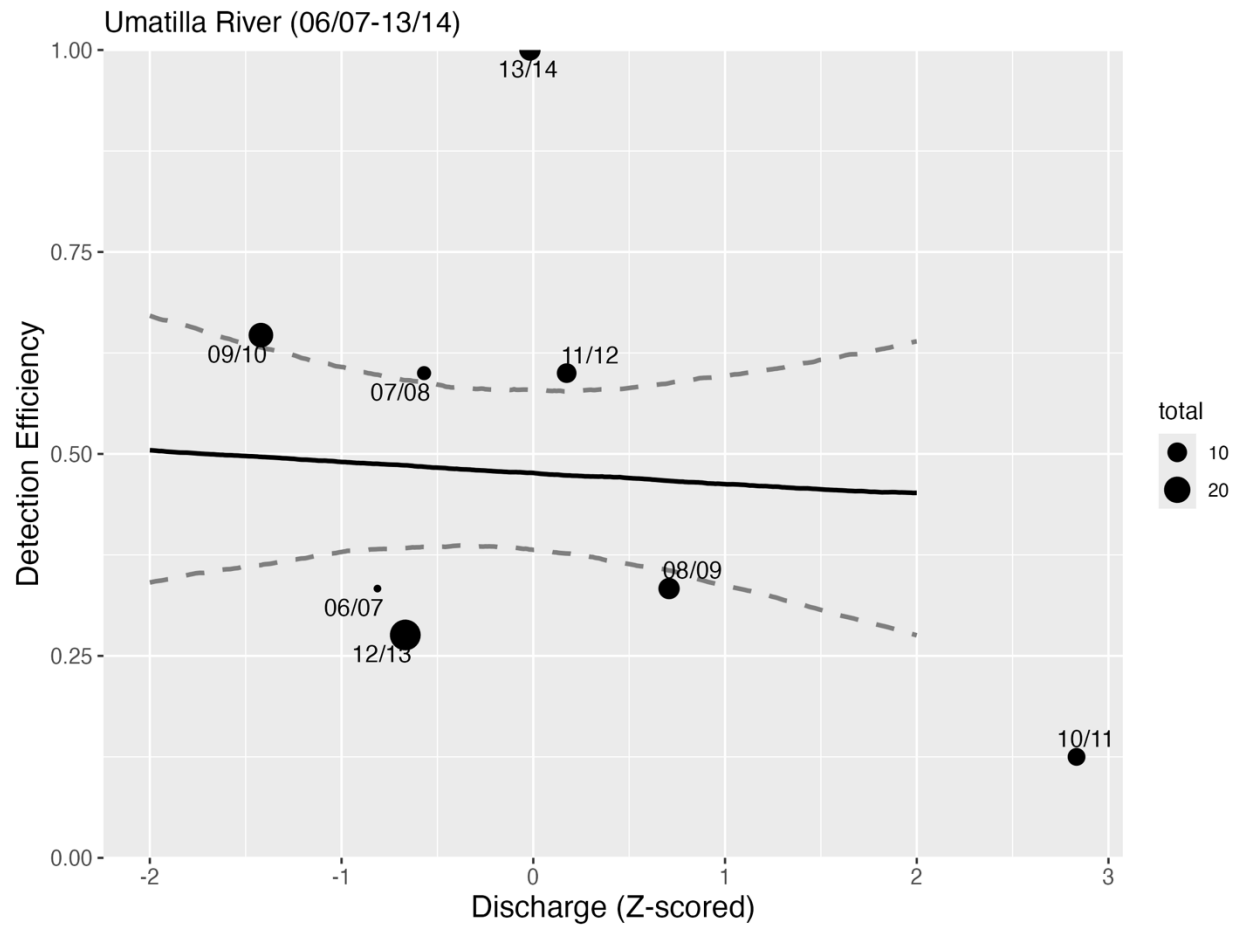


Figure 4. Umatilla River, estimated detection efficiency in time period 1.

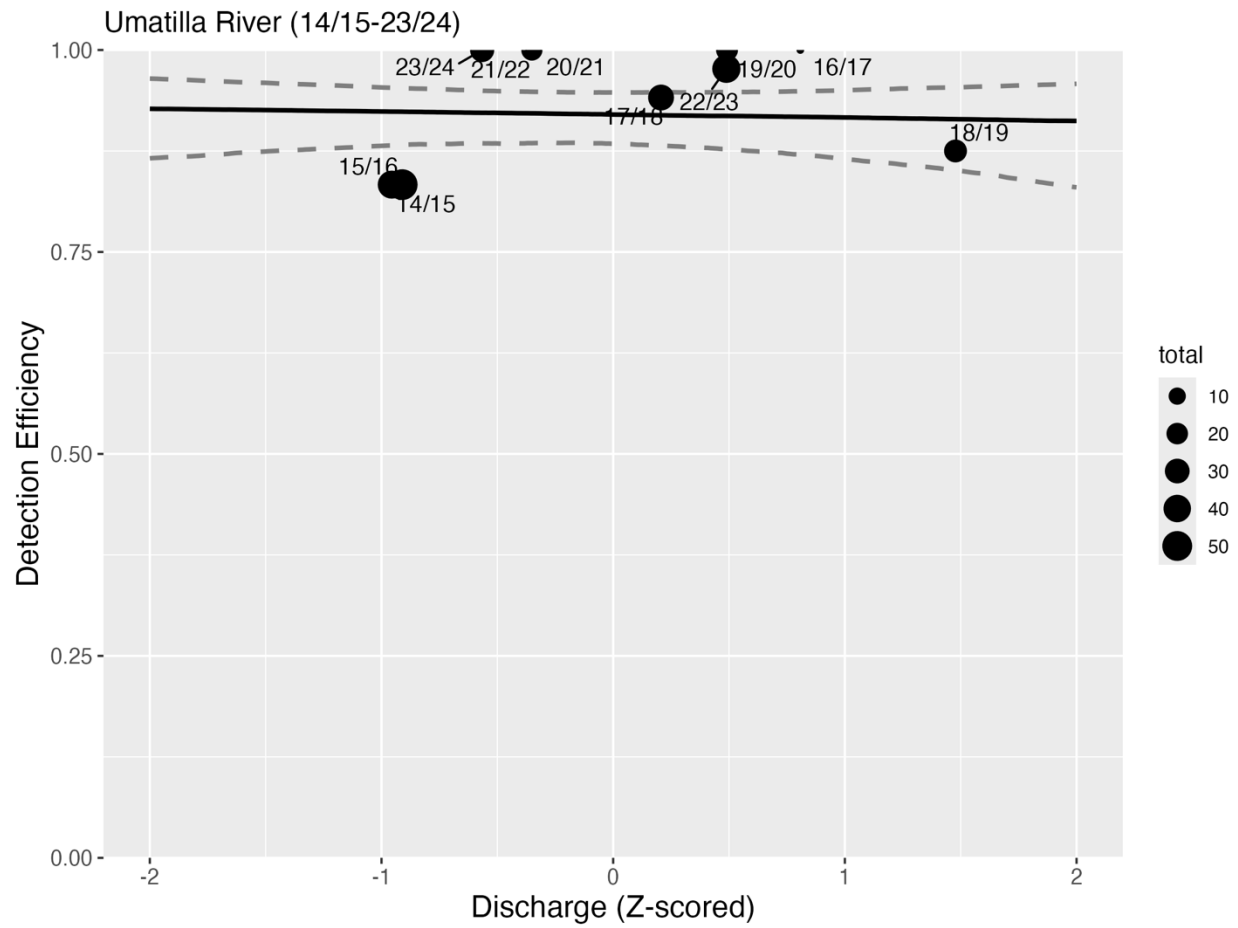


Figure 5. Umatilla River, estimated detection efficiency in time period 2.

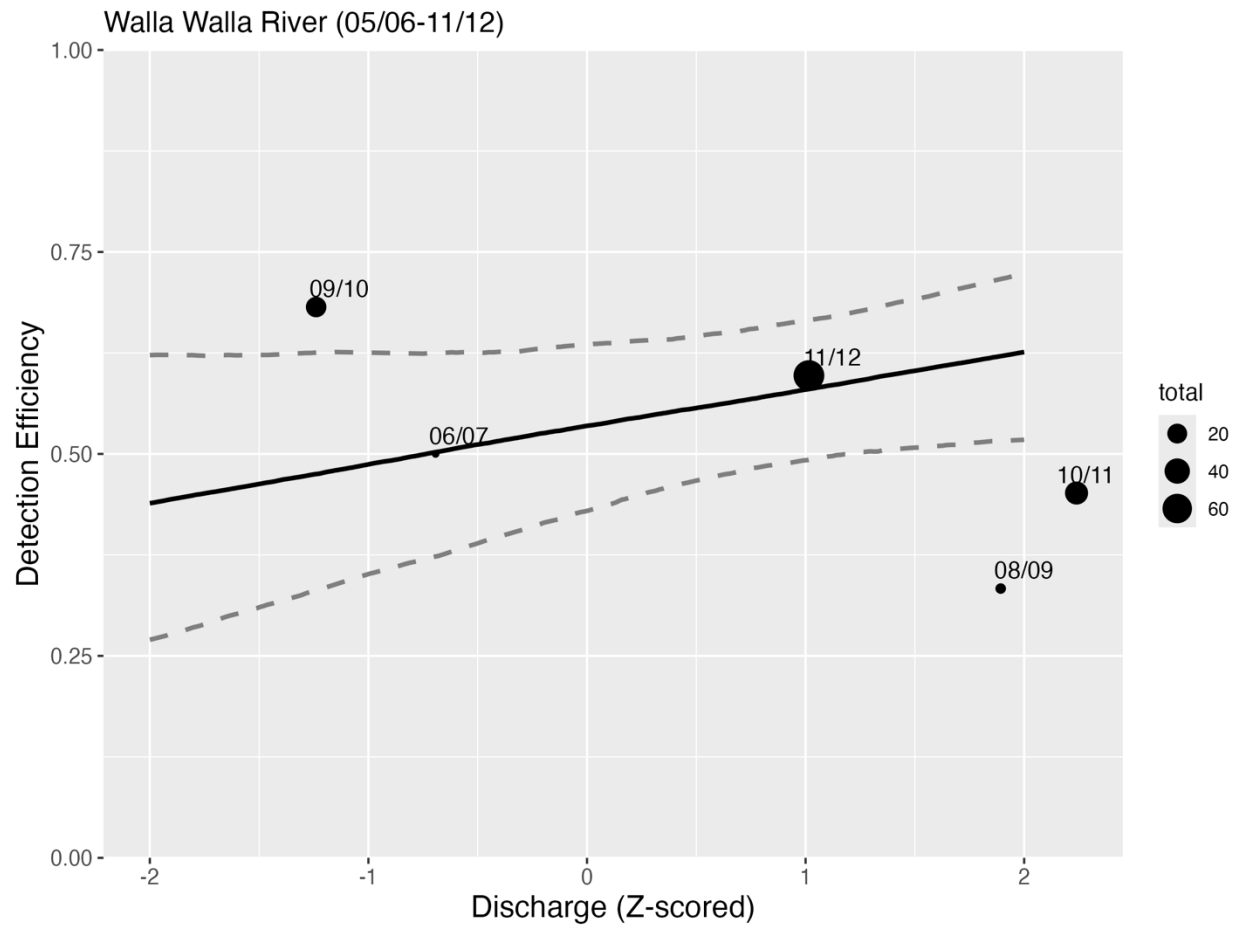


Figure 6. Walla Walla River, estimated detection efficiency in time period 1.

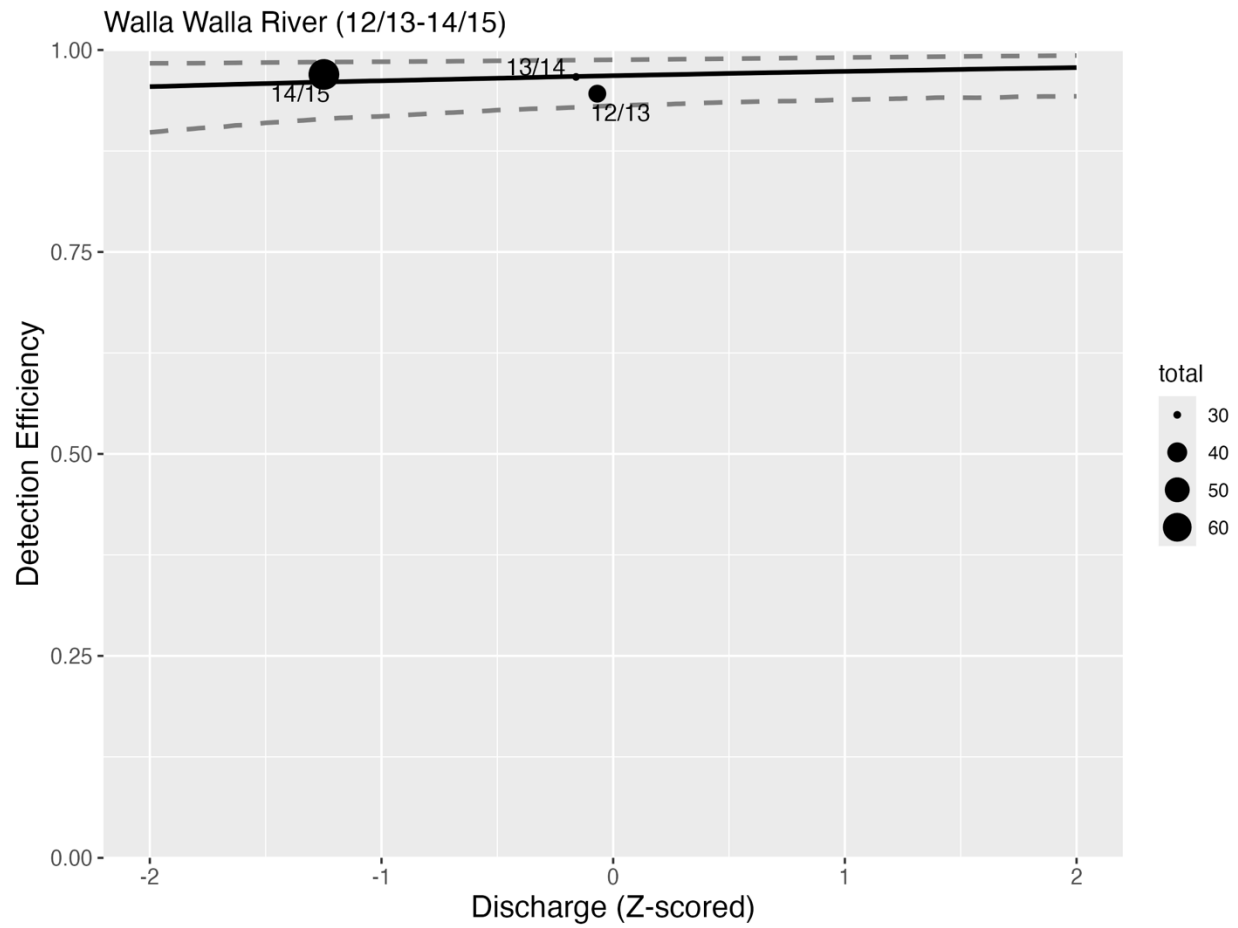


Figure 7. Walla Walla River, estimated detection efficiency in time period 2.

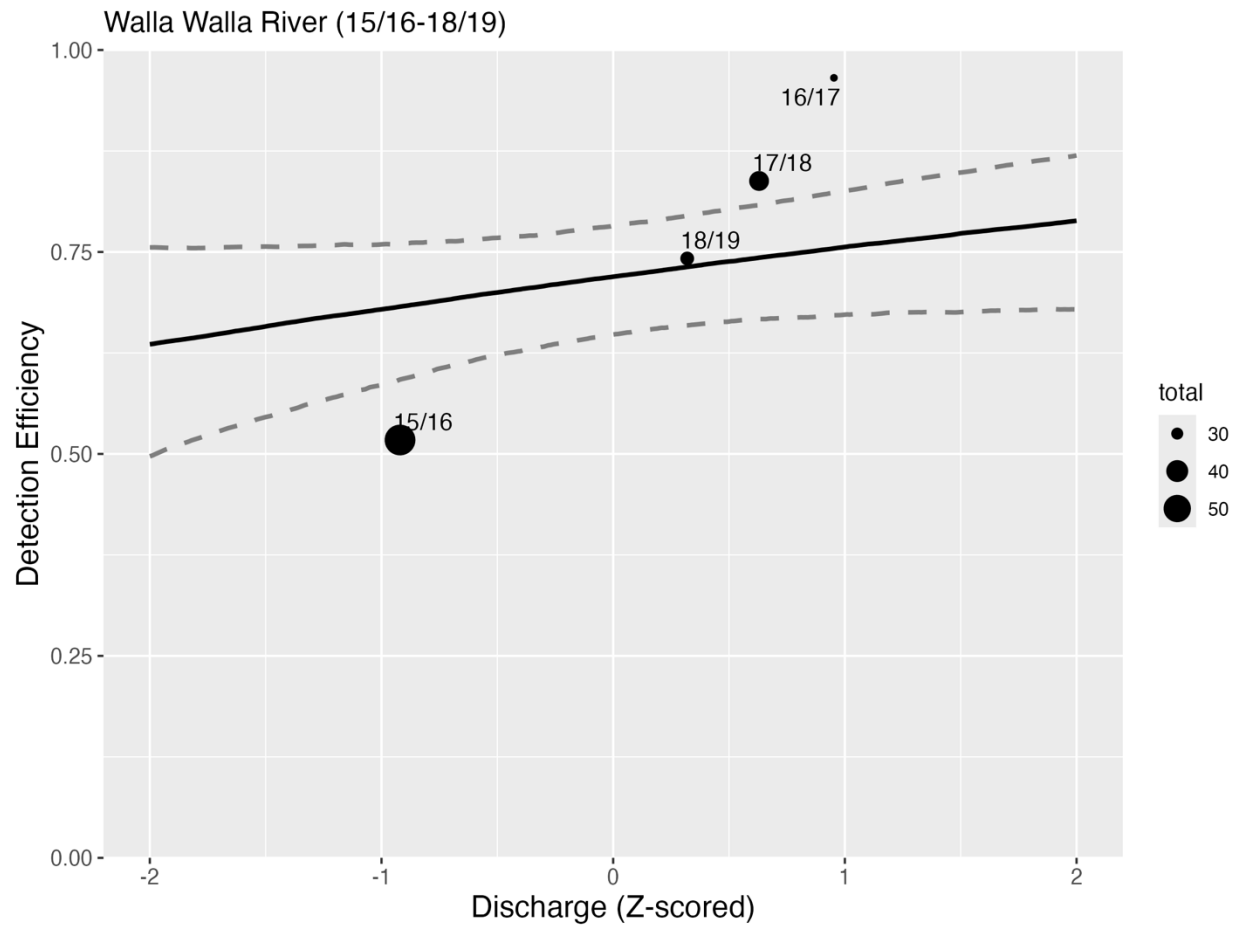


Figure 8. Walla Walla River, estimated detection efficiency in time period 3.

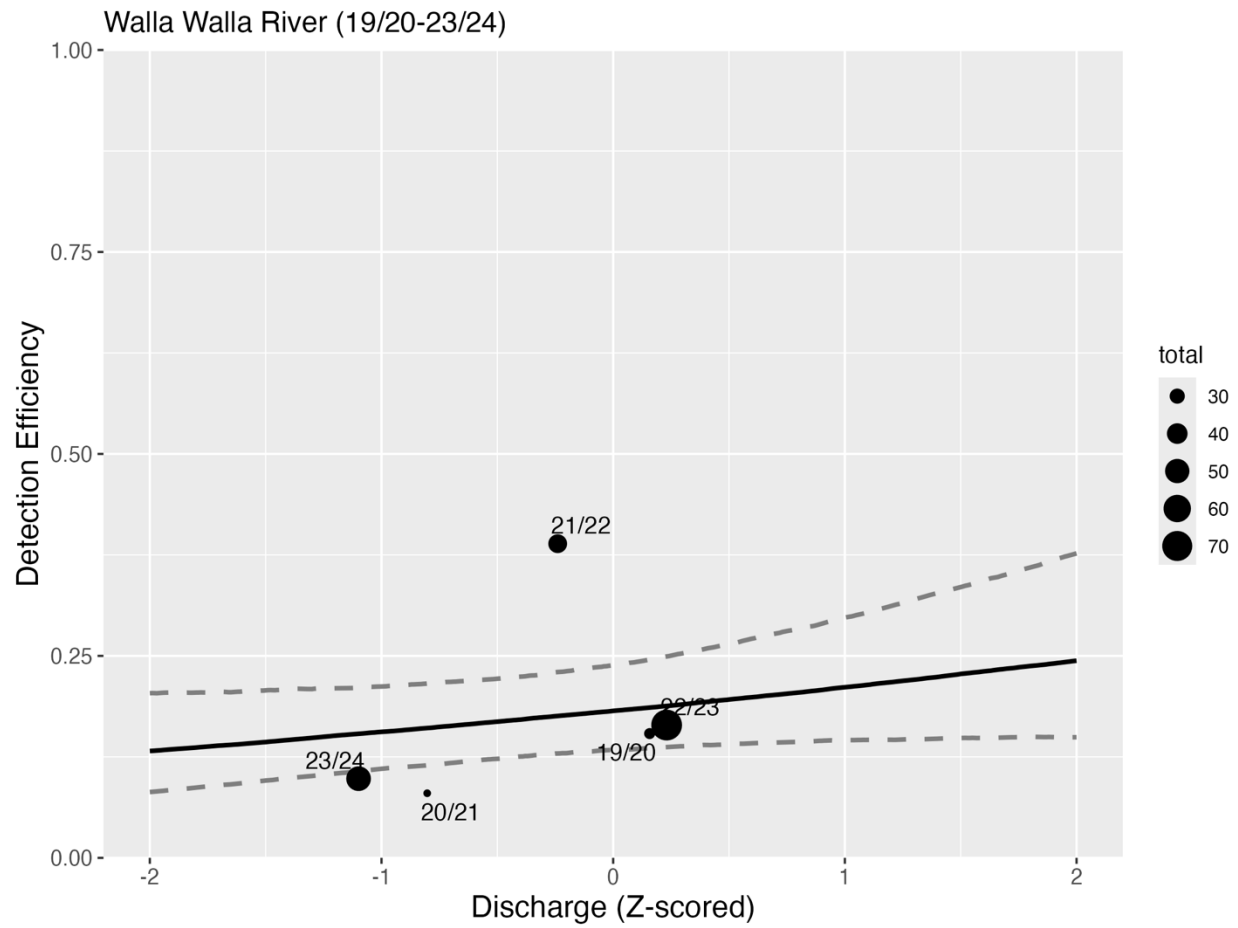


Figure 9. Walla Walla River, estimated detection efficiency in time period 3.

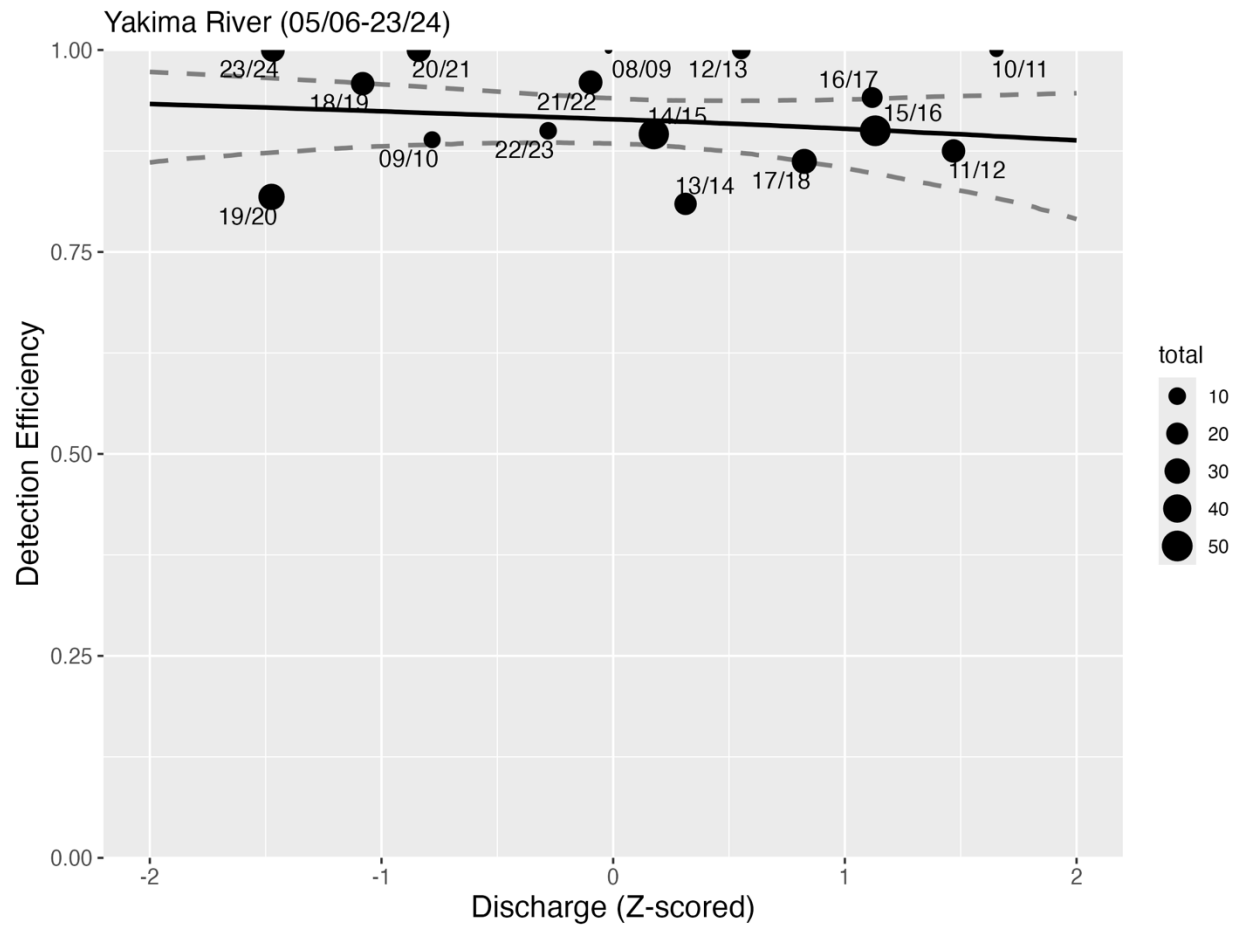


Figure 10. Yakima River, estimated detection efficiency.

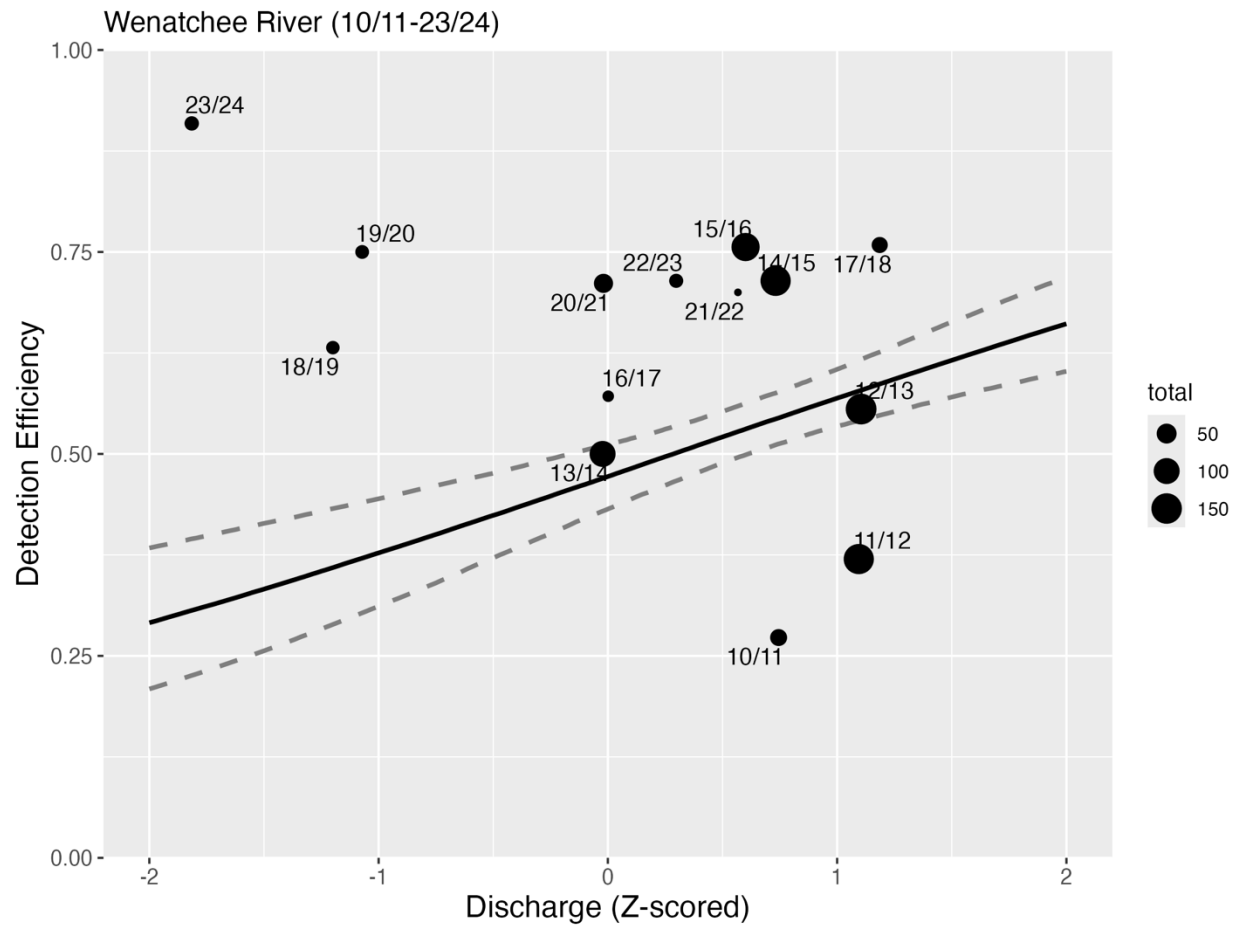


Figure 11. Wenatchee River, estimated detection efficiency.

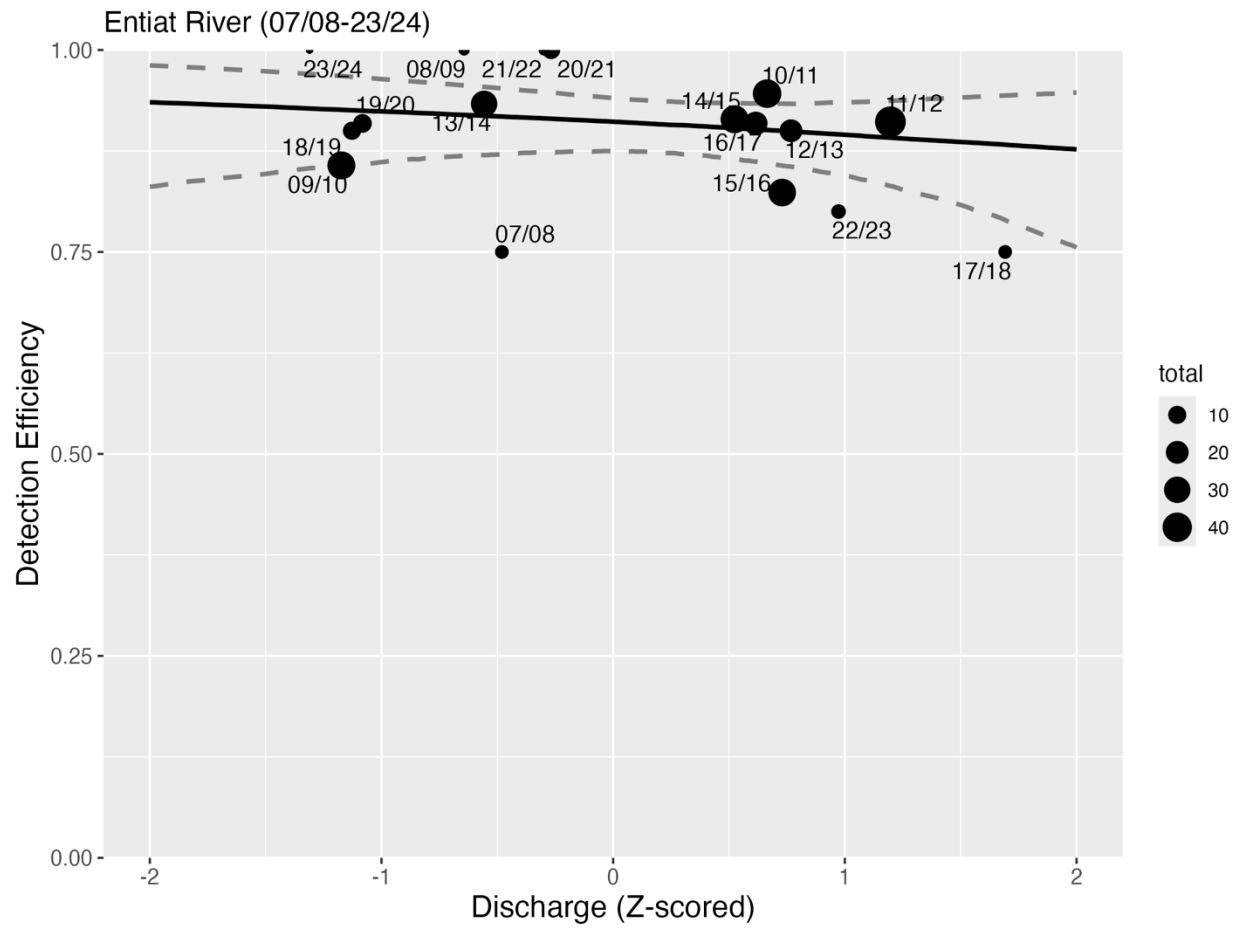


Figure 12. Entiat River, estimated detection efficiency.

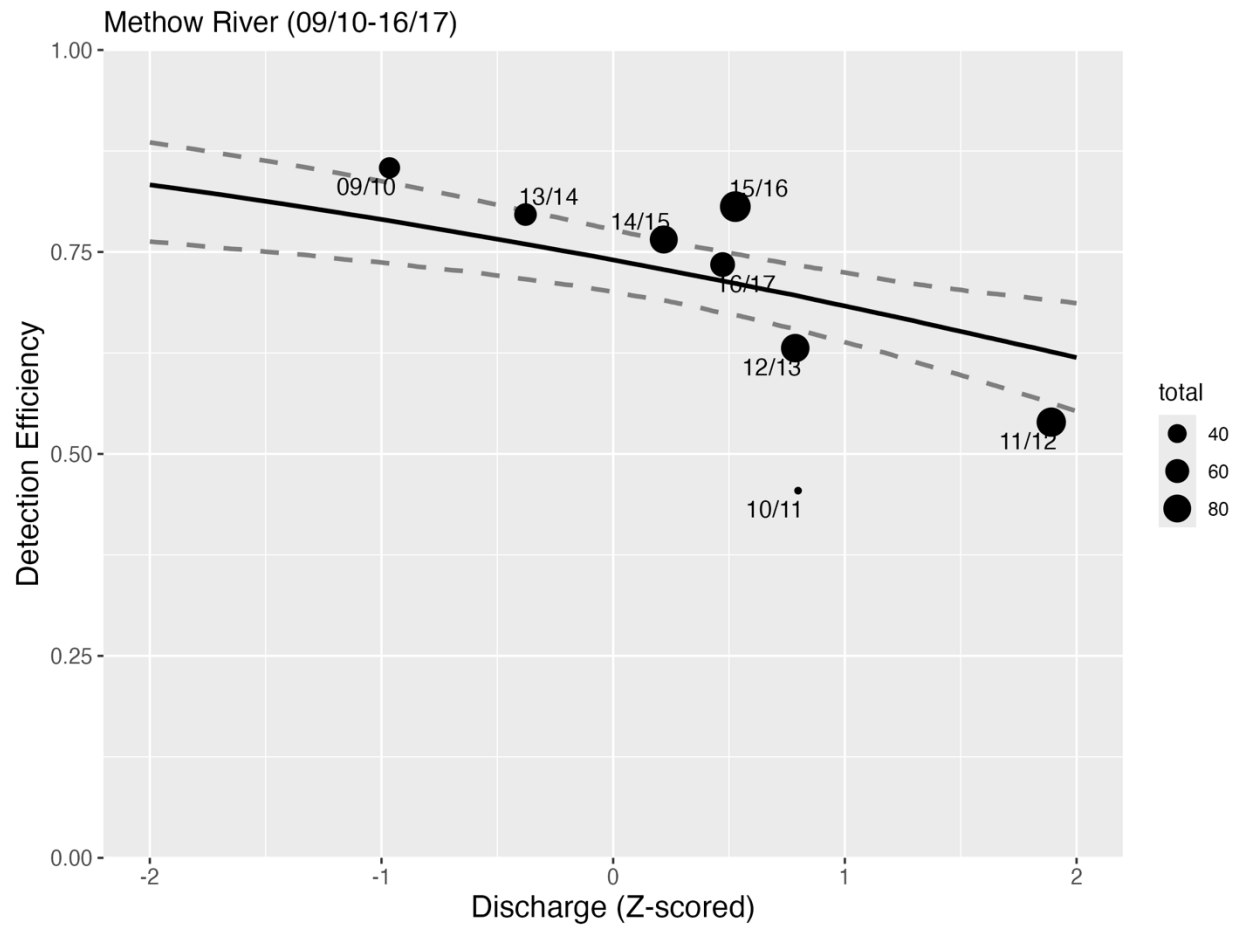


Figure 13. Methow River, estimated detection efficiency in time period 1.

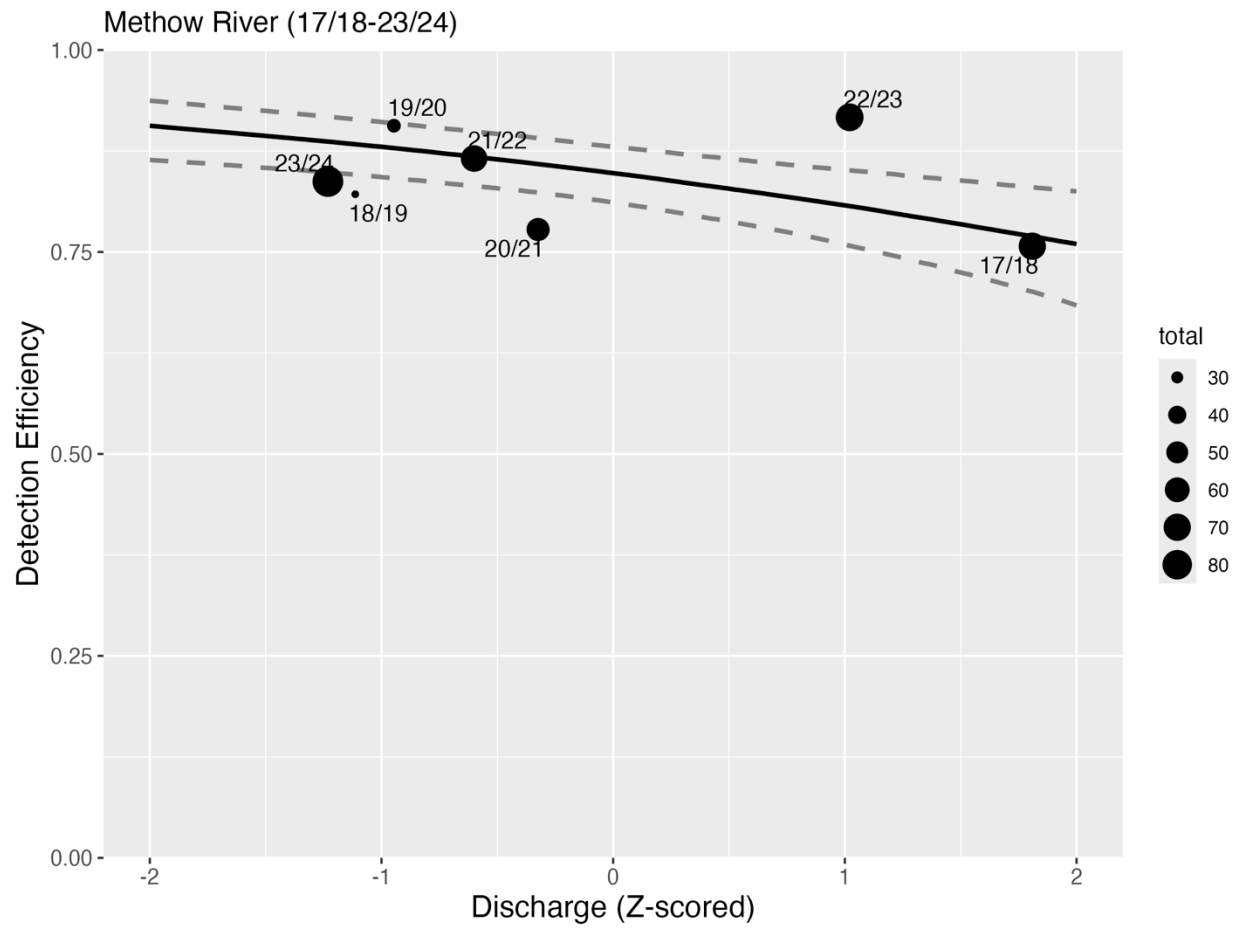


Figure 14. Methow River, estimated detection efficiency in time period 2.

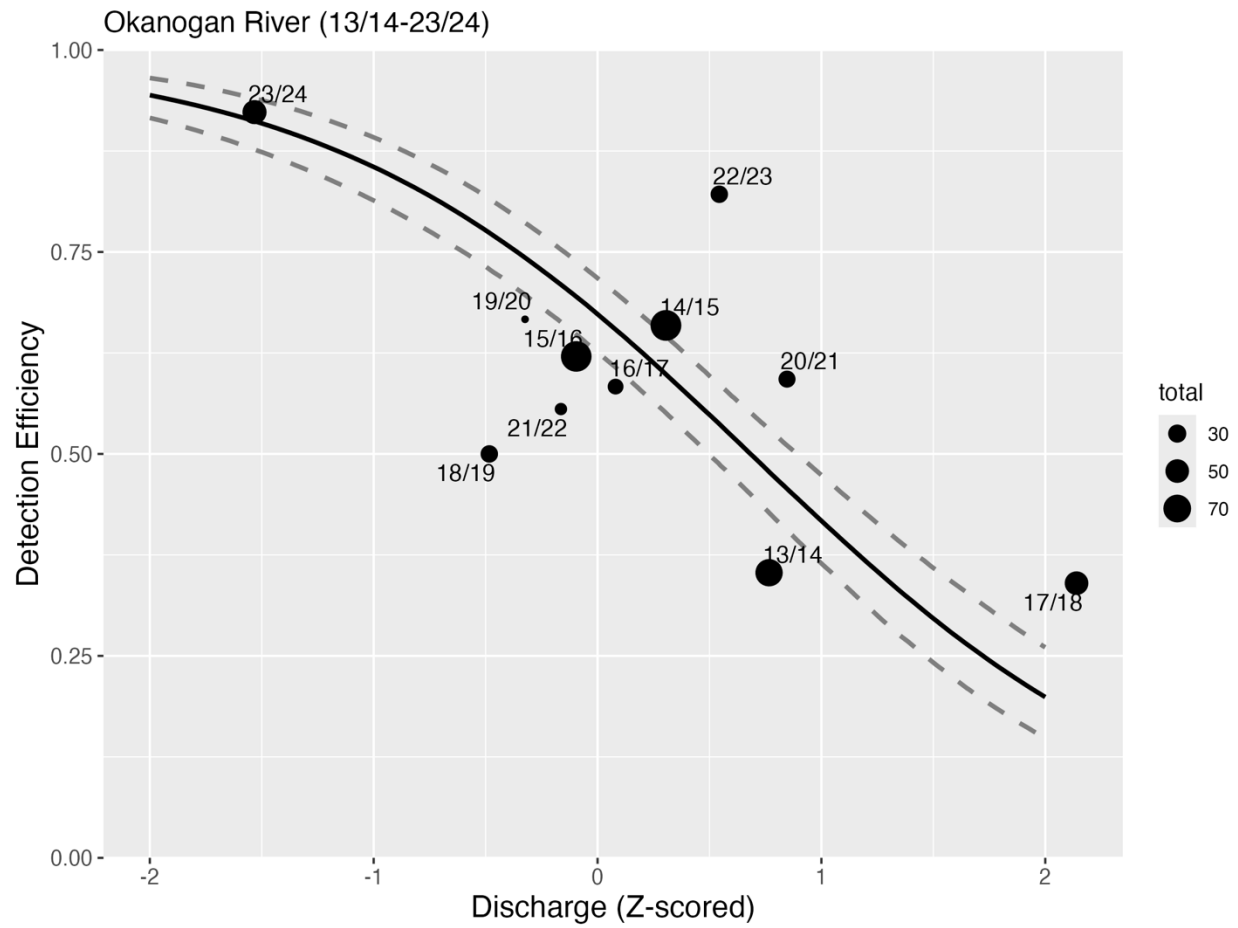


Figure 15. Okanogan River, estimated detection efficiency.

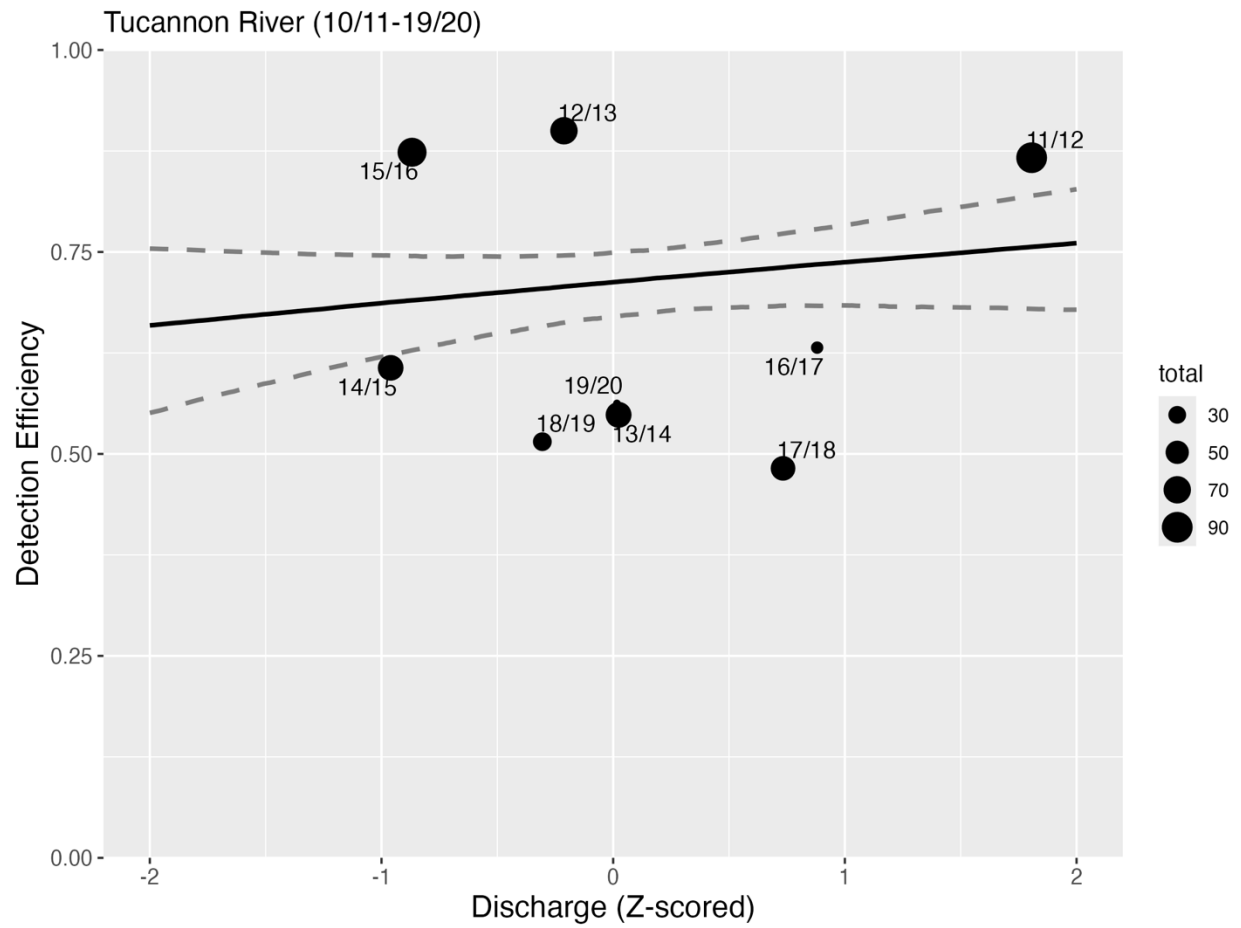


Figure 16. Tucannon River, estimated detection efficiency in time period 1.

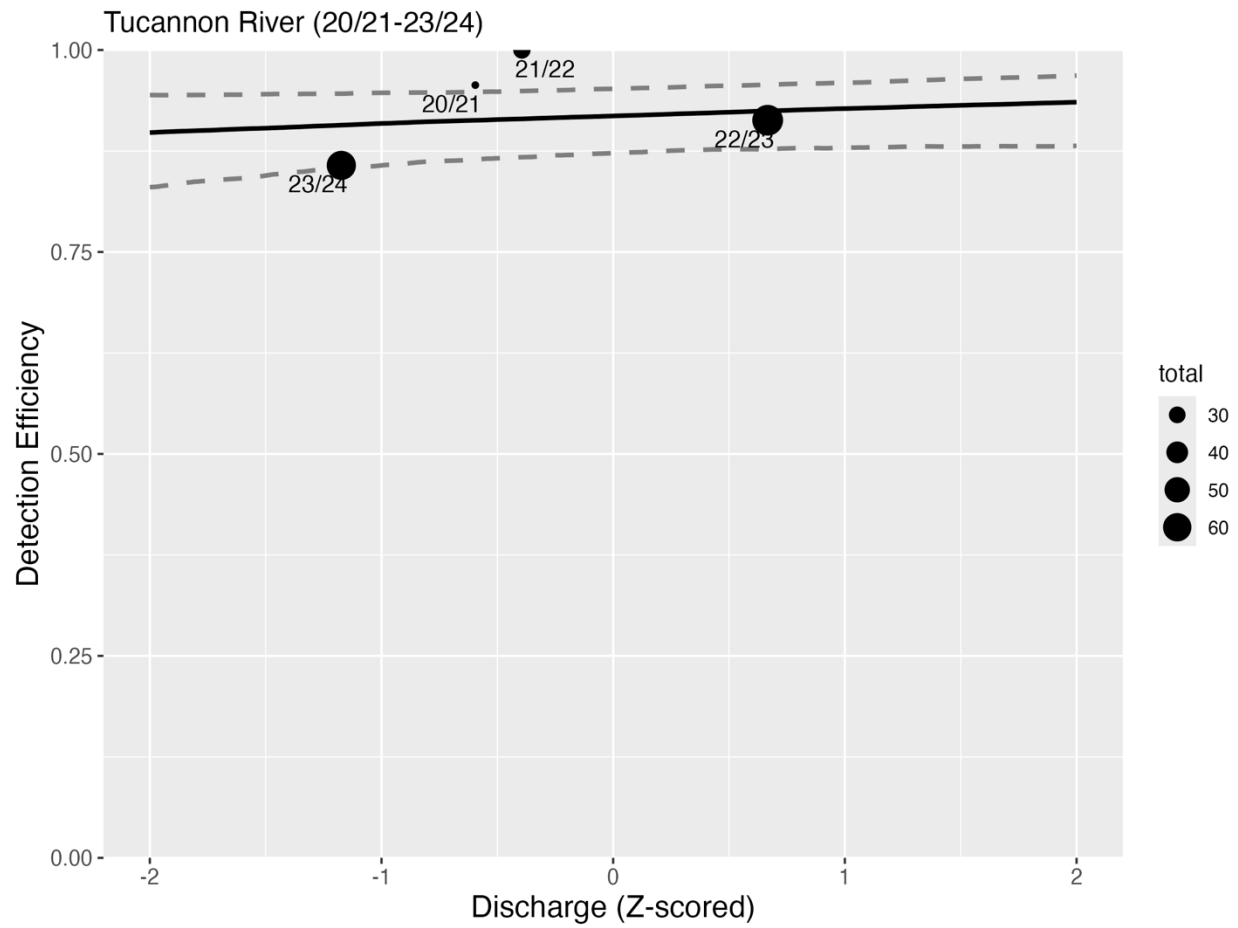


Figure 17. Tucannon River, estimated detection efficiency in time period 2.

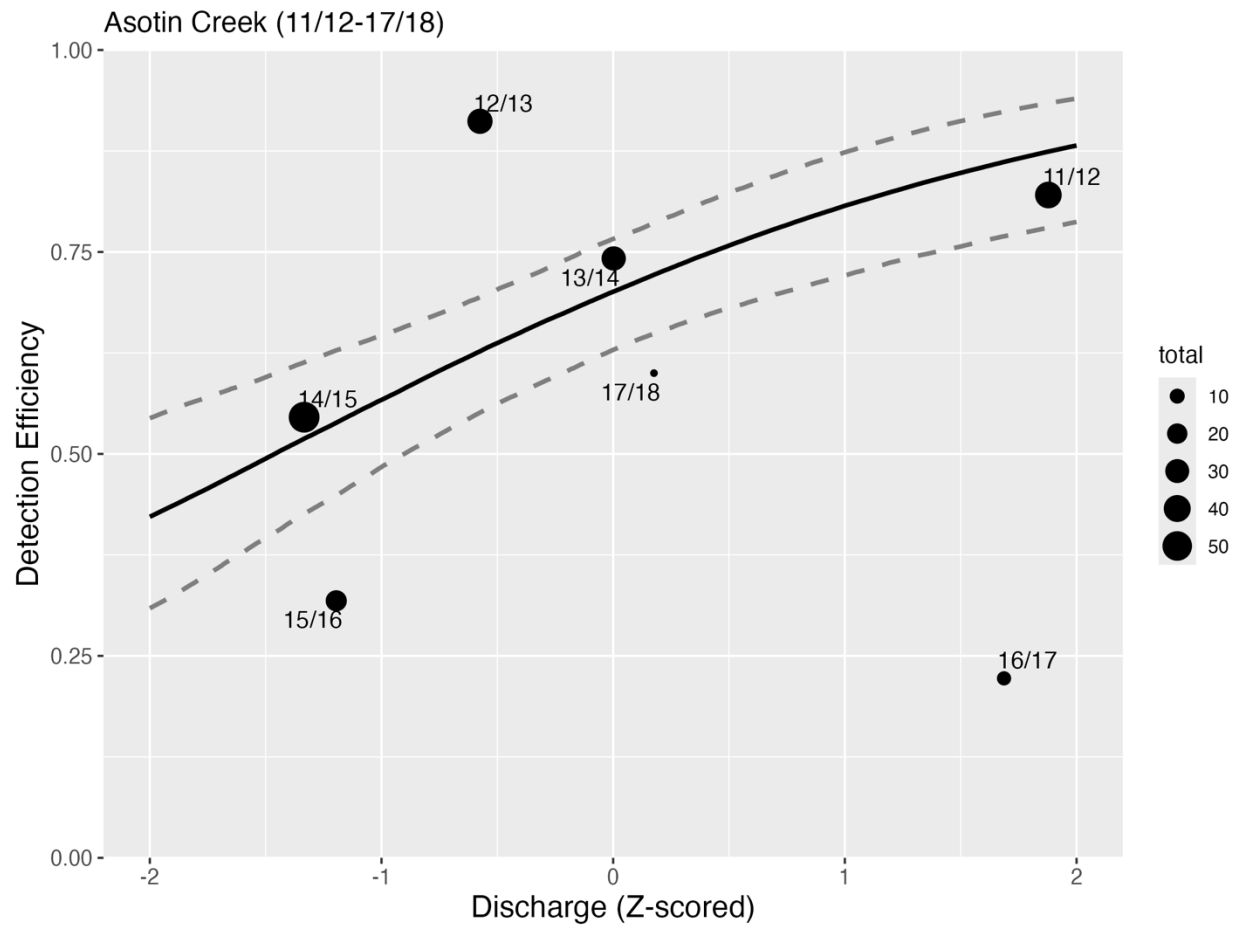


Figure 18. Asotin Creek, estimated detection efficiency in time period 1.

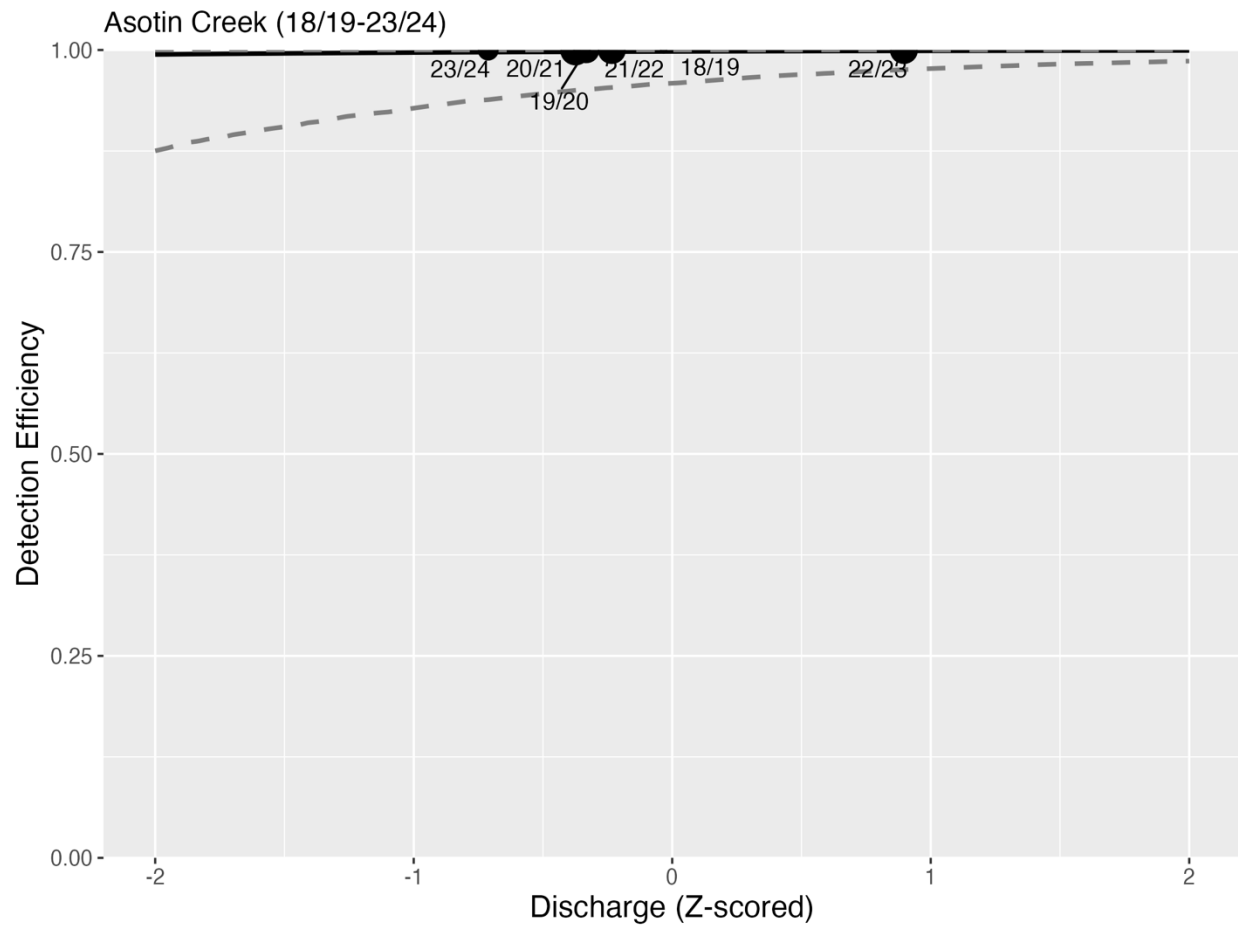


Figure 19. Asotin Creek, estimated detection efficiency in time period 2.

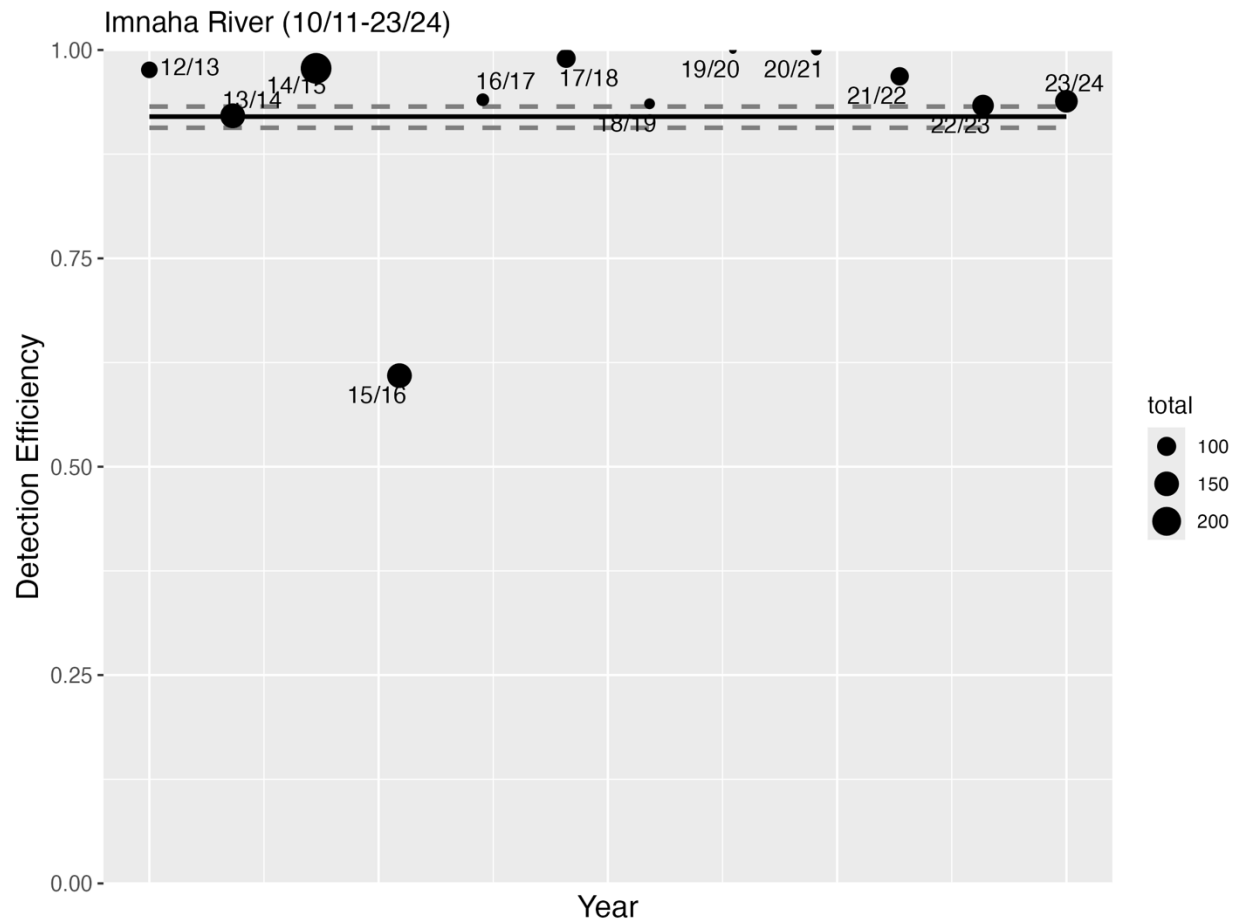


Figure 20. Imnaha River, estimated detection efficiency.

Appendix G. Model diagnostic figures

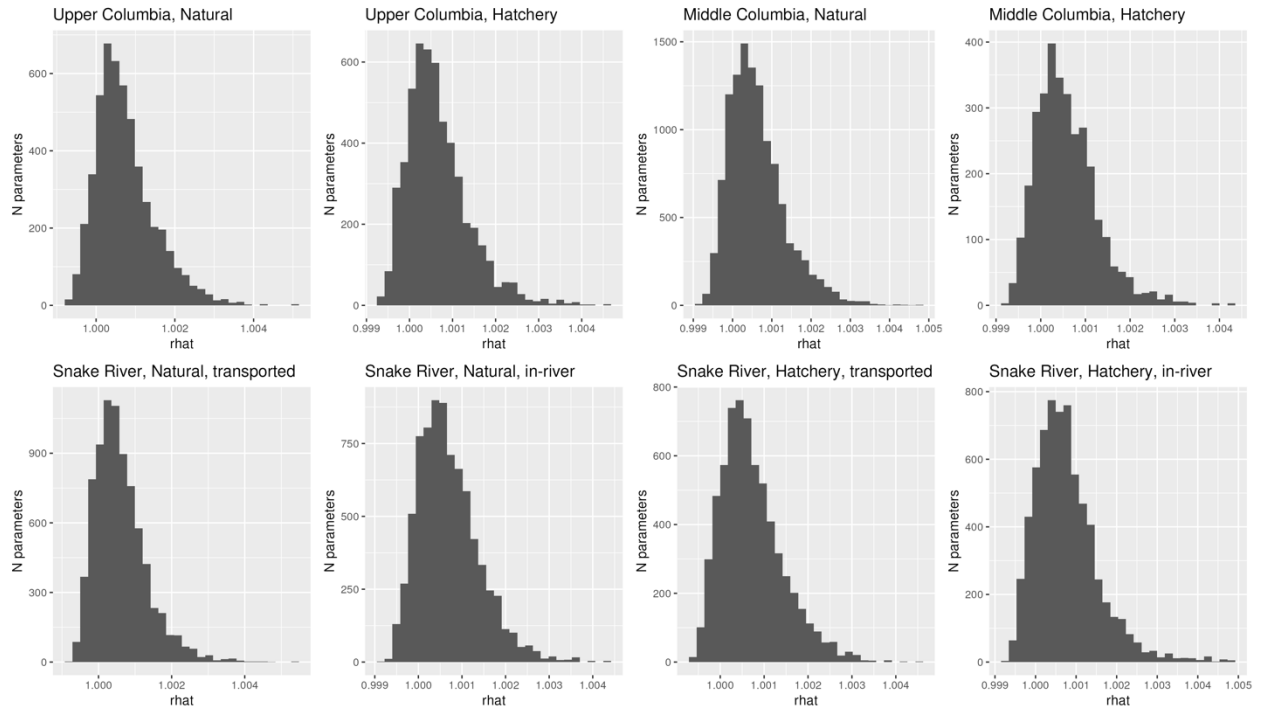


Figure 1. The R-hat convergence diagnostic for each of the six models run. The R-hat convergence diagnostic compares the between- and within-chain estimates for model parameters and other univariate quantities of interest. If chains have not mixed well (i.e., the between- and within-chain estimates don't agree), R-hat is larger than 1. R-hat values should be less than 1.05, and all parameters here have an R-hat of less than 1.01.

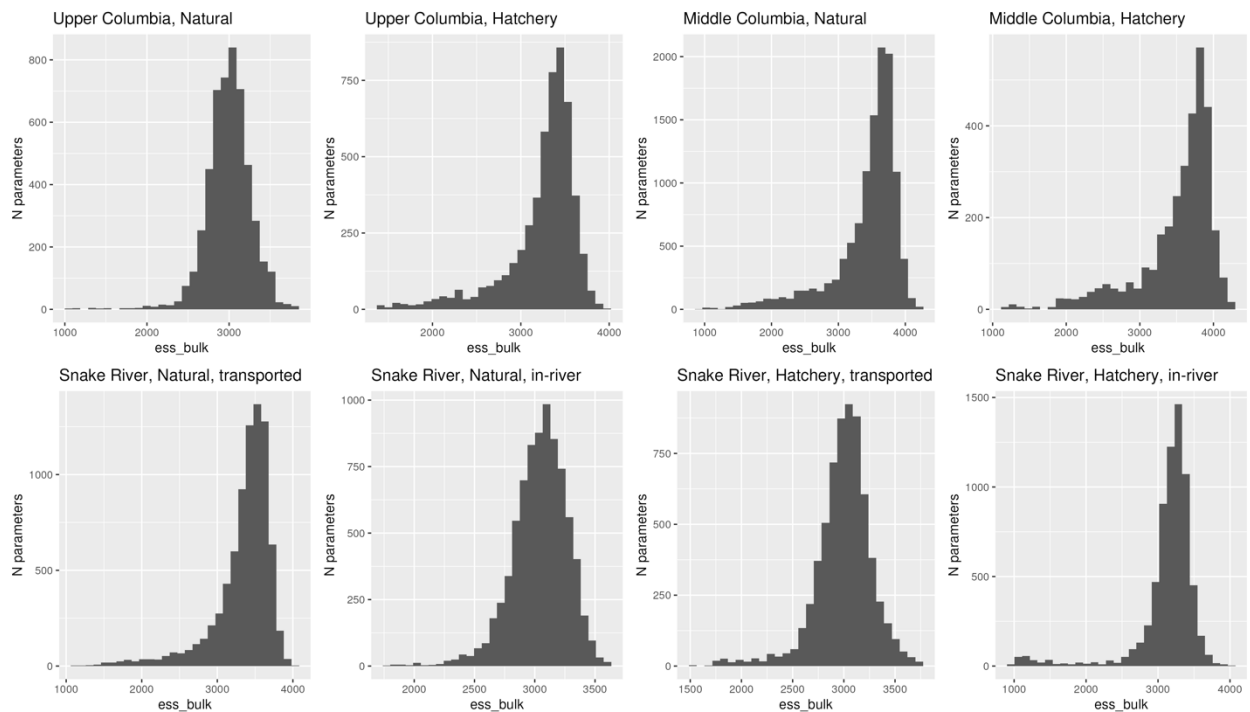


Figure 2. Bulk Effective Sample Size (bulk-ESS) using rank normalized draws, for each of the six models run. Bulk-ESS is useful measure for sampling efficiency in the bulk of the distribution (related to efficiency of mean and median estimates), and is well defined even if the chains do not have finite mean or variance. Both bulk-ESS and tail-ESS should be at least 100 (approximately) per Markov Chain in order to be reliable and indicate that estimates of respective posterior quantiles are reliable.

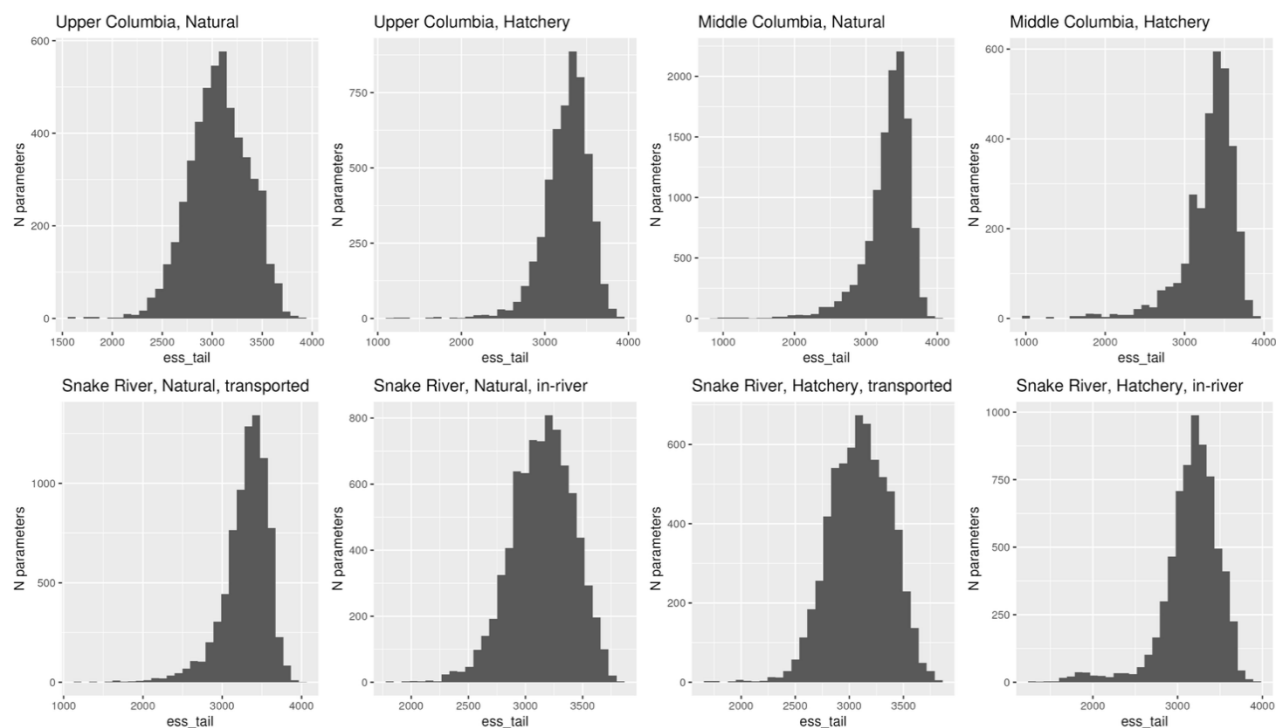


Figure 3. Tail Effective Sample Size (tail-ESS) using rank normalized draws, for each of the six models run. Tail-ESS is produced by computing the minimum of effective sample sizes for 5% and 95% quantiles. Tail-ESS is a useful measure for sampling efficiency in the tails of the distribution (related to efficiency of variance and tail quantile estimates). Both bulk-ESS and tail-ESS should be at least 100 (approximately) per Markov Chain in order to be reliable and indicate that estimates of respective posterior quantiles are reliable.

Appendix H. Covariate correlations

Table 1. Correlation between spill and flow across all run years in the dataset, by dam.

Dam	Mean Flow	Mean Spill	R-squared
Bonneville Dam	177.04	46.73	0.61

Table 1. Correlation between spill and flow across all run years in the dataset, by dam.

Dam	Mean Flow	Mean Spill	R-squared
McNary Dam	168.59	52.07	0.80
Priest Rapids Dam	117.07	20.84	0.72
Rock Island Dam	113.00	12.22	0.60
Rocky Reach Dam	109.27	8.12	0.61
Wells Dam	109.43	8.80	0.65
Ice Harbor Dam	45.87	18.17	0.82
Lower Granite Dam	45.33	12.23	0.71

Correlation between spill and temperature across all run years in the dataset, by dam.

Dam	Mean temp	Mean Spill	R-squared
Bonneville Dam	13.11	46.73	0.08
McNary Dam	12.32	52.07	0.04
Priest Rapids Dam	11.45	20.84	0.03
Rock Island Dam	11.07	12.22	0.04

Correlation between spill and temperature across all run years in the dataset, by dam.

Dam	Mean temp	Mean Spill	R-squared
Rocky Reach Dam	11.06	8.12	0.01
Wells Dam	10.87	8.80	0.01
Ice Harbor Dam	12.42	18.17	0.00
Lower Granite Dam	11.52	12.23	0.02

Appendix I. Final fates, under median conditions

The figures below show the predicted final fates of fish from different natal tributaries under the median conditions in our study system from 2005-2024. The final fates for hatchery and natural origin fish are shown on each plot. However, in the case of the six Snake River tributaries (Tucannon River, Clearwater River, Asotin Creek, Grande Ronde River, Salmon River, and Imnaha River), the difference between in-river and transported juvenile migrants is highlighted instead of the differences between rearing type, with a separate plot provided for each rearing type.

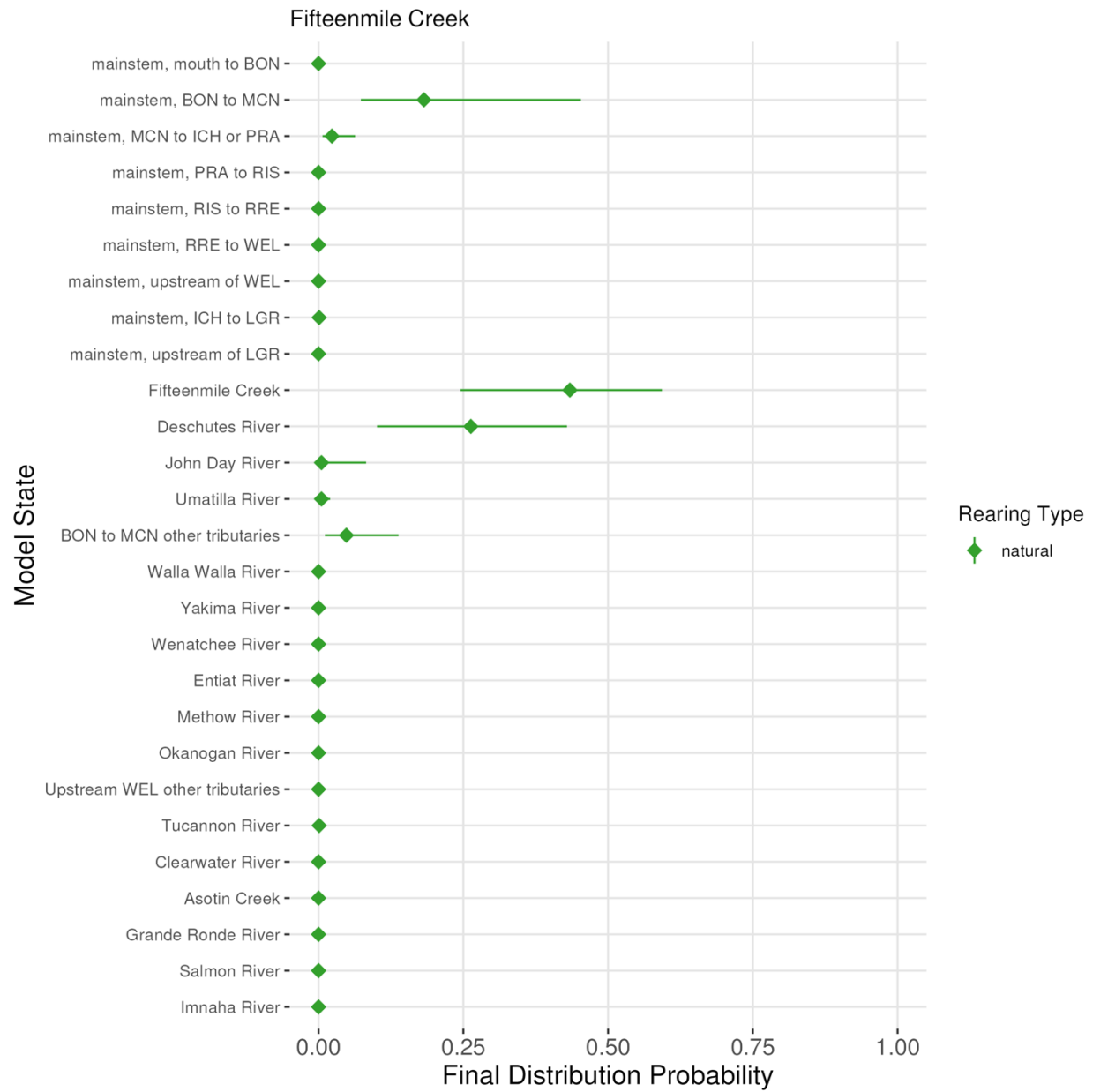


Figure 1. Fifteenmile Creek, estimated final fates under median conditions from 2005-2024.

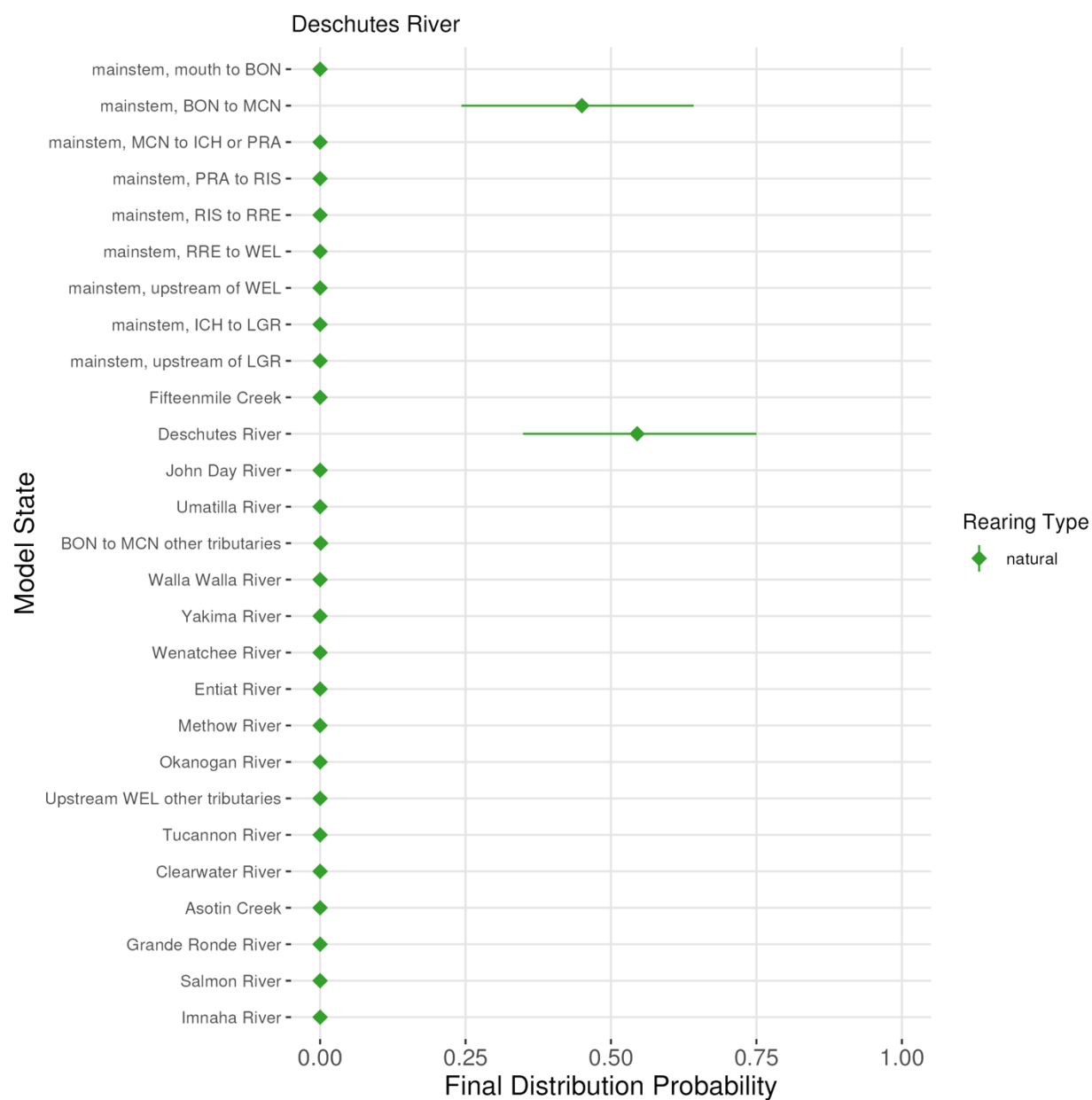


Figure 2. Deschutes River, estimated final fates under median conditions from 2005-2024.

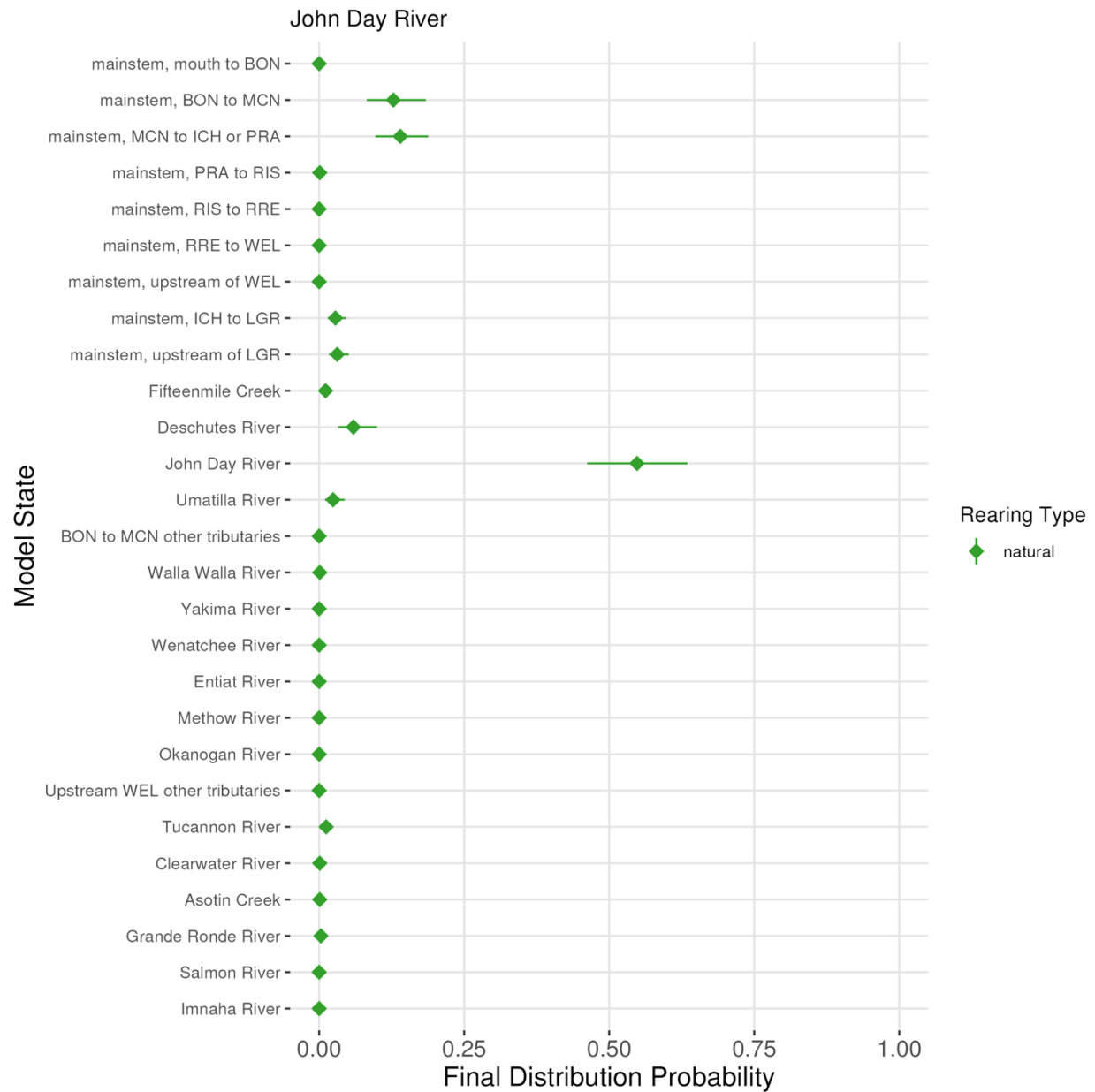


Figure 3. John Day River, estimated final fates under median conditions from 2005-2024.

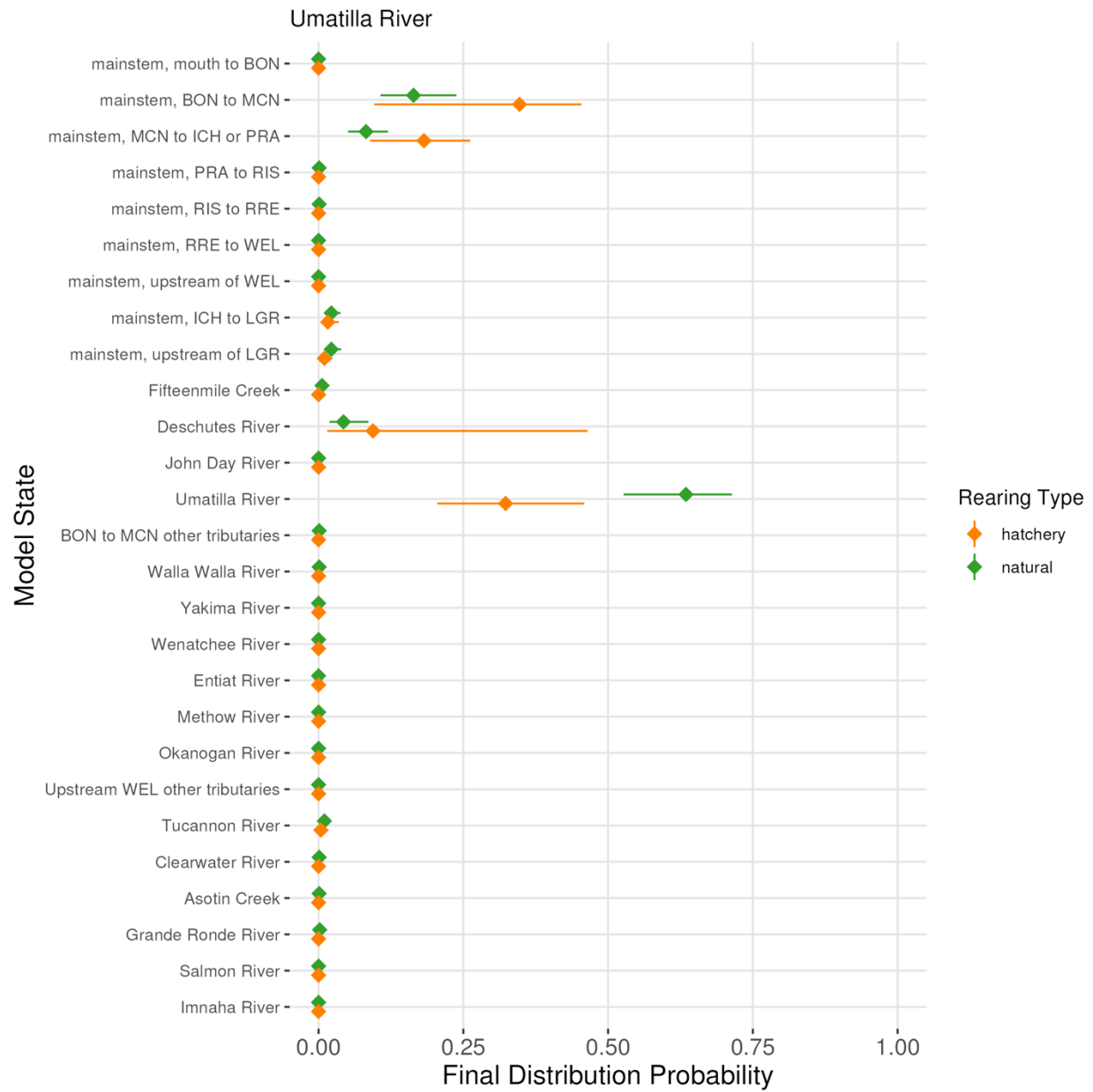


Figure 4. Umatilla River, estimated final fates under median conditions from 2005-2024.

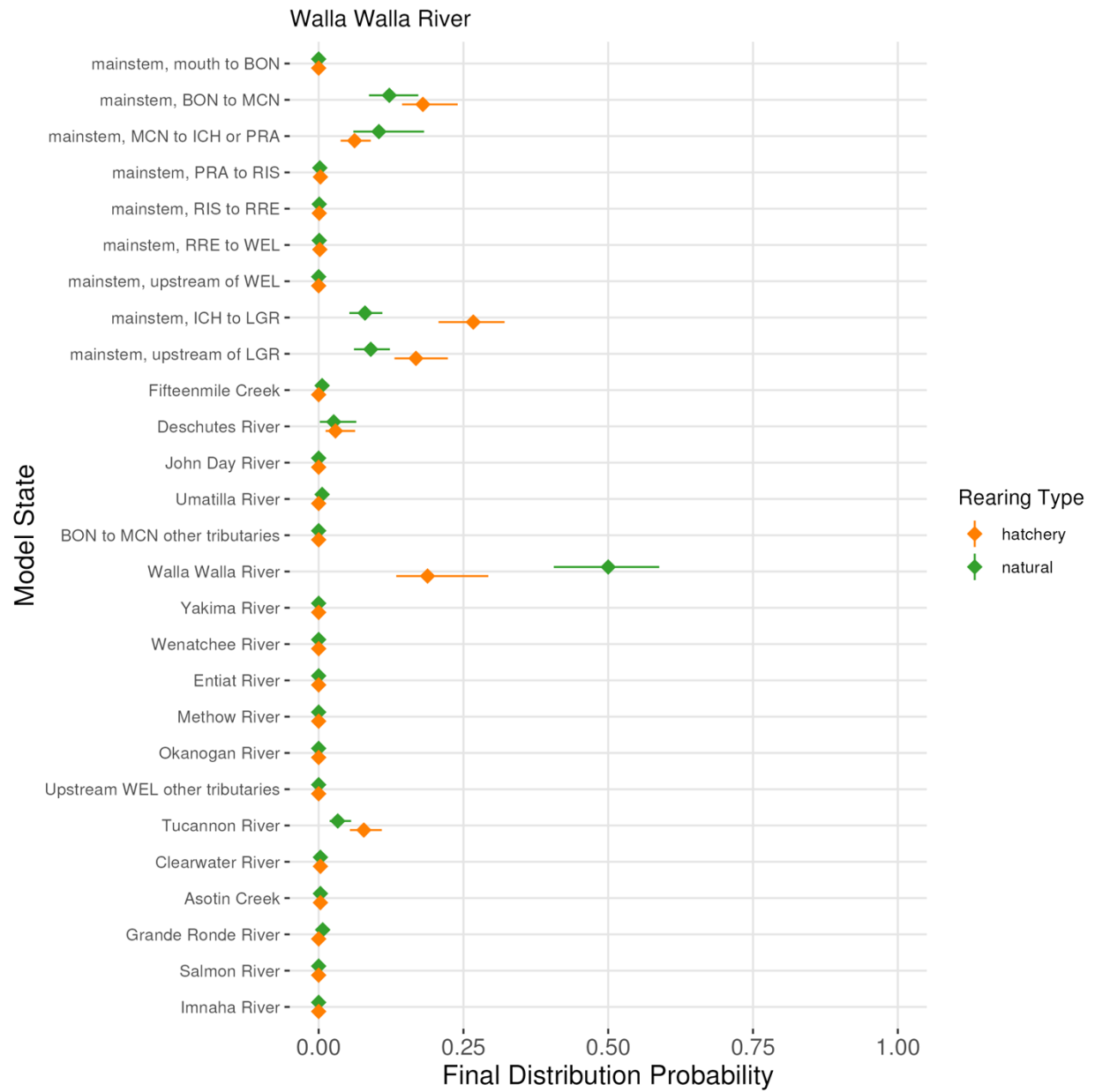


Figure 5. Walla Walla River, estimated final fates under median conditions from 2005-2024.

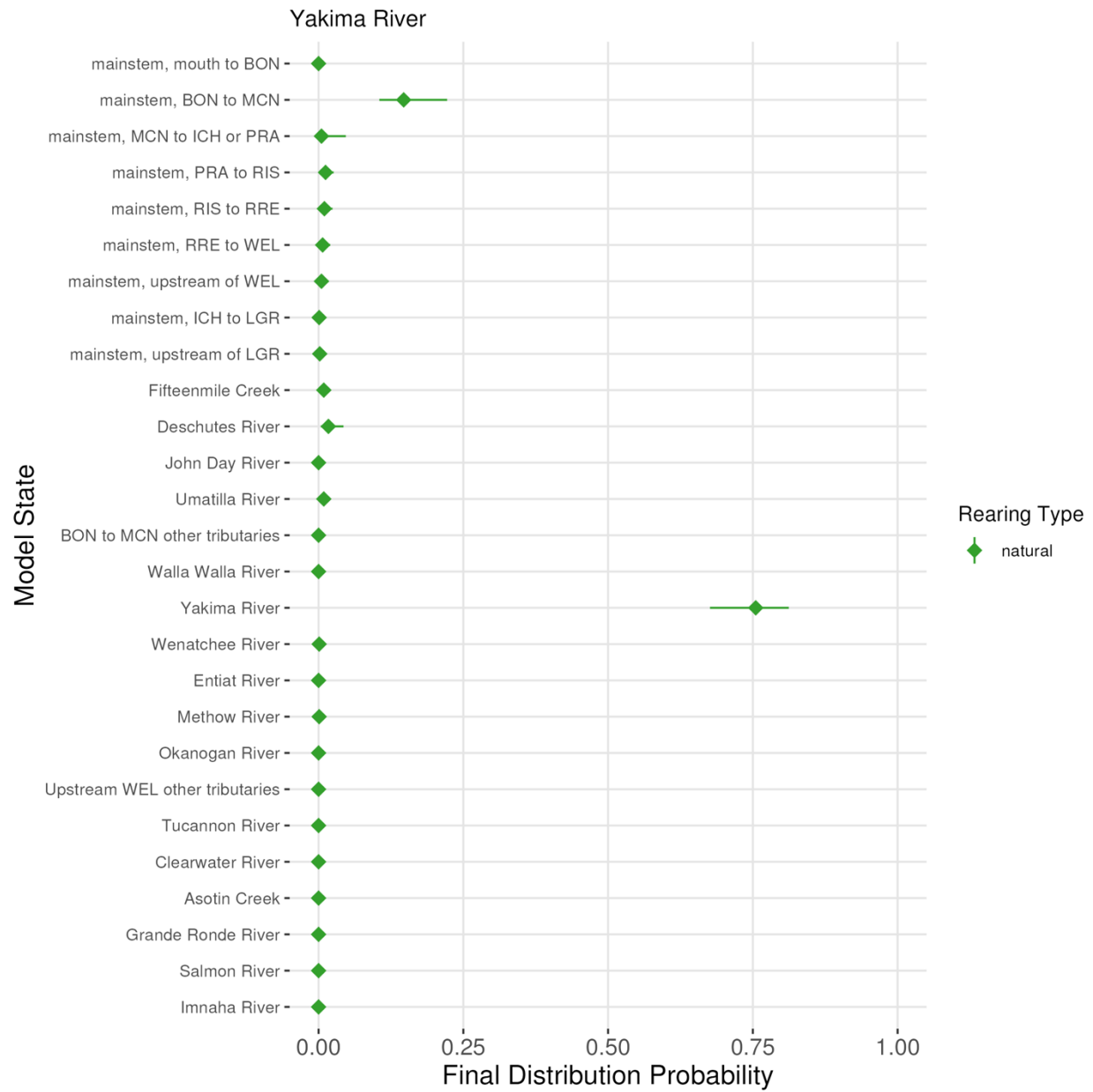


Figure 6. Yakima River, estimated final fates under median conditions from 2005-2024.

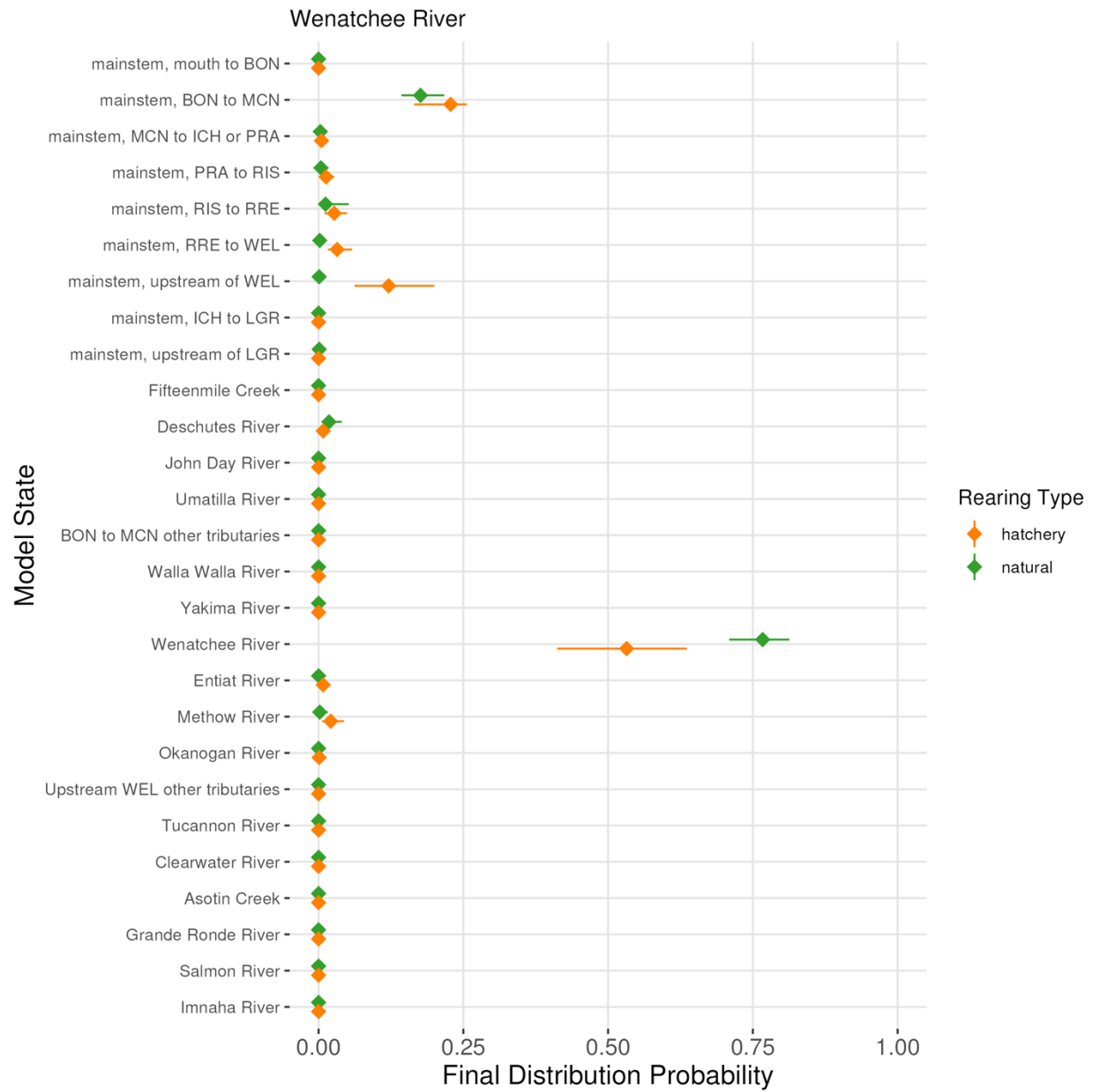


Figure 7. Wenatchee River, estimated final fates under median conditions from 2005-2024.

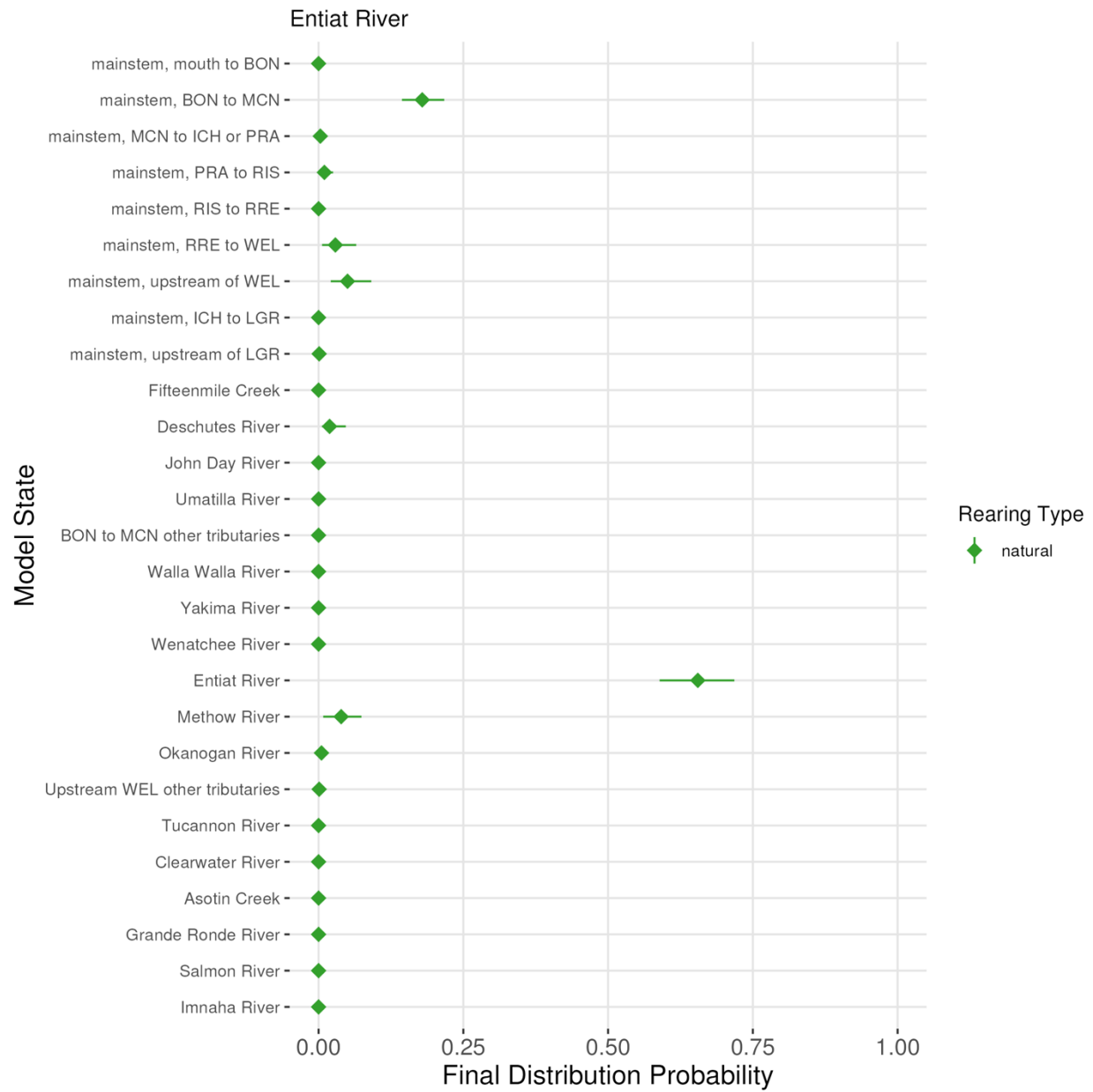


Figure 8. Entiat River, estimated final fates under median conditions from 2005-2024.

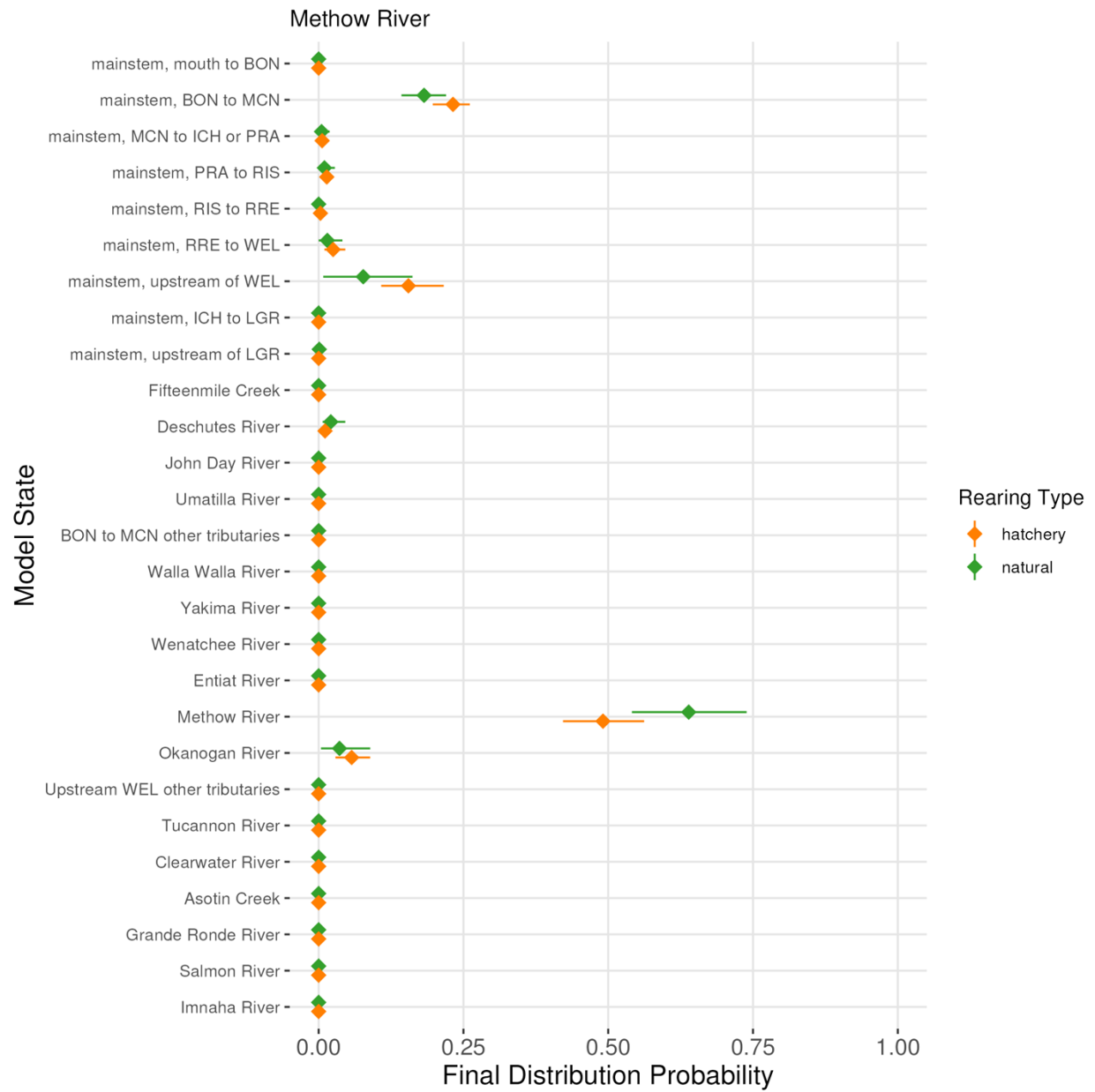


Figure 9. Methow River, estimated final fates under median conditions from 2005-2024.

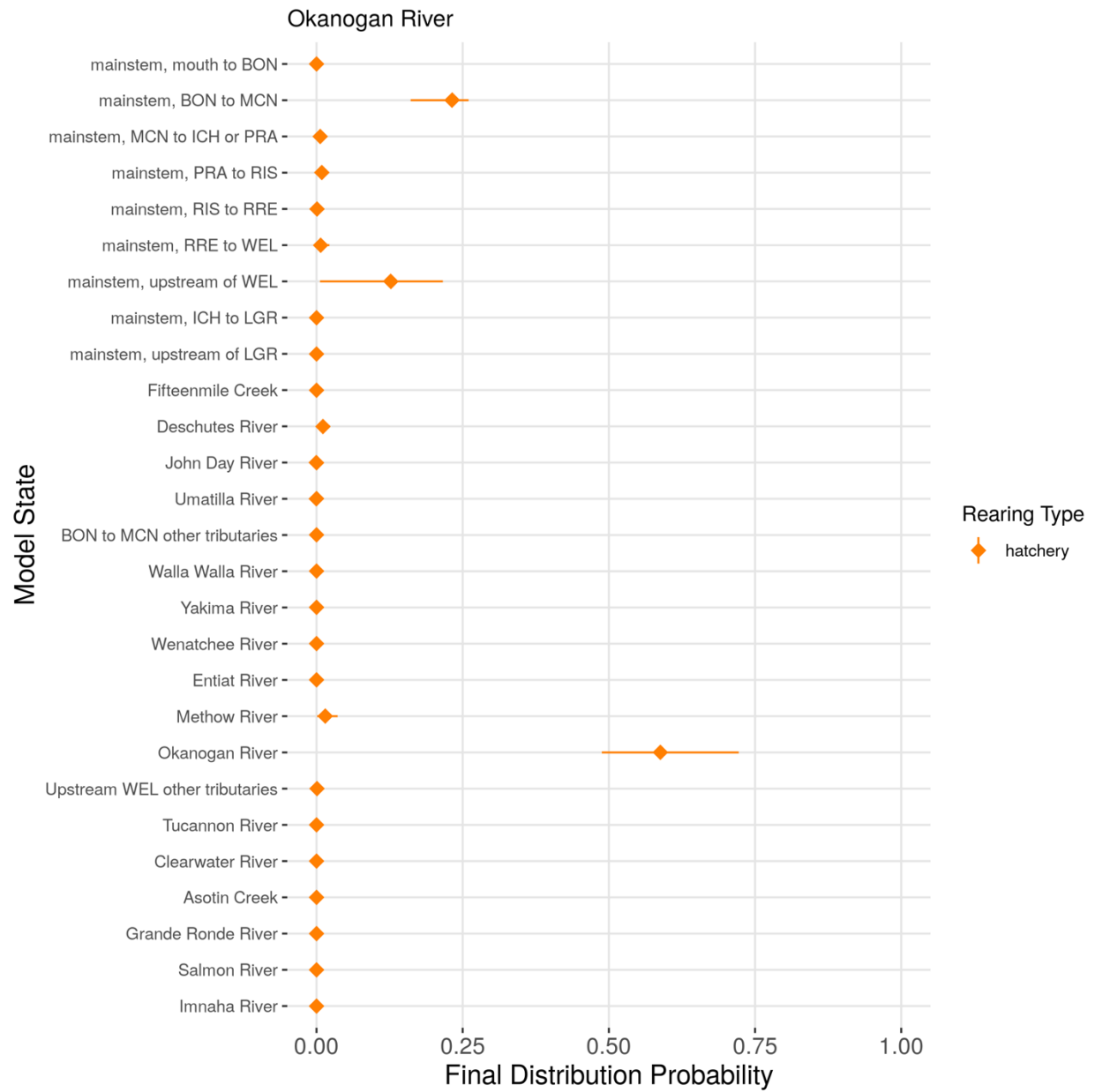


Figure 10. Okanogan River, estimated final fates under median conditions from 2005-2024.

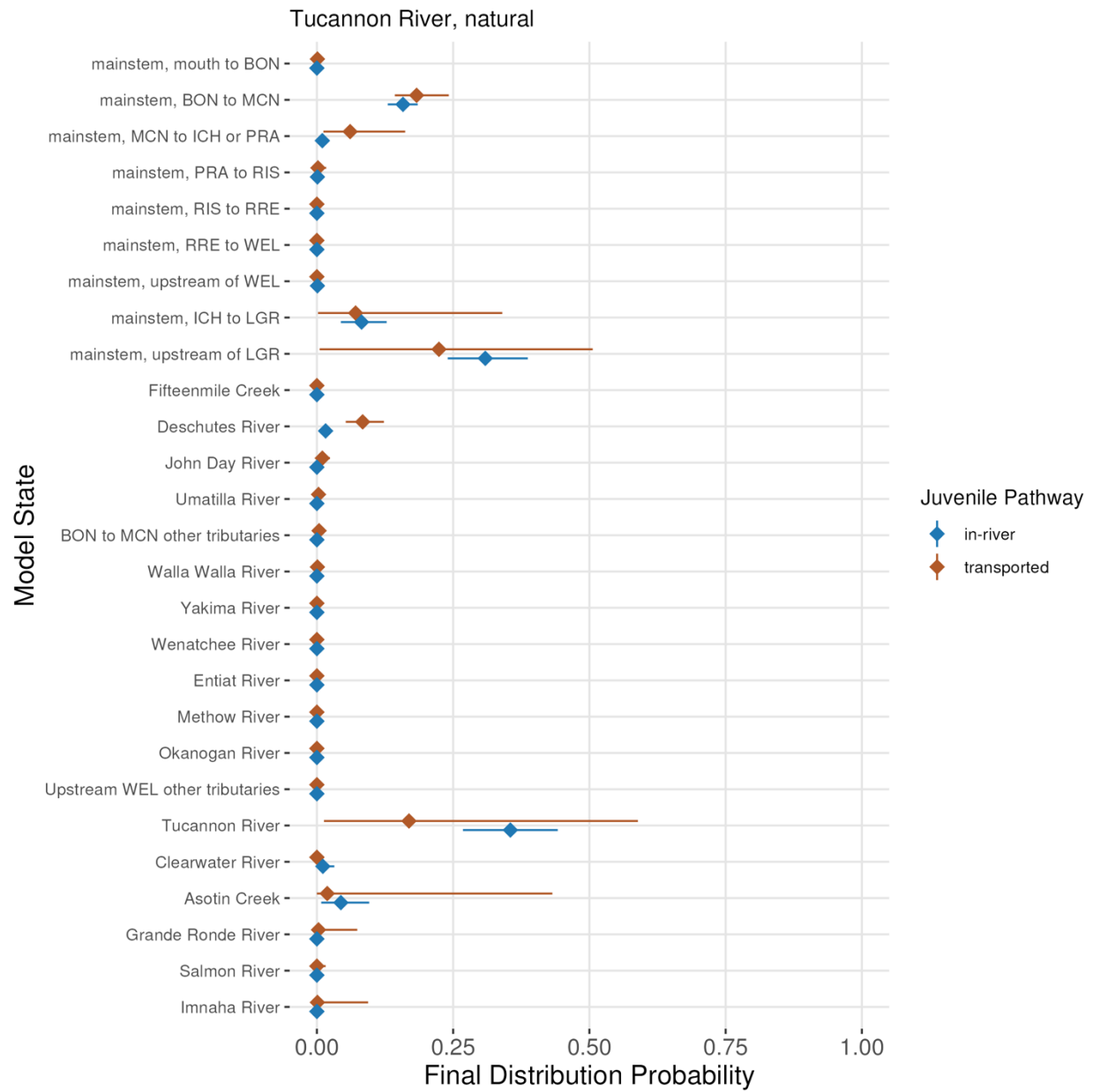


Figure 11. Tucannon River natural origin, estimated final fates under median conditions from 2005-2024.

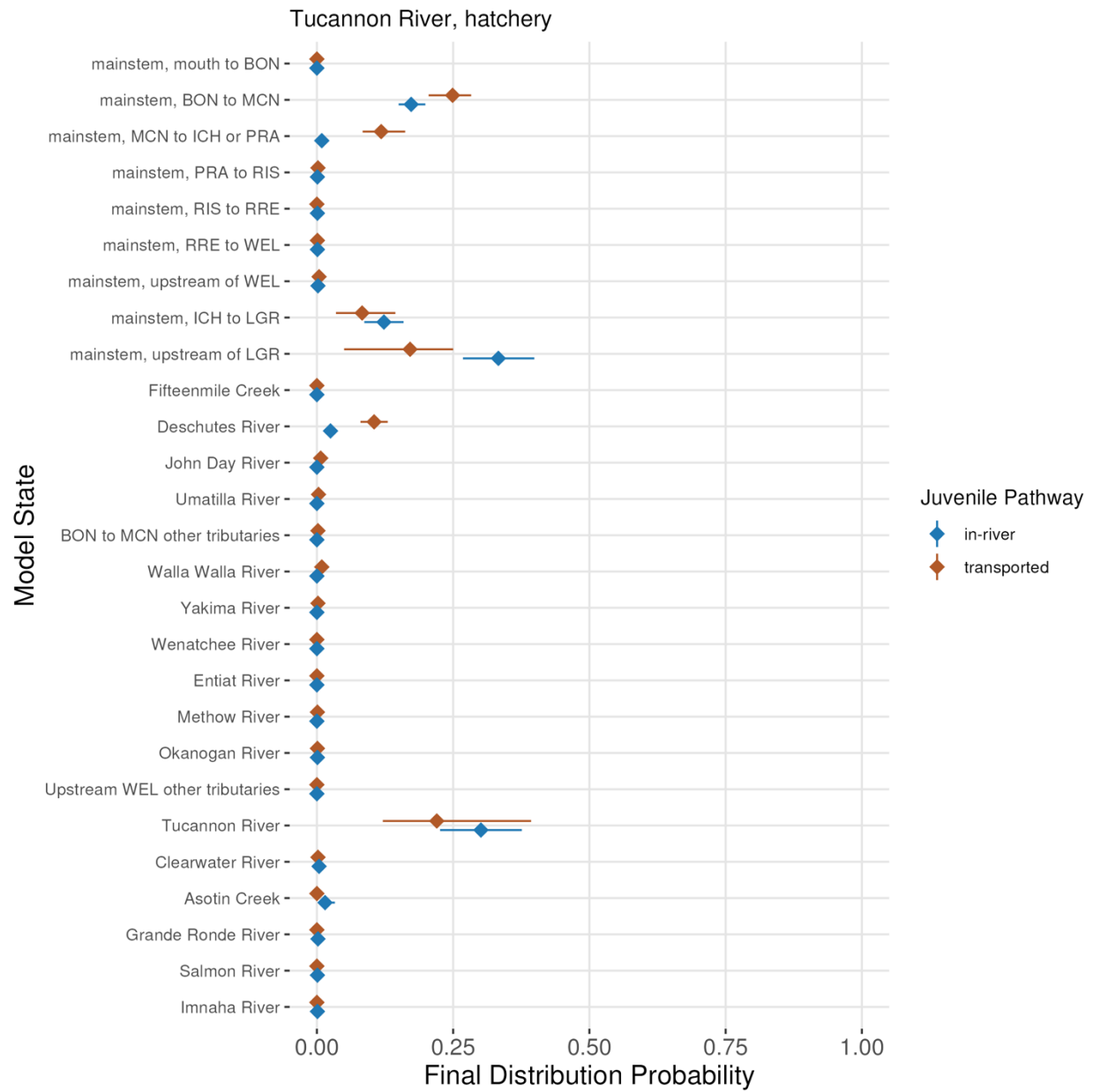


Figure 12. Tucannon River hatchery origin, estimated final fates under median conditions from 2005-2024.

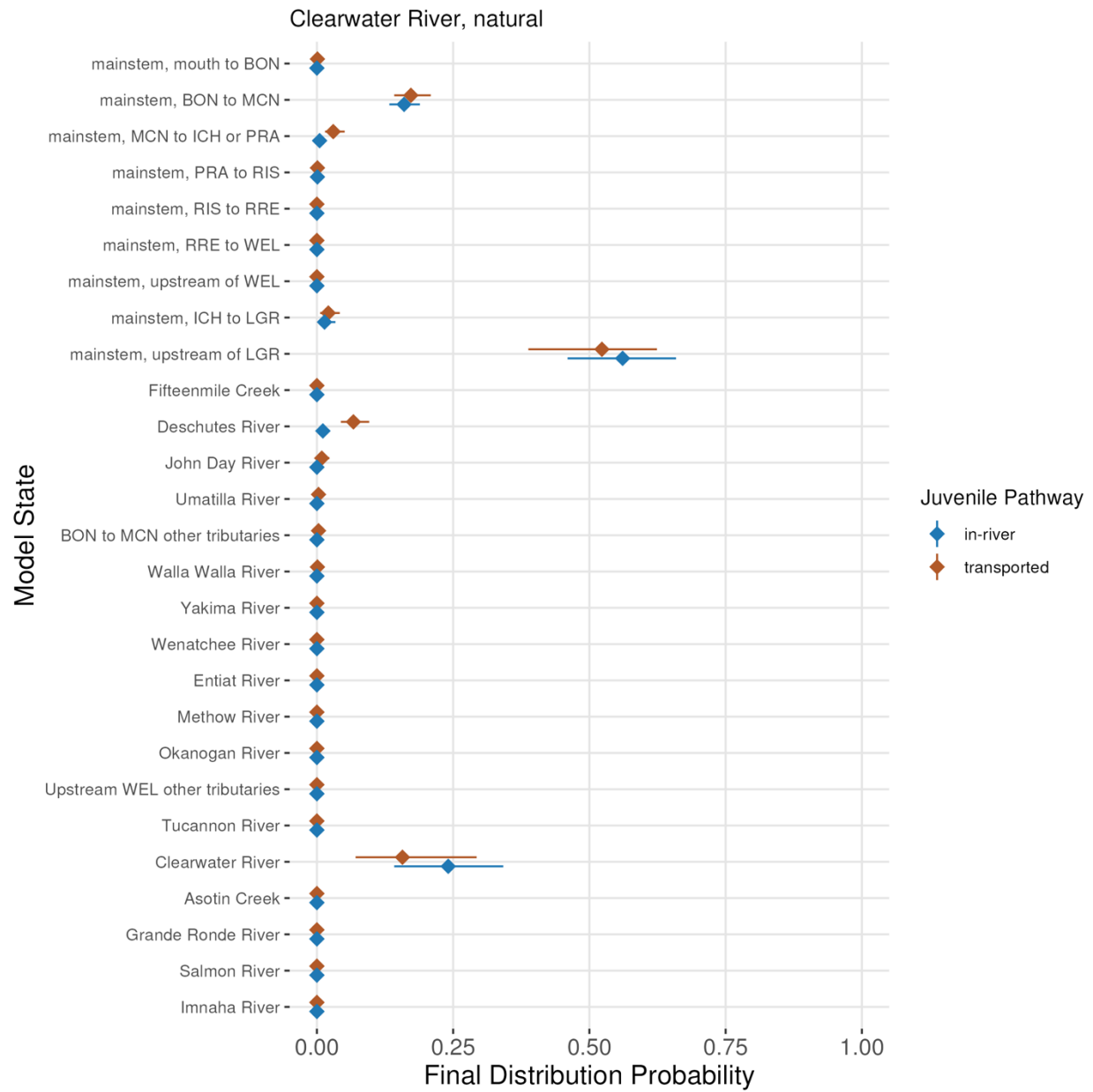


Figure 13. Clearwater River natural origin, estimated final fates under median conditions from 2005-2024.

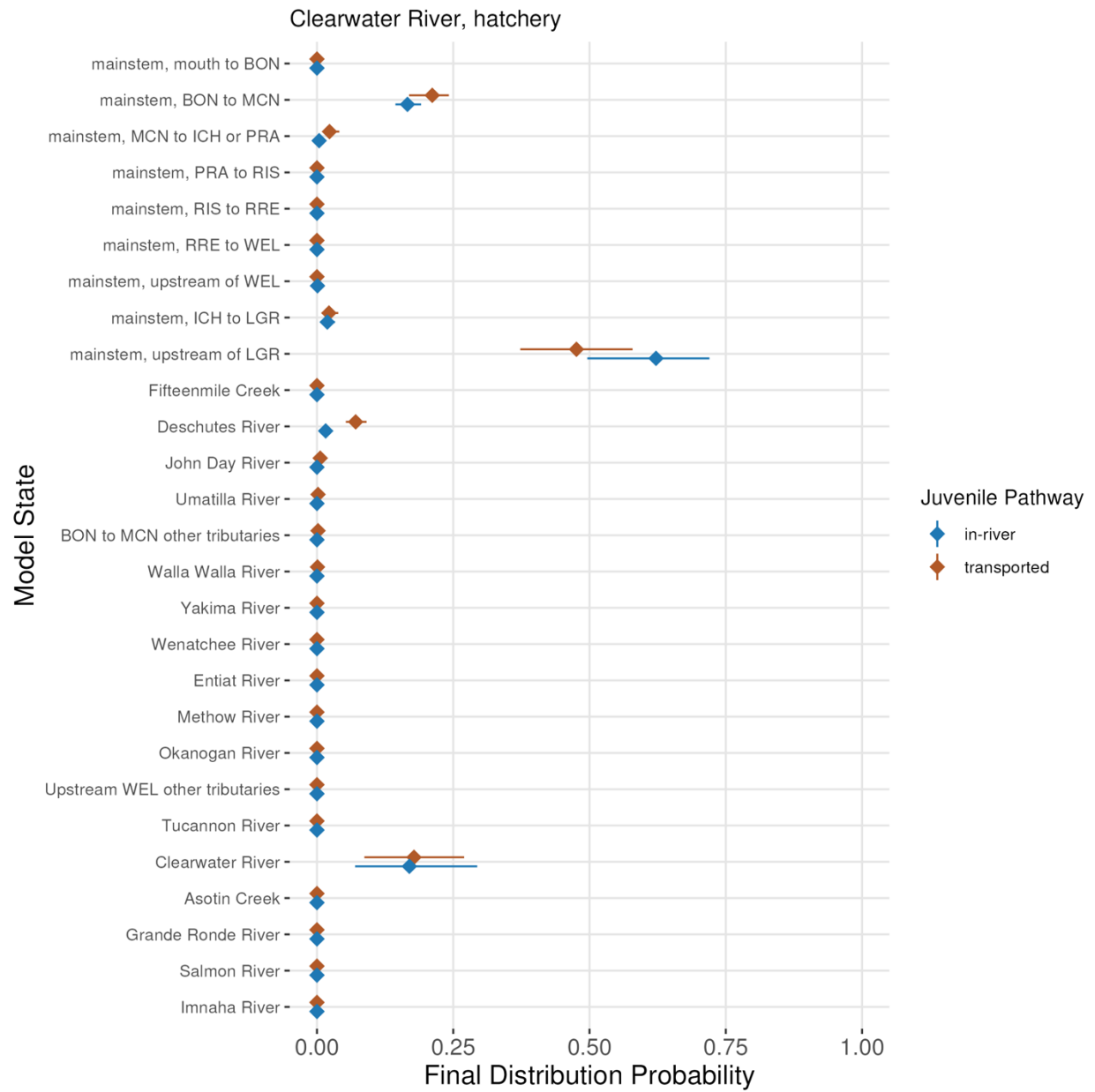


Figure 14. Clearwater River hatchery origin, estimated final fates under median conditions from 2005-2024.

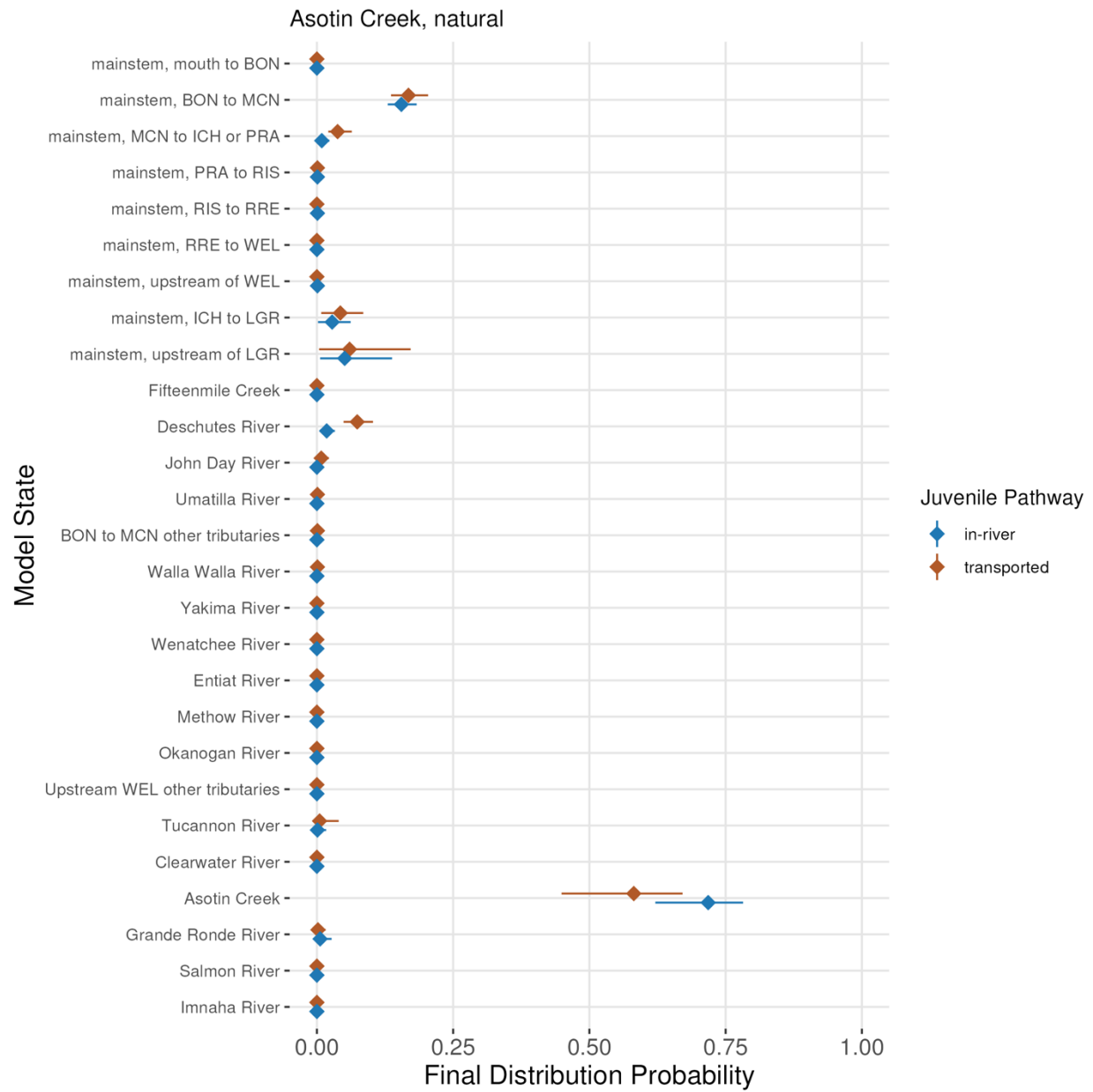


Figure 15. Asotin Creek natural origin, estimated final fates under median conditions from 2005-2024.

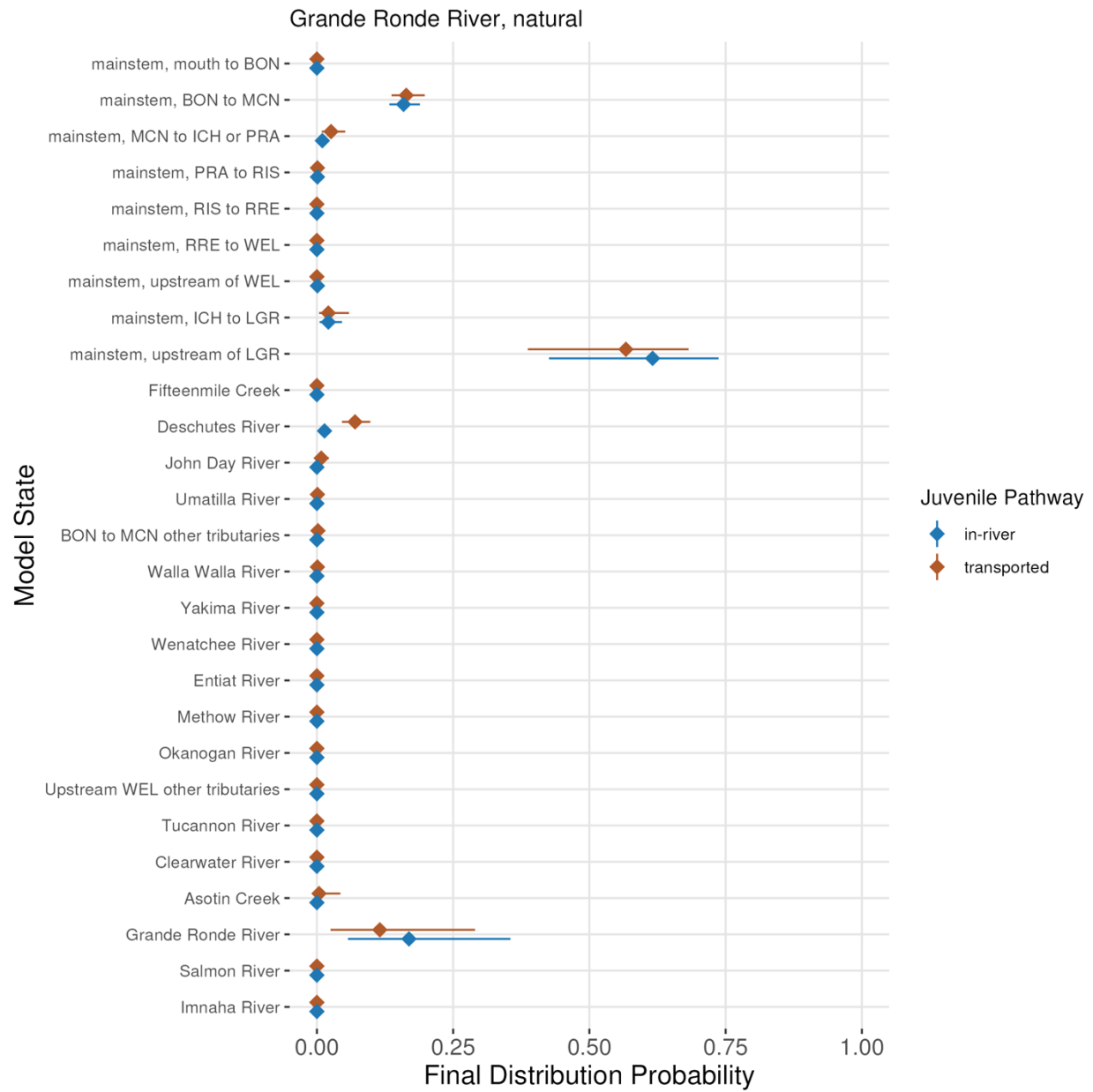


Figure 16. Grande Ronde River natural origin, estimated final fates under median conditions from 2005-2024.

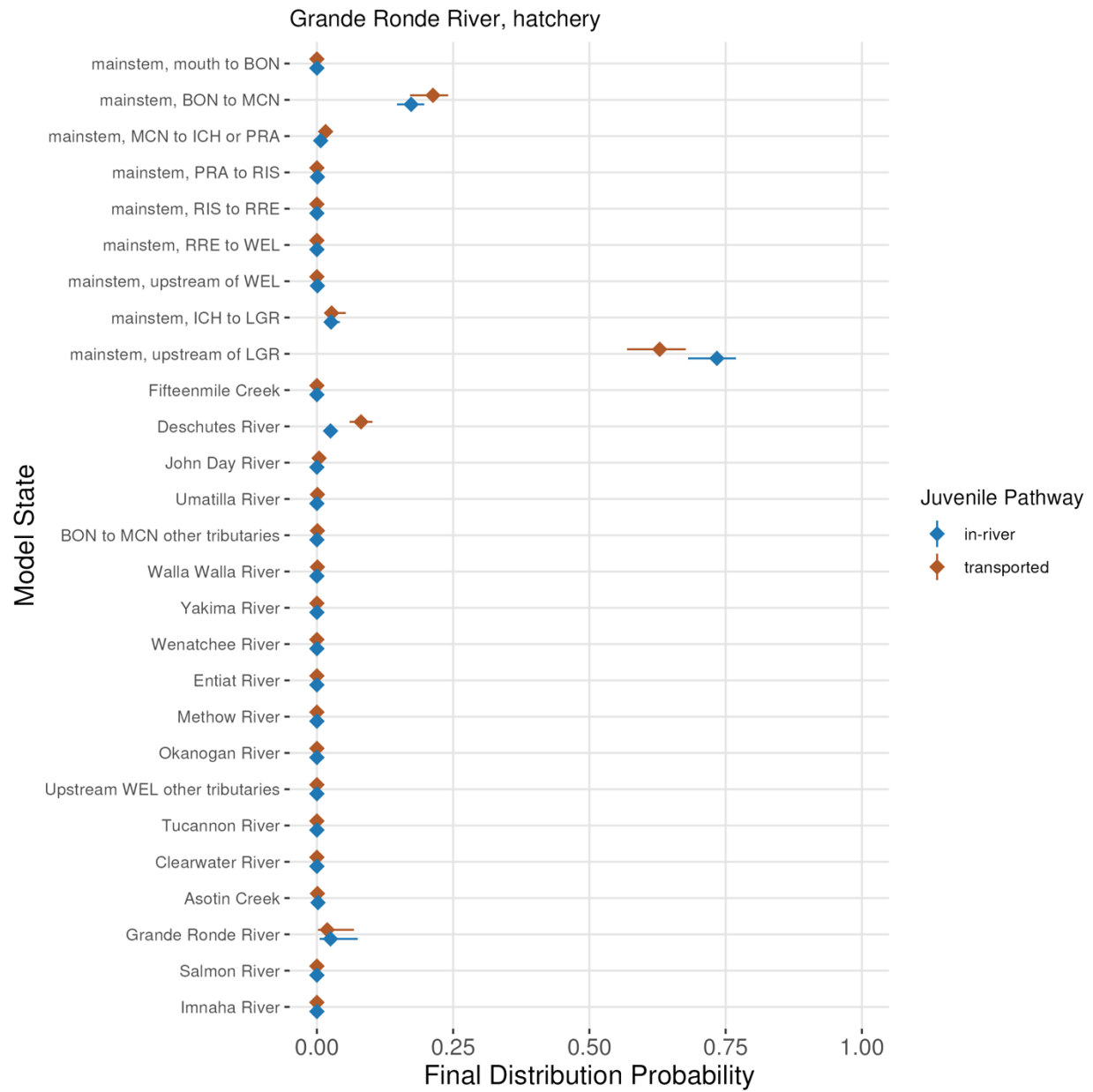


Figure 17. Grande Ronde River hatchery origin, estimated final fates under median conditions from 2005-2024.

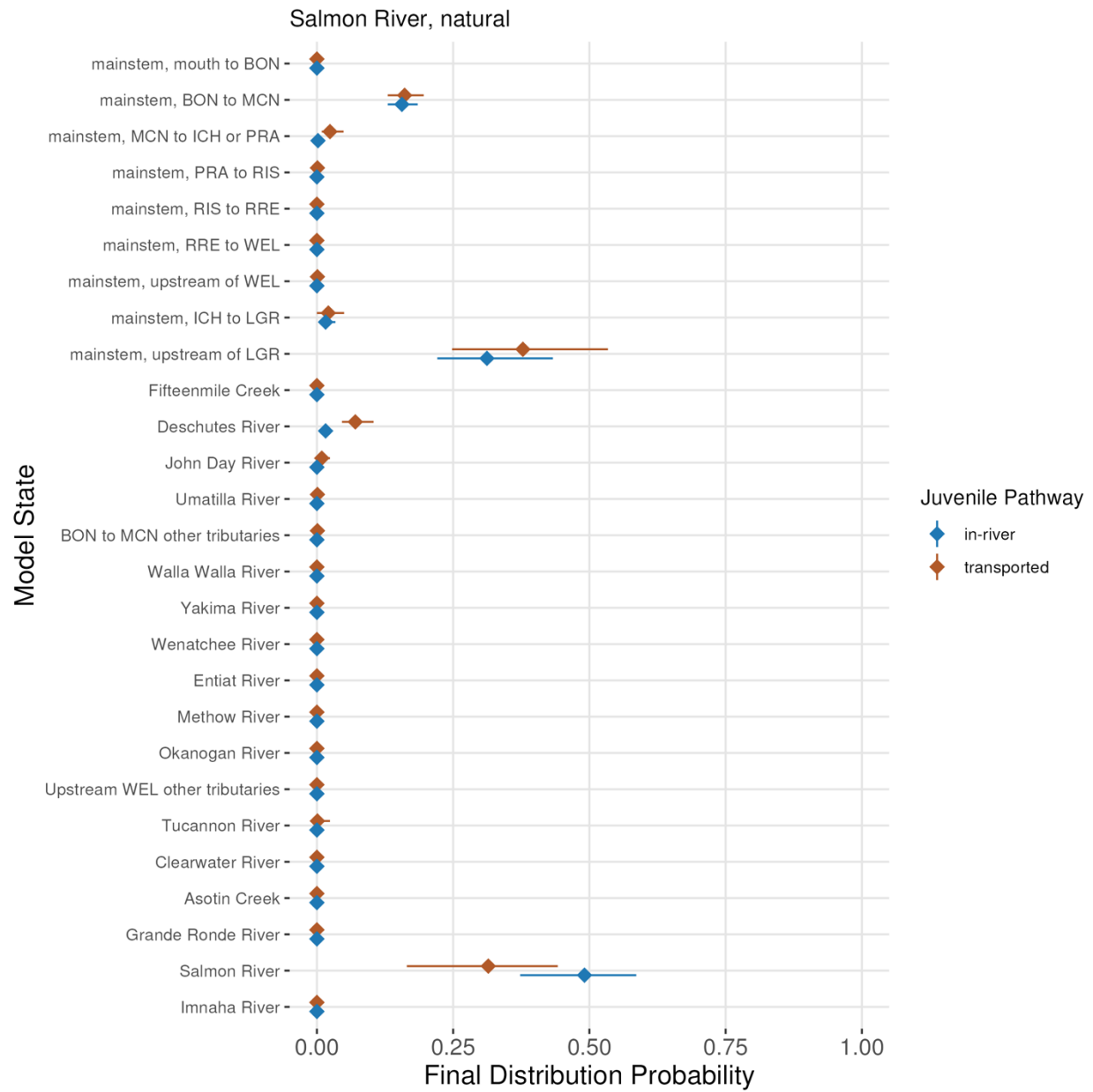


Figure 18. Salmon River natural origin, estimated final fates under median conditions from 2005-2024.

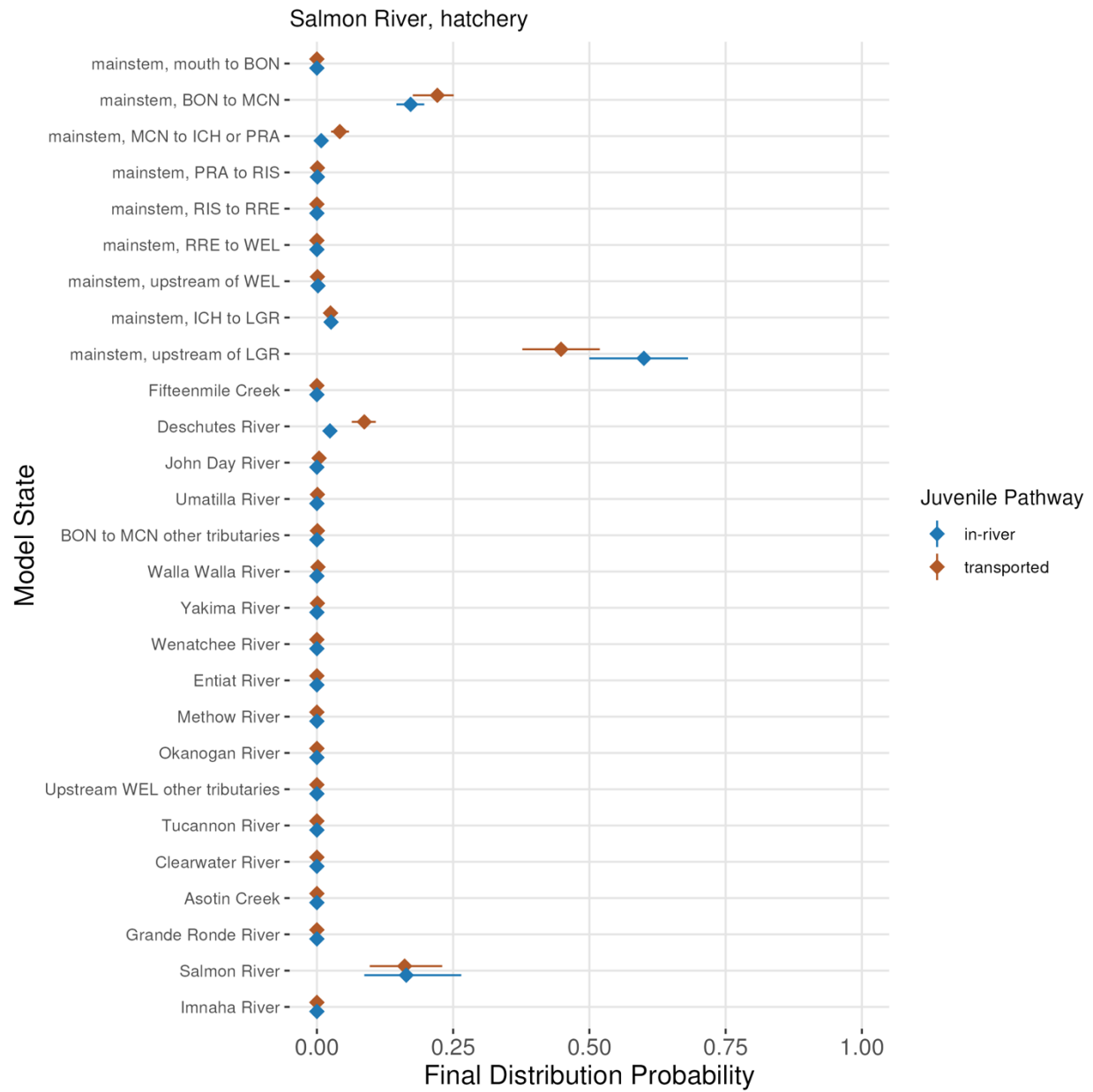


Figure 19. Salmon River hatchery origin, estimated final fates under median conditions from 2005-2024.

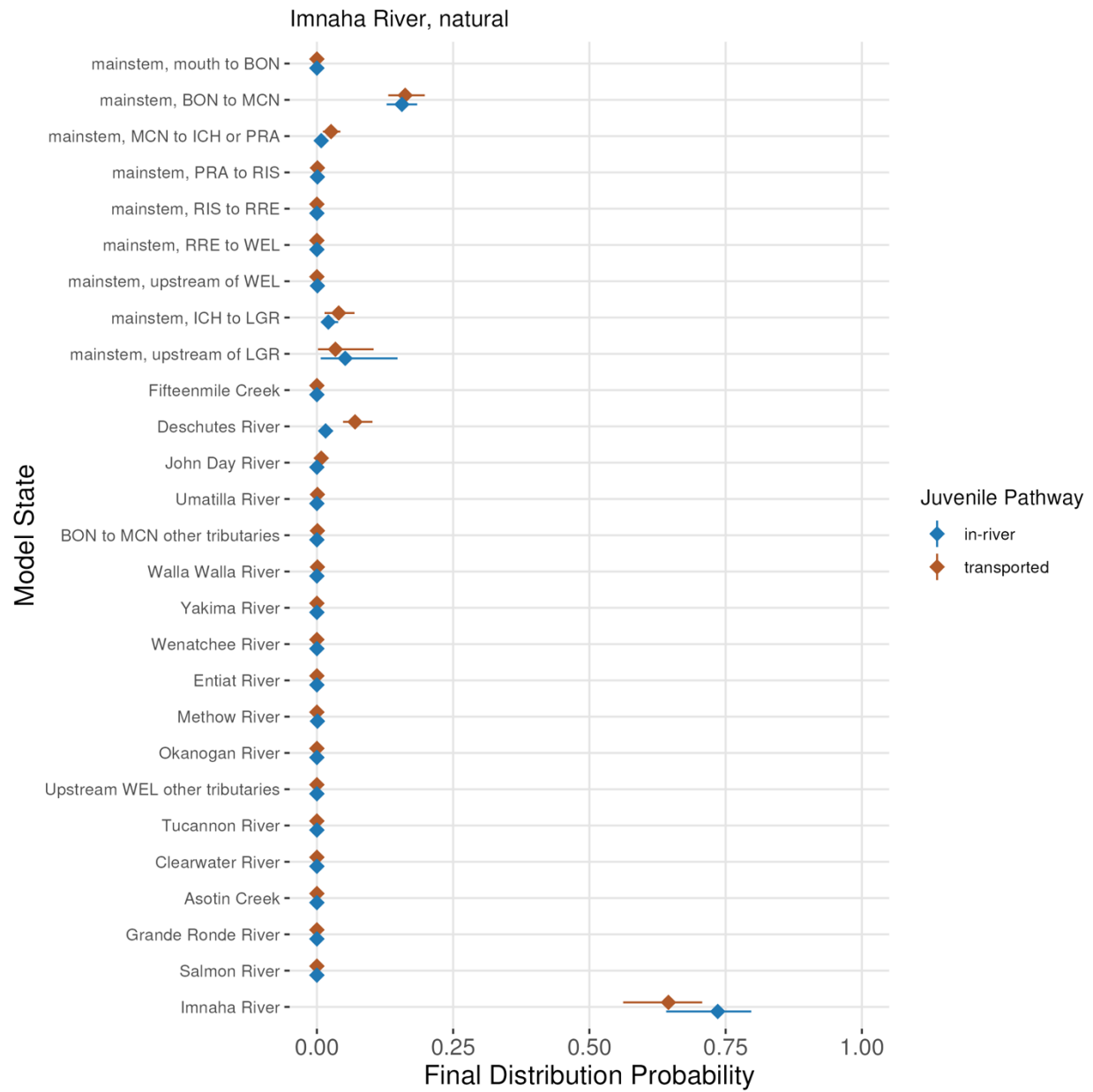


Figure 20. Imnaha River natural origin, estimated final fates under median conditions from 2005-2024.

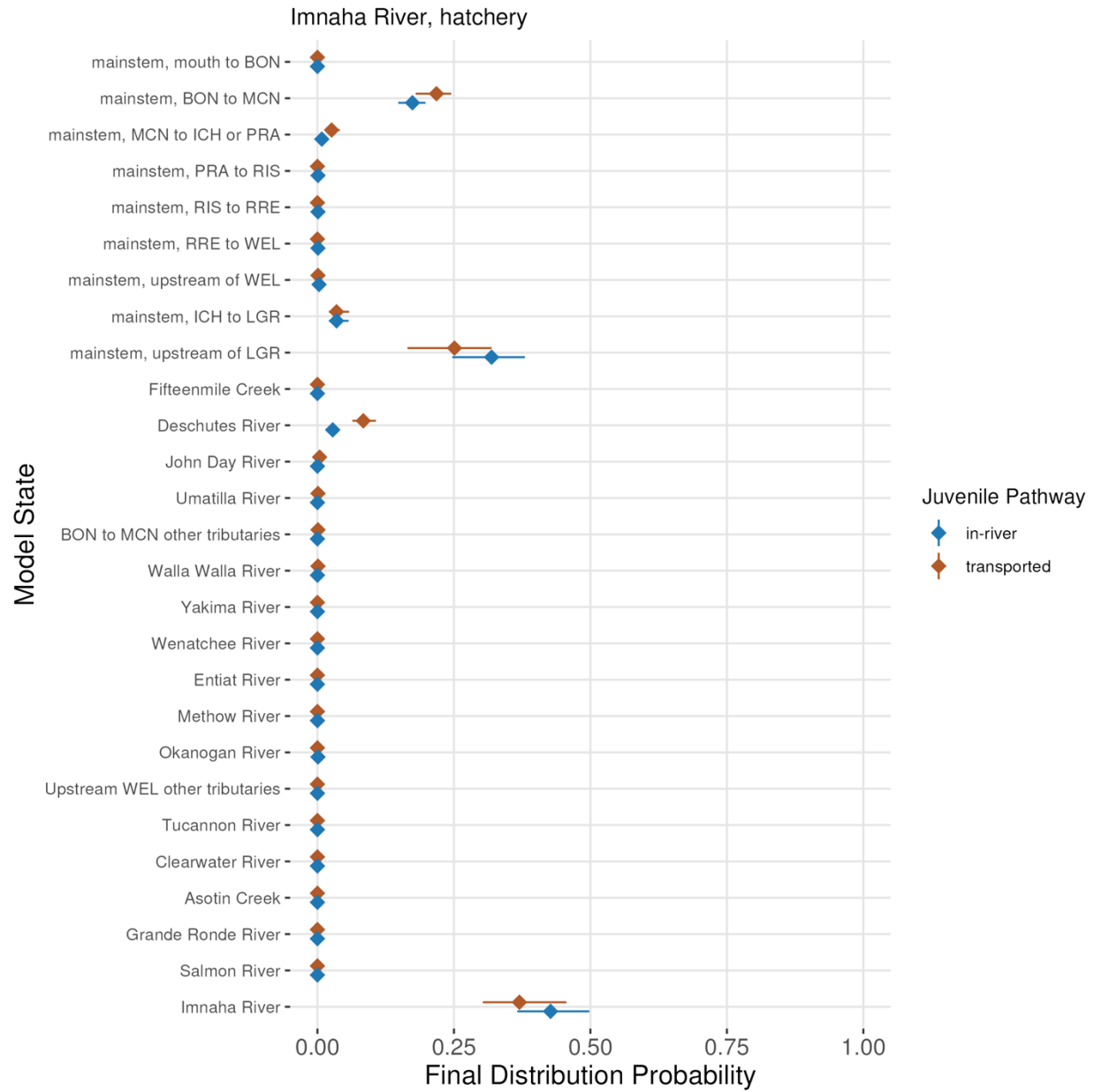


Figure 21. Imnaha River hatchery origin, estimated final fates under median conditions from 2005-2024.

Appendix J. Overshoot probabilities and homing

Table 1. Probability (with 95% credible interval) of overshooting one or two or more dams by population. The Entiat River and Tucannon River populations are only able to overshoot one dam in our model (Wells Dam and Lower Granite Dam, respectively).

Population	1	2+
John Day River, Natural	0.32 (0.23 - 0.4)	0.11 (0.07 - 0.16)
Umatilla River, Natural	0.26 (0.18 - 0.35)	0.1 (0.06 - 0.15)
Umatilla River, Hatchery	0.25 (0.14 - 0.35)	0.06 (0.02 - 0.11)
Walla Walla River, Natural	0.26 (0.2 - 0.32)	0.16 (0.11 - 0.22)
Walla Walla River, Hatchery	0.35 (0.28 - 0.41)	0.27 (0.21 - 0.34)
Yakima River, Natural	0.1 (0.06 - 0.15)	0.05 (0.02 - 0.08)
Wenatchee River, Natural	0.03 (0 - 0.07)	0.02 (0 - 0.05)
Wenatchee River, Hatchery	0.05 (0.03 - 0.09)	0.16 (0.09 - 0.25)
Entiat River, Natural	0.36 (0.28 - 0.47)	•
Tucannon River, Natural (not transported)	0.53 (0.45 - 0.61)	•
Tucannon River, Natural (transported)	0.42 (0.03 - 0.71)	•
Tucannon River, Hatchery (not transported)	0.51 (0.44 - 0.58)	•
Tucannon River, Hatchery (transported)	0.24 (0.07 - 0.34)	•

Table 2. Probability (with 95% credible interval) of homing, conditional on ascending the dam directly downstream of the natal tributary but not overshooting (No overshoot), overshooting one dam (1), or overshooting two or more dams (2+) by population. The Entiat River and Tucannon River populations are only able to overshoot one dam in our model (Wells Dam and Lower Granite Dam, respectively).

Population	No overshoot	1	2+
John Day River, Natural	0.66 (0.55 - 0.75)	0.5 (0.42 - 0.57)	0.15 (0.07 - 0.25)
Umatilla River, Natural	0.68 (0.56 - 0.78)	0.67 (0.58 - 0.75)	0.26 (0.13 - 0.39)
Umatilla River, Hatchery	0.34 (0.2 - 0.51)	0.3 (0.2 - 0.42)	0.12 (0.04 - 0.25)
Walla Walla River, Natural	0.79 (0.62 - 0.89)	0.55 (0.44 - 0.65)	0.15 (0.1 - 0.23)
Walla Walla River, Hatchery	0.71 (0.6 - 0.84)	0.15 (0.1 - 0.35)	0.05 (0.02 - 0.11)
Yakima River, Natural	0.99 (0.93 - 1)	0.87 (0.75 - 0.95)	0.3 (0.12 - 0.55)
Wenatchee River, Natural	0.98 (0.93 - 1)	0.91 (0.67 - 1)	0.57 (0.17 - 1)
Wenatchee River, Hatchery	0.95 (0.89 - 0.98)	0.47 (0.33 - 0.63)	0.05 (0.02 - 0.1)
Entiat River, Natural	0.95 (0.89 - 0.99)	0.71 (0.6 - 0.82)	•
Tucannon River, Natural (not transported)	0.74 (0.6 - 0.86)	0.29 (0.21 - 0.37)	•

Table 2. Probability (with 95% credible interval) of homing, conditional on ascending the dam directly downstream of the natal tributary but not overshooting (No overshoot), overshooting one dam (1), or overshooting two or more dams (2+) by population. The Entiat River and Tucannon River populations are only able to overshoot one dam in our model (Wells Dam and Lower Granite Dam, respectively).

Population	No overshoot	1	2+
Tucannon River, Natural (transported)	0.69 (0.03 - 1)	0.14 (0.01 - 0.41)	•
Tucannon River, Hatchery (not transported)	0.6 (0.46 - 0.74)	0.28 (0.22 - 0.34)	•
Tucannon River, Hatchery (transported)	0.66 (0.29 - 0.9)	0.25 (0.14 - 0.37)	•

Appendix K. Deschutes River movement

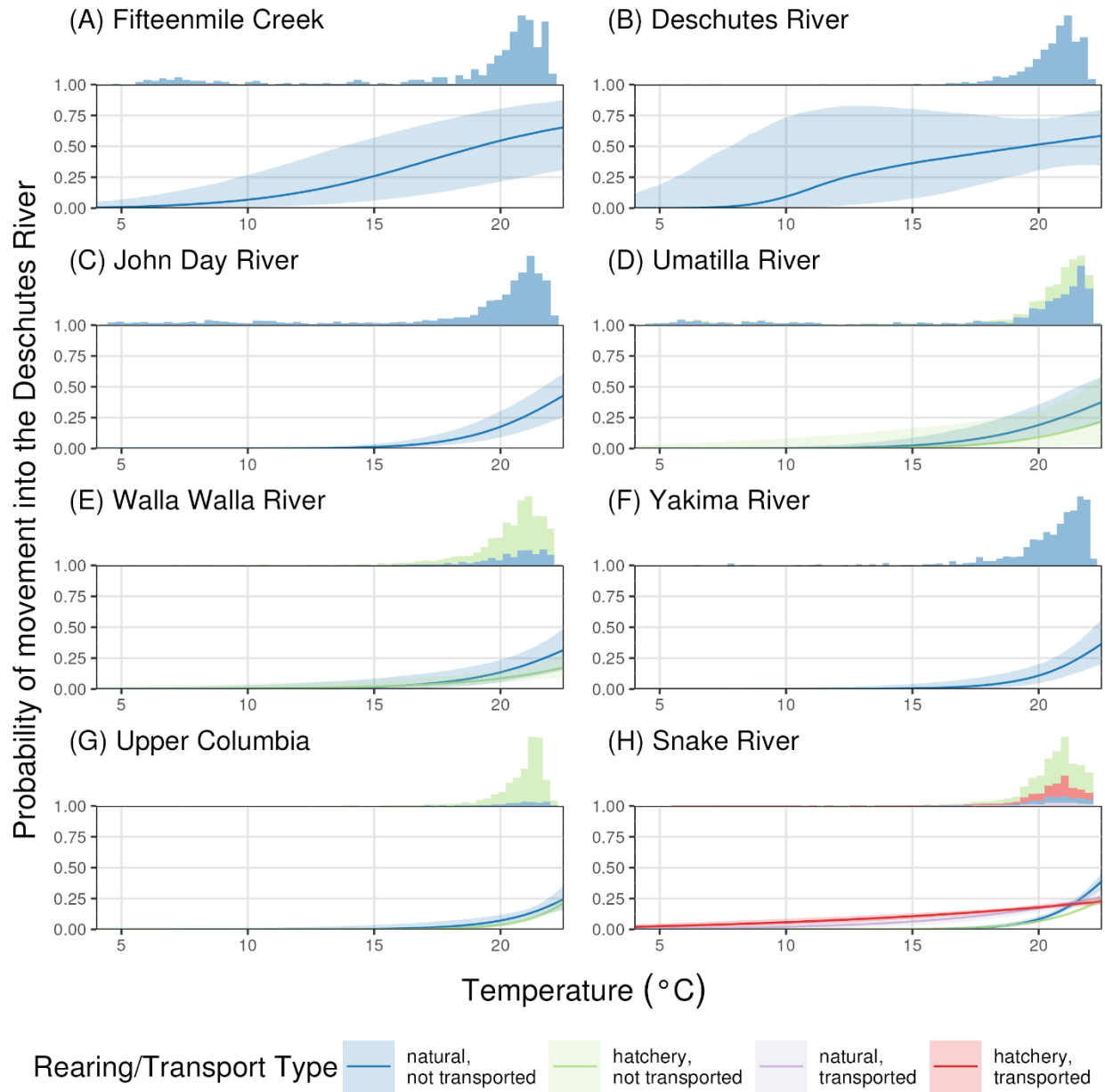


Figure 1. Probability of movement into the Deschutes River by temperature, conditional on being in the reach of the mainstem Columbia between Bonneville and McNary Dam. Histograms on the plot margins indicate the temperature experiences of individual fish. Because this movement occurs within the Middle Columbia DPS, those populations have separate probabilities of movement, and are shown in panels A-F, while fish from the Upper Columbia DPS and the Snake River DPS have shared movement probabilities for this movement and are shown in panels G and H. Please note that in panel H, “not transported” refers to in-river juvenile migrants.

Appendix L. Post-overshoot fallback by dam

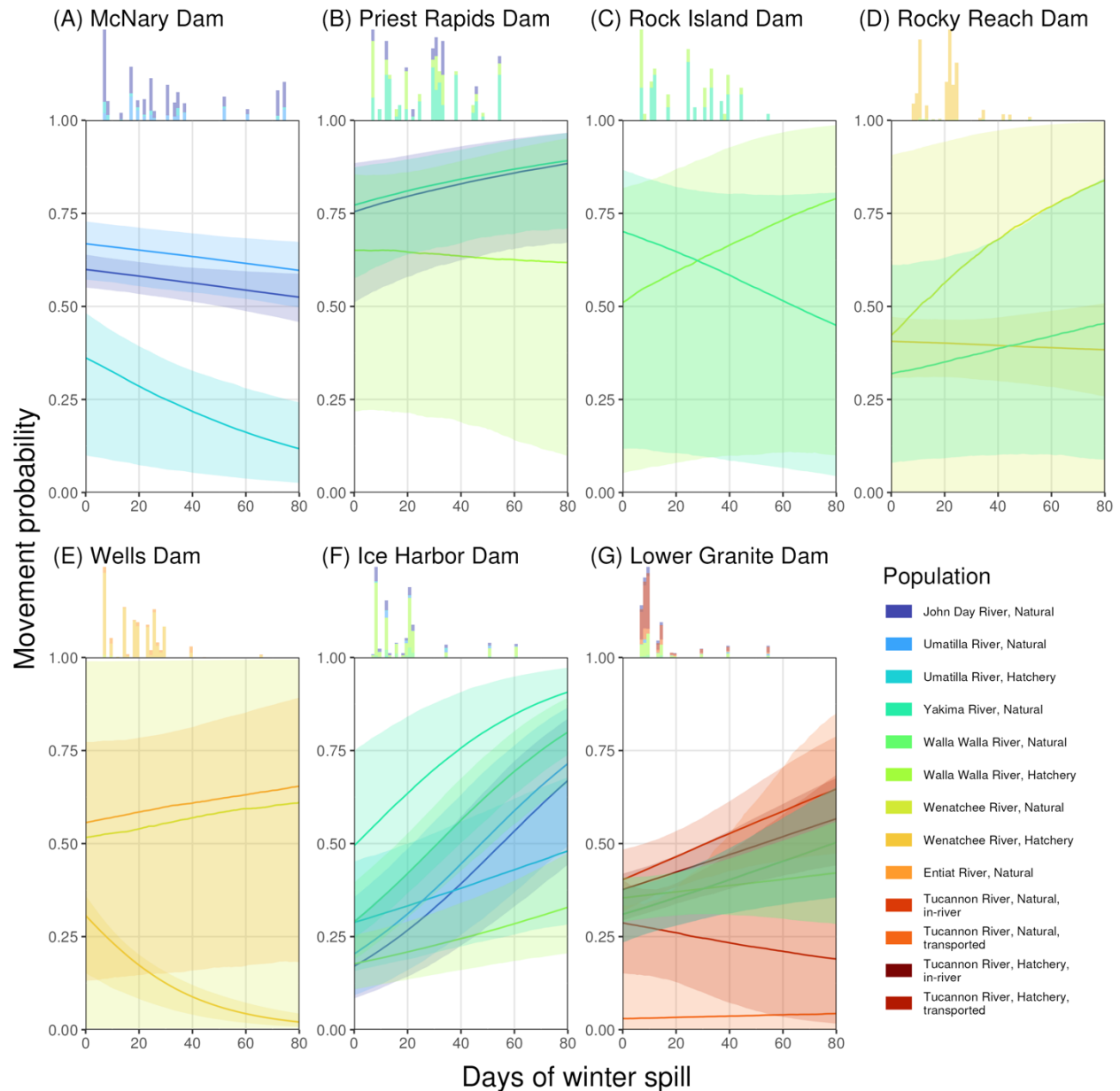


Figure 1. The effect of winter spill days on post-overshoot fallback at each of the seven overshoot dams in this study. For each dam, populations are only visualized if there were at least 10 fish that both overshoot the dam may have been affected by winter spill, based on their movement timing.

Appendix M. En-route fallback as a function of spill volume

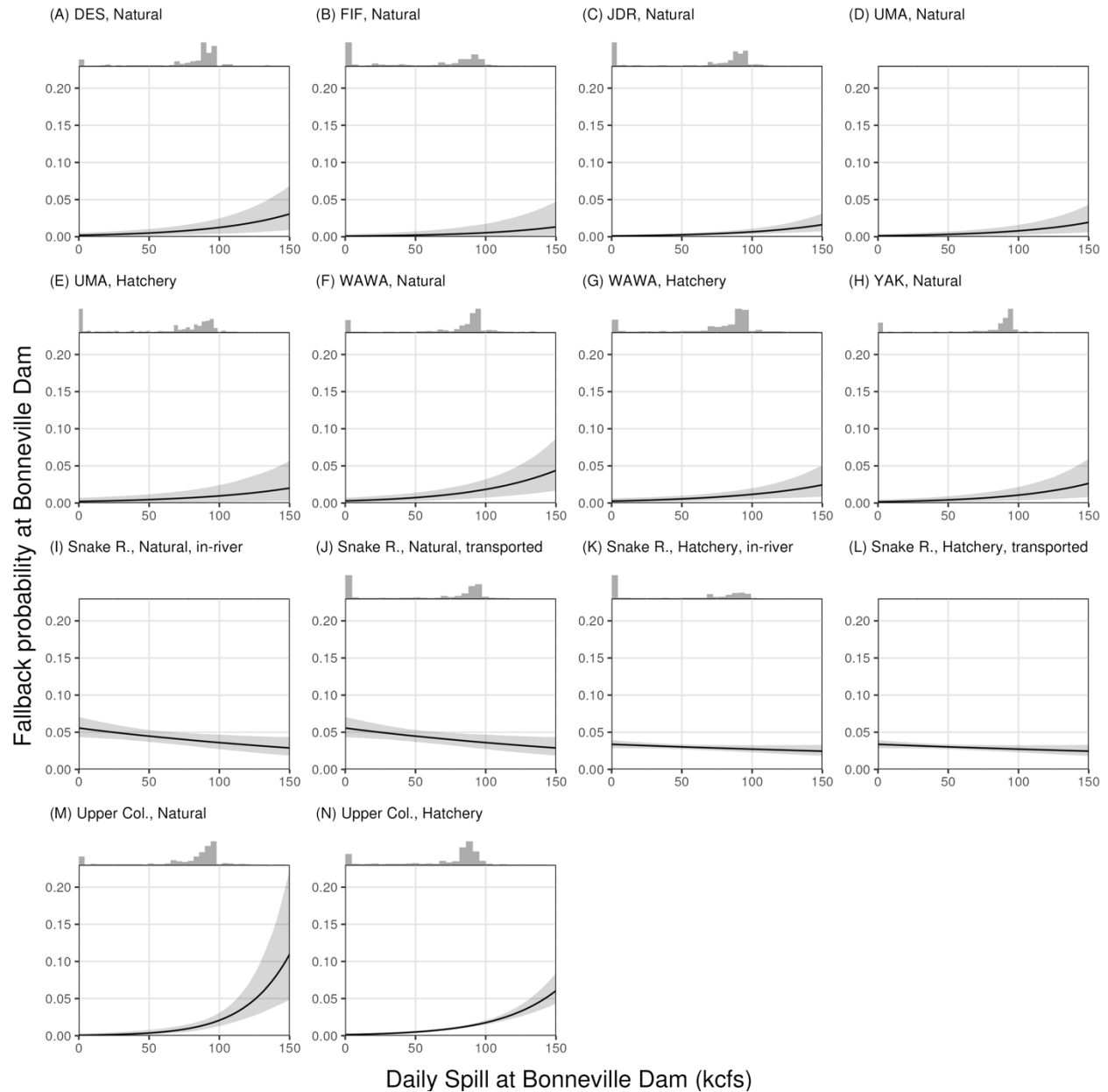


Figure 1. Probability of fallback at Bonneville Dam, by volume of spill. Because this movement occurs within the Middle Columbia DPS, those populations have separate probabilities of movement, and are shown in panels A-H, while fish from the Upper Columbia DPS and the Snake River DPS have shared movement probabilities for this movement and are shown in panels I-L. Histograms on the plot margins indicate the spill experiences of individual fish.

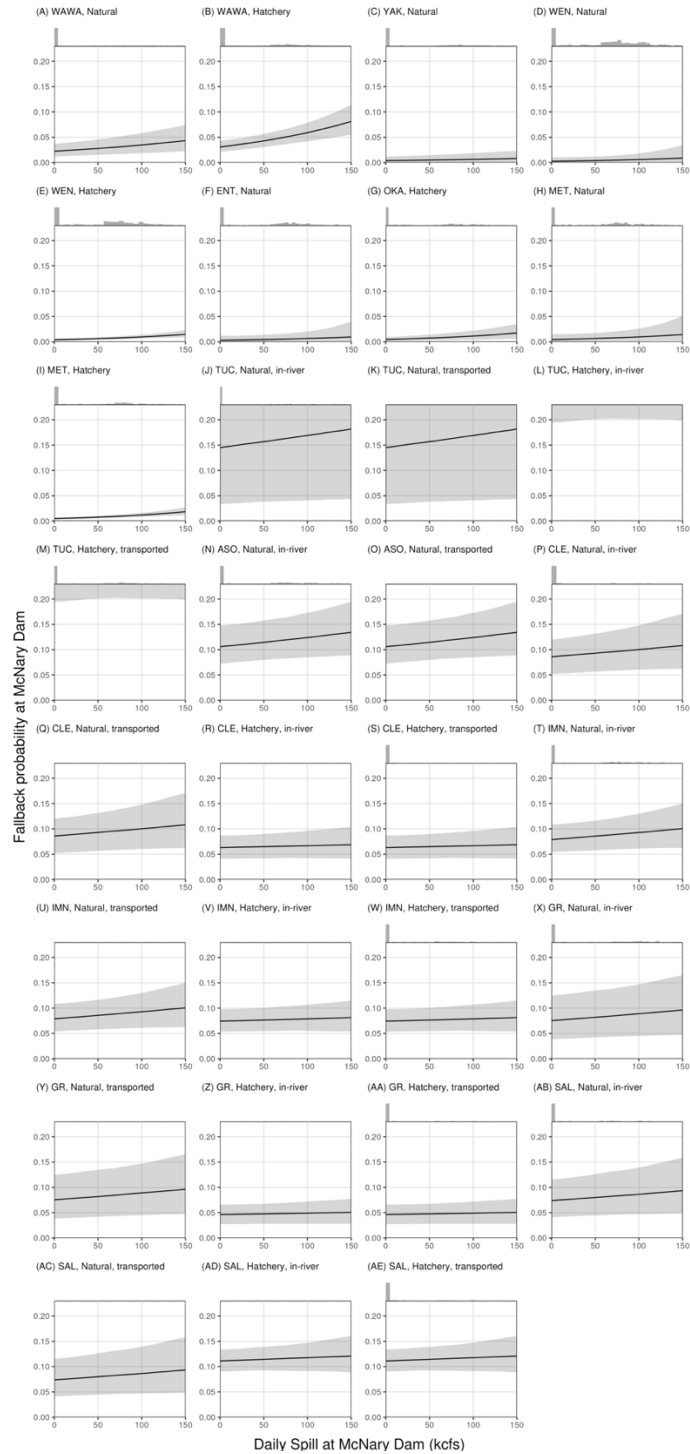


Figure 2. Probability of fallback at McNary Dam, by volume of spill. Because this movement at the juncture between the Middle Columbia, Upper Columbia, and Snake River DPS boundaries, every population has a unique probability of movement. All populations that are downstream of McNary Dam (the Fifteenmile Creek, Deschutes River, John Day River, and Umatilla River) are not shown because they are affected by winter spill days rather than spill volume for this movement, as it is a post-overshoot fallback movement. Histograms on the plot margins indicate the spill experiences of individual fish.

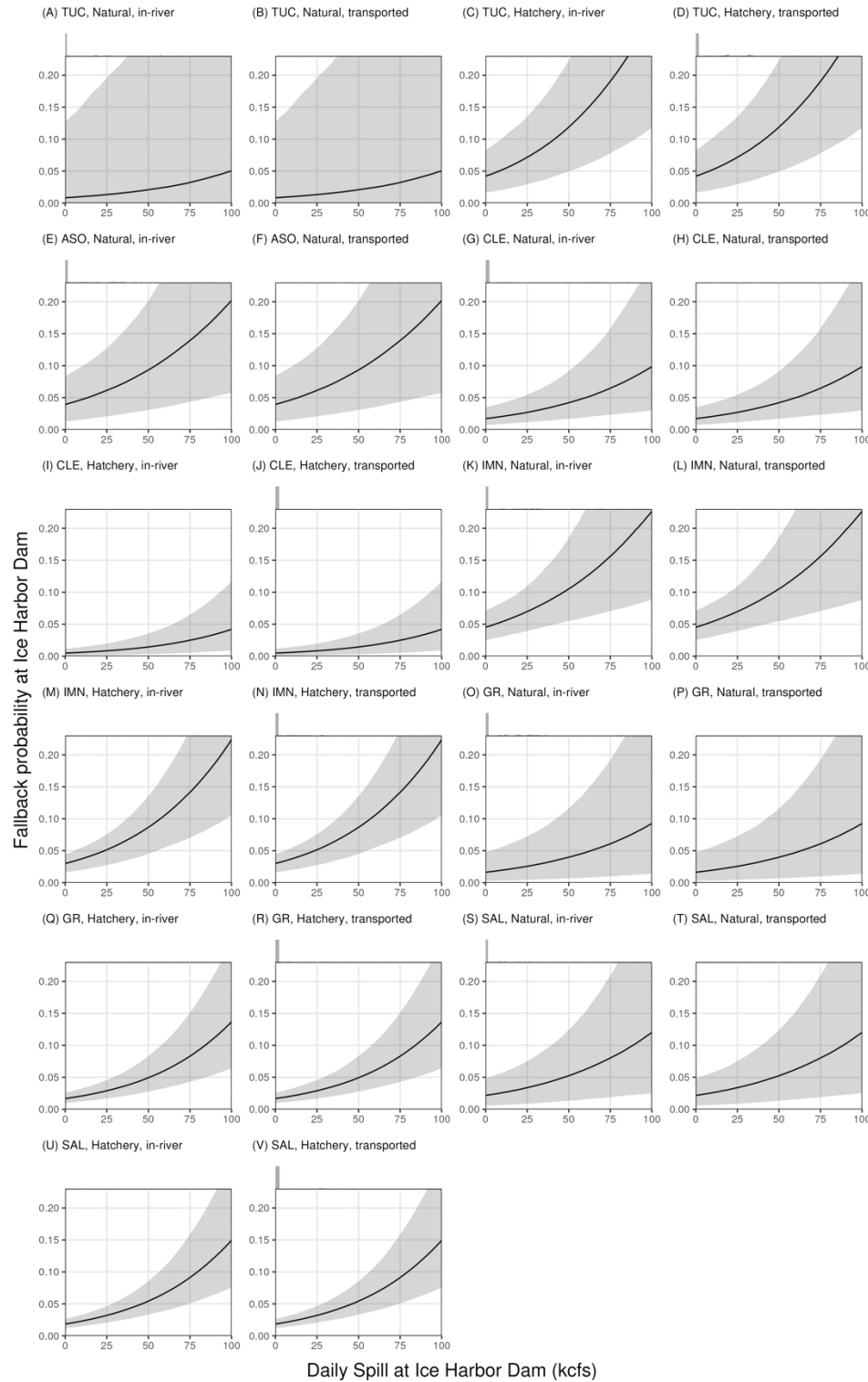


Figure 3. Probability of fallback at Ice Harbor Dam, by volume of spill. Only Snake River populations are shown because an ascent of Ice Harbor Dam by any populations from the Middle or Upper Columbia would be overshoot and therefore the probability of fallback is affected by winter spill days rather than spill volume. Histograms on the plot margins indicate the spill experiences of individual fish.

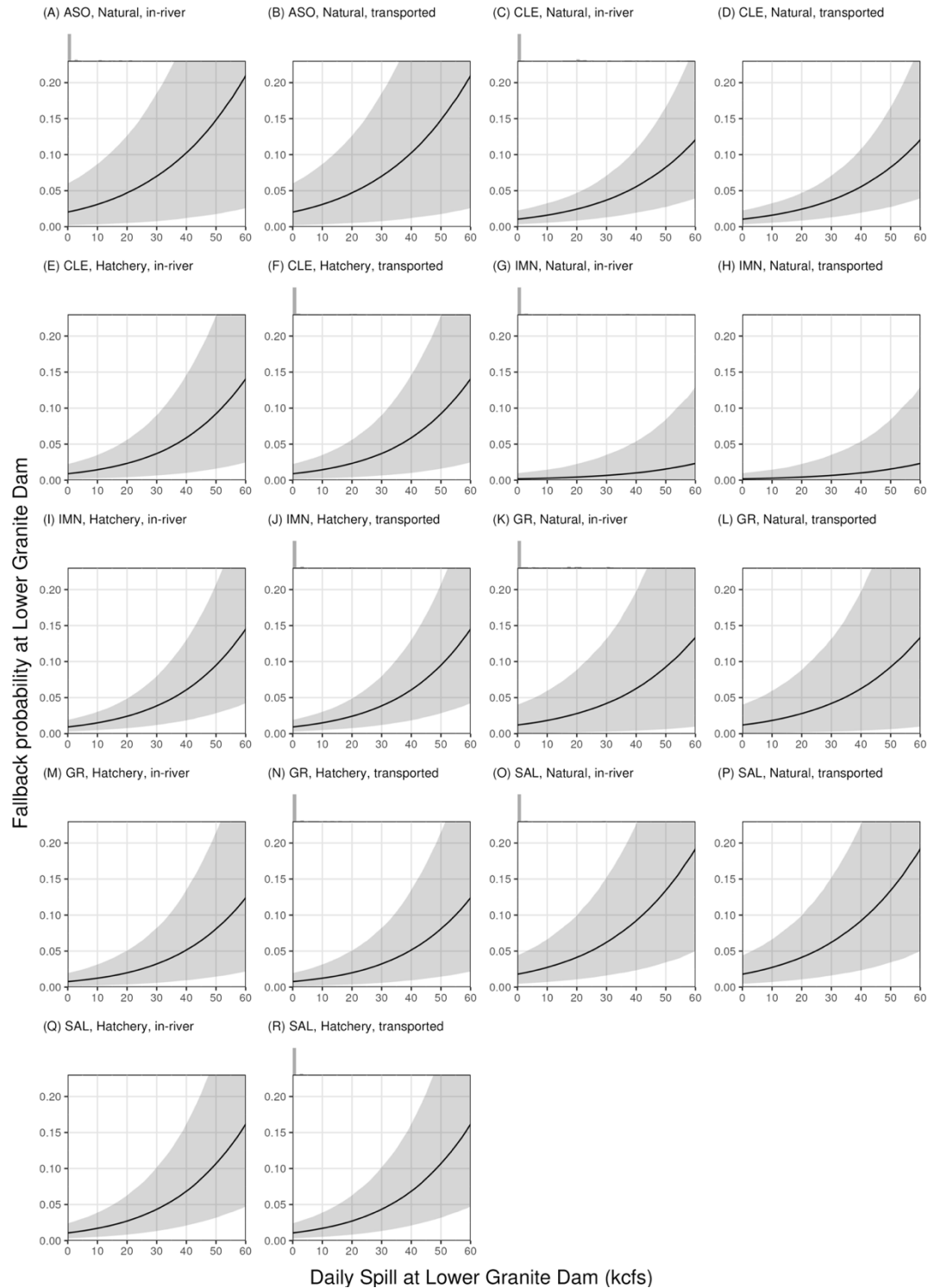


Figure 4. Probability of fallback at Lower Granite Dam, by volume of spill. Only Snake River populations are shown because an ascent of Lower Granite Dam by any populations from the Middle or Upper Columbia would be overshoot and therefore the probability of fallback is affected by winter spill days rather than spill volume. The Tucannon River is also not shown because Lower Granite Dam is an overshoot for that population. Histograms on the plot margins indicate the spill experiences of individual fish.

Appendix N. Post-overshoot fallback as a function of March spill

This section presents shows Figures 5 and 6 from the main manuscript where the model is re-run where only days of spill in March are used as a covariate instead of days of spill in January, February, and March (as is used in the base model).

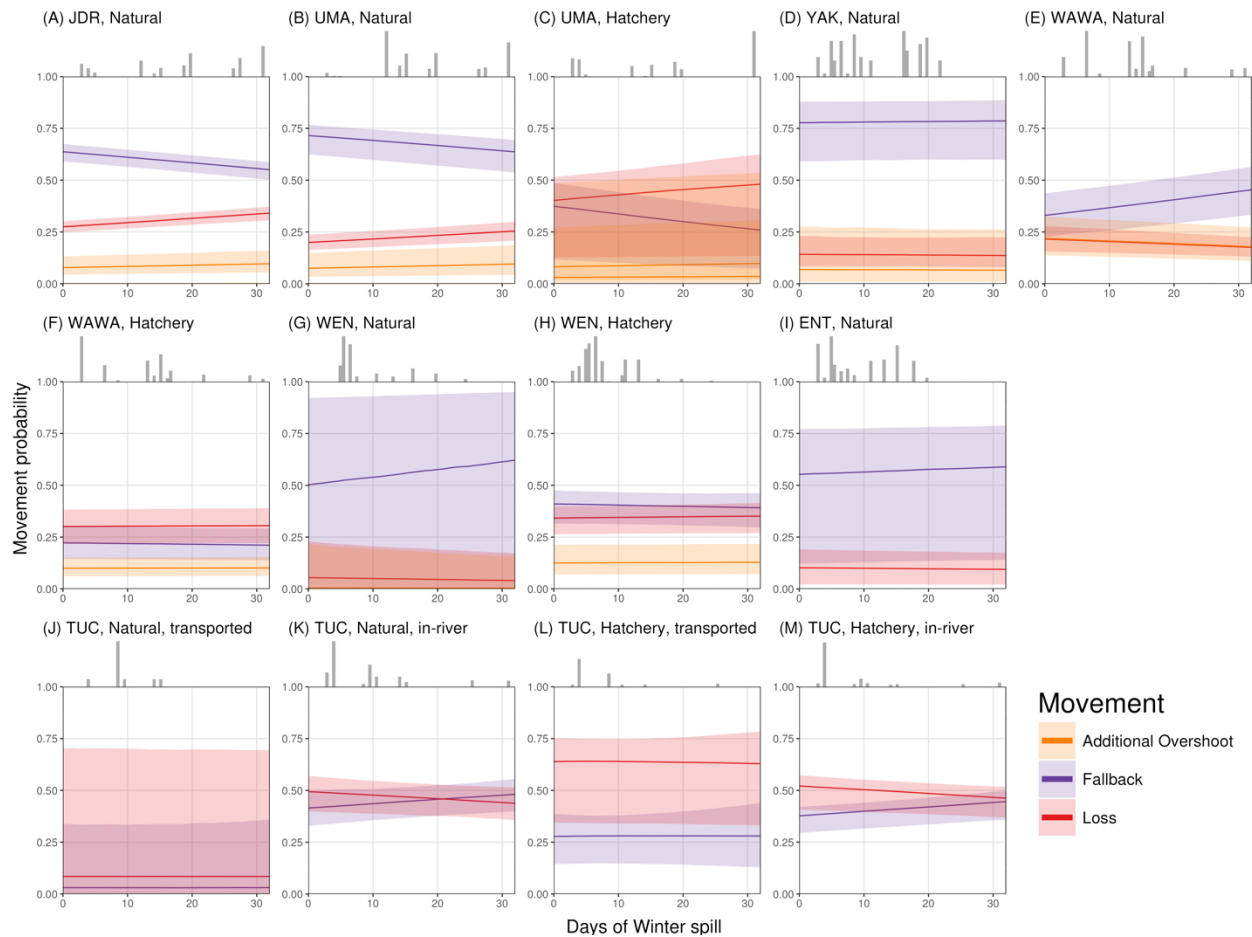


Figure 1. The effect of March spill days on movement probabilities out of the mainstem state directly upstream of the mainstem state that connects to the natal tributary for (A) John Day River natural origin Steelhead, (B) Umatilla River natural origin Steelhead, (C) Umatilla River hatchery origin Steelhead, (D) Yakima River natural origin Steelhead, (E) Walla Walla River natural origin Steelhead, (F) Walla Walla River hatchery origin Steelhead, (G) Wenatchee River natural origin Steelhead, (H) Wenatchee River hatchery origin Steelhead, (I) Entiat River natural origin Steelhead, (J) Tucannon River natural origin transported Steelhead, (K) Tucannon River natural origin in-river Steelhead, (L) Tucannon River hatchery origin transported Steelhead, and (M) Tucannon River hatchery origin in-river Steelhead. Histograms on the plot margins indicate the temperature experiences of individual fish.

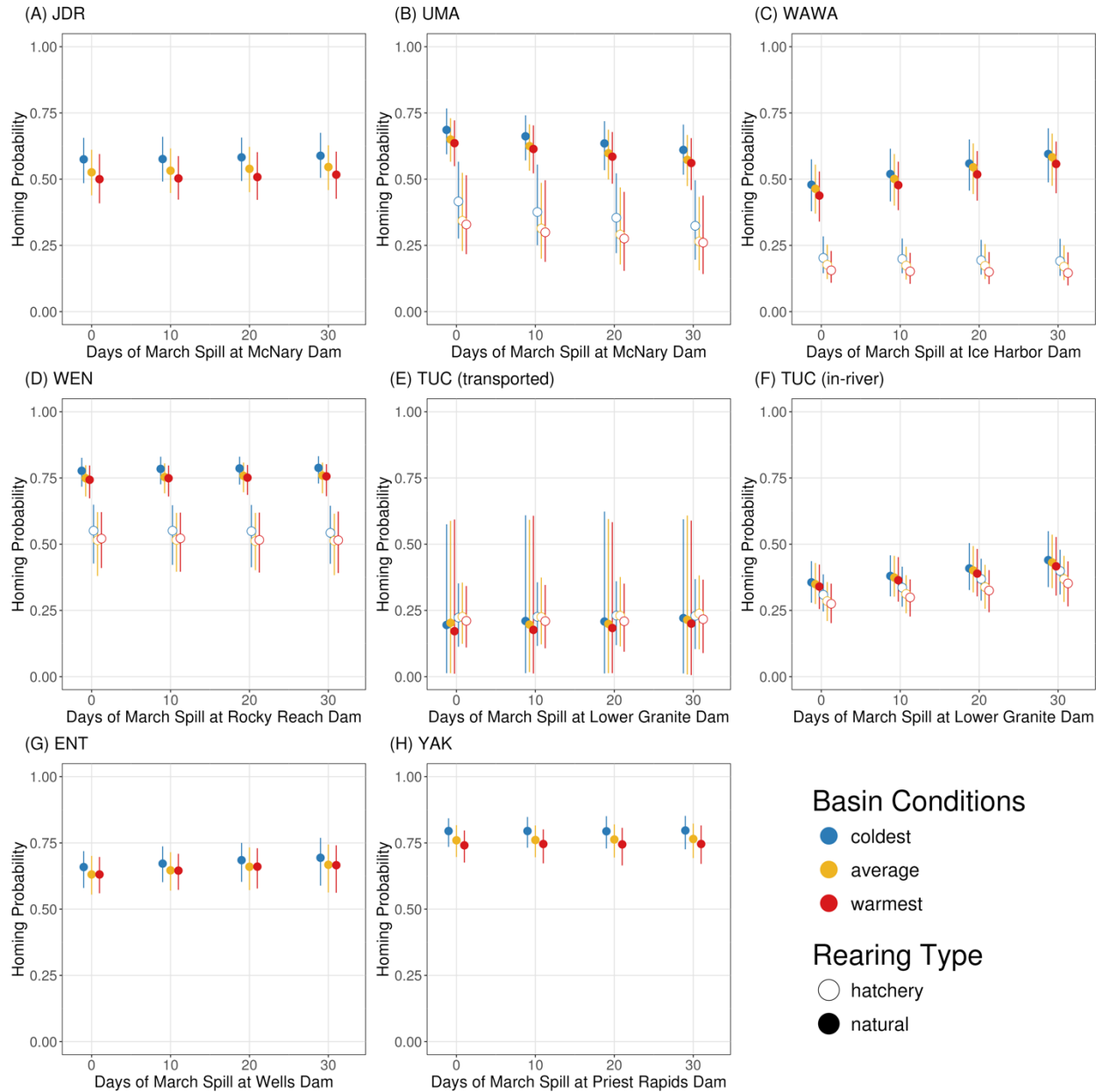


Figure 2. The homing probability for (A) John Day River, (B) Umatilla River, (C) Walla Walla River, (D) Wenatchee River, (E) Tucannon River transported, (F) Tucannon River in-river, (G) Entiat River, and (H) Yakima River Steelhead under different scenarios for basin-wide temperature and March spill days (0, 10, 20, or 30 days) at the overshoot dam. The temperature scenarios are specific run years from the dataset, with the coldest year being the 2011/2012 run year, the average year being the 2005/2006 run year, and the warmest year being the 2015/2016 run year.

Chapter 2 Appendix References

Benaglia, T., D. Chauveau, D. R. Hunter, and D. S. Young. 2010. mixtools: an R package for analyzing mixture models. *Journal of statistical software* 32:1–29.

- Connolly, P. J., I. G. Jezorek, K. D. Martens, and E. F. Prentice. 2008. Measuring the Performance of Two Stationary Interrogation Systems for Detecting Downstream and Upstream Movement of PIT-Tagged Salmonids. *North American Journal of Fisheries Management* 28:402–417.
- Greenberg, L. A., and P. S. Ciller. 2000. The potential of flat-bed passive integrated transponder antennae for studying habitat use by stream fishes. *Ecology of Freshwater Fish* 9:74–80.
- Holmes, E. E., E. J. Ward, and K. Wills. 2012. MARSS: Multivariate autoregressive state-space models for analyzing time-series data. *R Journal* 4:11–19.

Chapter 3 Appendix

Appendix A. Survey Descriptions

Appendix A.1. Juvenile Salmon and Ocean Ecosystem Survey (JSOES)

Surface trawl sampling

The Juvenile Salmon and Ocean Ecosystem Survey (JSOES) targets juvenile salmonids and other pelagic nekton in the upper 20 m of the water column by towing a 264 Nordic trawl for 30 minutes at a speed of approximately 6.5 km/h. The rope trawl is 108 m long, with a mouth opening that measures 30 m wide by 20 m deep. The net has variable and graded mesh sizes, ranging from 162.6 cm in the throat to 8.9 cm in the cod end, with the cod end having a further 0.8 m liner sewn into it to capture small fish and other nekton.

Genetic assignment of Chinook Salmon to stock groups

Juvenile Chinook Salmon caught by the JSOES were assigned to specific run and life history groups using genetic methods and catch per unit effort was then calculated for each genetic stock group. For each juvenile Chinook Salmon caught by the JSOES, caudal fin clips were stored in 100% ethanol and DNA subsequently extracted. The genetic stock identification methods used varied between the time periods 2003-2012 and 2013-2022. For the time period 2003-2012, polymerase chain reaction (PCR) was conducted to amplify 13 microsatellite DNA loci, whereas for the time period 2013-2022 PCR was used to genotype individuals using 185 single-nucleotide polymorphism loci. In both cases, the results were compared to a genetic baseline to assign individual fish to stock groups using the genetic stock identification program ONCOR (Kalinowski et al., 2007). More detail on stock assignment methods from 2003-2012 can be found in Teel et al. (2015) and more detail on the methods used from 2013-2022 can be found in Hess et al. (2013) and Van Doornik et al. (2019). Because of the genetic legacy of broodstock

transfers between stocks from the Columbia and Snake Rivers, genetic stock identification cannot distinguish among certain Chinook Salmon populations upstream of Bonneville Dam. As such, ocean-caught juveniles were necessarily combined into an interior fall stock group, which is composed mostly of Upper Columbia River Summer/Fall and Snake River Fall Chinook Salmon. ONCOR (Kalinowski et al., 2007) was used to compute the catch per unit effort of each genetic stock group in each tow by allocating each individual to the different stock groups proportional to the probability of assignment in that stock group. Combined with the size-based life history classifications, the genetic stock identification methods allowed us to analyze the ocean distributions of two Chinook Salmon groups: Interior Fall subyearlings and Interior Fall yearlings.

Bongo net sampling

Bongo net tows were conducted using a 0.6 m bongo net with 335 μm mesh. Sampling with this net was conducted by letting out 60 m of cable before retrieving the net at a rate of 30 m/min while being towed at 2 knots. As such, the net was towed obliquely from the surface, to depth, and back again, reaching a maximum depth of 20-30 m. Samples were preserved in 5% buffered formalin/seawater solution for laboratory analysis. In the laboratory, samples were rinsed and organisms identified to the lowest taxonomic level and life history stage and enumerated. More detail on the laboratory procedure can be found in Morgan et al. (2005). We then assigned each taxon identified in the JSOES Bongo data to a functional group in alignment with yearling and subyearling Chinook Salmon diet items (Daly et al., 2009, 2017). Ultimately, four functional groups were extracted for investigation as potential juvenile salmon prey items: shrimp larvae, non-Cancer crab larvae, Cancer crab larvae, and hyperiid amphipods. The life history stages of each of these groups that are typically consumed by juvenile salmonids (i.e., excluding any adults for the larval groups) were exported for further modeling. The assignment of each taxon to a functional group can be found in Appendix B. As a proxy for energy availability from prey, biomass was used as the unit of measurement. Biomass for each combination of taxonomic level and life history stage in a sample was calculated by multiplying the density (number per m^3) by the carbon weight of individuals of that developmental stage, with carbon content estimates derived from the literature or from estimates of dry weight (Morgan et al., 2005).

Seabird observations

Seabird observations were collected early in the morning, beginning between 0450 and 0515 hours, prior to trawl or bongo net sampling. This ensured that seabirds were not attracted to the ship by fishing activity. Observations were collected by a trained seabird observer as the vessel transited west to east along each transect. This observer made continuous observations within a

300-m-wide bow-to-beam strip transect on the side of the vessel with the best visibility, which was almost always the south-facing (starboard) side to minimize morning sun glare that interferes with an observer's ability to detect birds. Seabird counts and the area surveyed in each year were assigned to the nearest trawl station, with the density of each species (number per square kilometer) calculated by dividing the count by the area surveyed for each station.

Pacific Whiting Conservation Cooperative (PWCC)/Pre-Recruit Survey (PRS)

The Pacific Whiting Conservation Cooperative (PWCC) survey, which was conducted from 2001-2009, and the Pre-Recruit Survey (PRS), conducted most years since 2011, were used to provide data on young-of-year (YOY) rockfishes, a key prey item for juvenile Chinook. While the PRS samples fixed transects perpendicular to the coast, the PWCC survey did not have a fixed sampling design but typically conducted transects while transiting south. The varying spatial coverage of each of these surveys can be found in Appendix F. As mentioned in the main text, these two surveys used the same fishing gear and sampling methods and therefore are treated as one continuous time series in our analysis. These surveys deployed a modified-Cobb midwater trawl with a 26 m headrope, a net opening with a height and width of 12 m, and a 9.5 mm cod-end liner to retain micronekton. The target depth of the headrope is 30 m. This net was towed for 15 minutes at approximately 2 knots.

The contents of each trawl were sorted and identified to the lowest possible taxonomic level onboard. Although the PWCC survey and the PRS capture many taxa that are salmon forage (Friedman et al., 2018), the PWCC taxonomic assignments are only considered reliable for YOY rockfishes (John Field, pers. comm.). Therefore, we only use the combined PWCC/PRS time series of YOY rockfishes for this analysis.

Joint U.S. and Canada Pacific Hake Integrated Acoustic and Trawl Survey (Hake Survey)

The Joint U.S. and Canada Pacific Hake Integrated Acoustic and Trawl Survey (Hake Survey) is a biennial survey targeting Pacific Hake (*Merluccius productus*) on the West Coasts of the United States and Canada. This proceeds south to north from Point Conception in California to Dixon Entrance in British Columbia. Transects, spaced 10 nautical miles apart, are conducted east-west perpendicular to the coast, with transects extending from approximately the 50 m isobath to the 1500 m isobath. In this survey, downward-looking Simrad EK60 echosounders operating at multiple frequencies (18, 38, 70, 120, and/or 200kHz, depending on the year) recorded acoustic backscatter from the sea surface to a depth of 750 m continuously during daylight hours. Midwater and bottom trawls were conducted opportunistically and adaptively during the survey and used to assign species, size, age, and sex composition to the acoustic

backscatter. The specific trawl nets deployed depended on the vessel, and a more detailed description of the trawl nets and biological sampling can be found in de Blois (2020). For this study, acoustic backscatter (measured as nautical-area-backscattering coefficient, or NASC, m² nmi⁻²) attributed to adult (age 2+) Pacific Hake were binned into 2.5 nautical mile (4.63 km) bins (Appendix F). Survey data from 2001-2021, odd years (plus 2012) were included in this study.

Appendix B. JSOES Bongo functional groups

Table 1. The taxa assigned to each of the four functional groups from the JSOES Bongo data, along with the proportion of that functional group that this taxon represents.

Taxonomy	Life History Stages	Functional Group	Proportion of Functional Group
Cancer oregonensis/productus	Zoea, Megalopa	Cancer crab larvae	0.77743429
Cancer antennarius/gracilis	Zoea, Megalopa	Cancer crab larvae	0.17774435
Cancer magister	Zoea, Megalopa	Cancer crab larvae	0.04473821
Themisto pacifica	Juvenile	Hyperiid amphipod	0.93919456
Hyperoche	Juvenile	Hyperiid amphipod	0.04354812
Vibilia australis	Juvenile	Hyperiid amphipod	0.00673086
Hyperia medusarum	Juvenile	Hyperiid amphipod	0.0057213
Lycaea pulex	Juvenile	Hyperiid amphipod	0.00230065
Vibilia pyripes	Juvenile	Hyperiid amphipod	0.00192206
Phronima spp.	Juvenile	Hyperiid amphipod	0.00019657
Dairella californica	Juvenile	Hyperiid amphipod	0.00016745
Streetsia challengerii	Juvenile	Hyperiid amphipod	0.00015289
Primno spp.	Juvenile	Hyperiid amphipod	4.37E-05
Oxycephalus	Juvenile	Hyperiid amphipod	1.46E-05
Vibilia spp.	Juvenile	Hyperiid amphipod	7.28E-06
Porcellanidae	Zoea, Megalopa	Non-Cancer crab larvae	0.45116451
Fabia	Zoea, Megalopa	Non-Cancer crab larvae	0.20376583
Lophopanopeus	Zoea, Megalopa	Non-Cancer crab larvae	0.14010037

Paguridae	Zoea, Megalopa	Non-Cancer crab larvae	0.0655097
Emerita analoga	Zoea	Non-Cancer crab larvae	0.03887514
Pinnixa	Zoea, Megalopa	Non-Cancer crab larvae	0.03734507
Pugettia	Zoea, Megalopa	Non-Cancer crab larvae	0.02912942
Hemigrapsus	Zoea, Megalopa	Non-Cancer crab larvae	0.01457134
Grapsidae	Zoea, Megalopa	Non-Cancer crab larvae	0.0106525
Majidae	Zoea, Megalopa	Non-Cancer crab larvae	0.00438301
Pinnotheridae	Zoea, Megalopa	Non-Cancer crab larvae	0.00290432
Oregonia gracilis	Megalopa	Non-Cancer crab larvae	0.00099207
Pinnixa littoralis	Zoea, Megalopa	Non-Cancer crab larvae	0.00015914
Rhithropanopeus harrisi	Megalopa	Non-Cancer crab larvae	0.00015914
Pachycheles	Megalopa	Non-Cancer crab larvae	9.95E-05
Xanthidae	Zoea, Juvenile	Non-Cancer crab larvae	8.95E-05
Hemigrapsus nudus	Megalopa	Non-Cancer crab larvae	5.97E-05
Crabs	Juvenile	Non-Cancer crab larvae	2.98E-05
Telmessus cheiragonus	Juvenile	Non-Cancer crab larvae	9.95E-06
Neotrypaea californiensis	Zoea, Megalopa	Shrimp larvae	0.82857322
Crangonidae	Juvenile, Larva	Shrimp larvae	0.12487467
Hippolytidae	Juvenile, Larva	Shrimp larvae	0.03040009
Cumacea	Juvenile, Larva	Shrimp larvae	0.01404462
Neomysis kadiakensis	Juvenile, Larva	Shrimp larvae	0.00045905
Pandalidae	Juvenile, Larva	Shrimp larvae	0.00043177
Sergestidae	Juvenile, Larva	Shrimp larvae	0.00041994

Alienacanthomysis macropsis	Larva	Shrimp larvae	0.00040965
Upogebia pugettensis	Zoea, Megalopa	Shrimp larvae	0.0001091
Mysidacea	Larva	Shrimp larvae	7.62E-05
Natantia	Larva	Shrimp larvae	6.59E-05
Neomysis rayii	Juvenile, Larva	Shrimp larvae	5.56E-05
Neomysis mercedis	Juvenile, Larva	Shrimp larvae	4.73E-05
Archaeomysis grebnitzkii	Larva	Shrimp larvae	2.68E-05
Exacanthomysis davisii	Juvenile	Shrimp larvae	2.06E-06
Lissocrangon stylirostris	Juvenile	Shrimp larvae	2.06E-06

Appendix C. Mesh and projection grids

Appendix C.1. JSOES Midwater Trawl

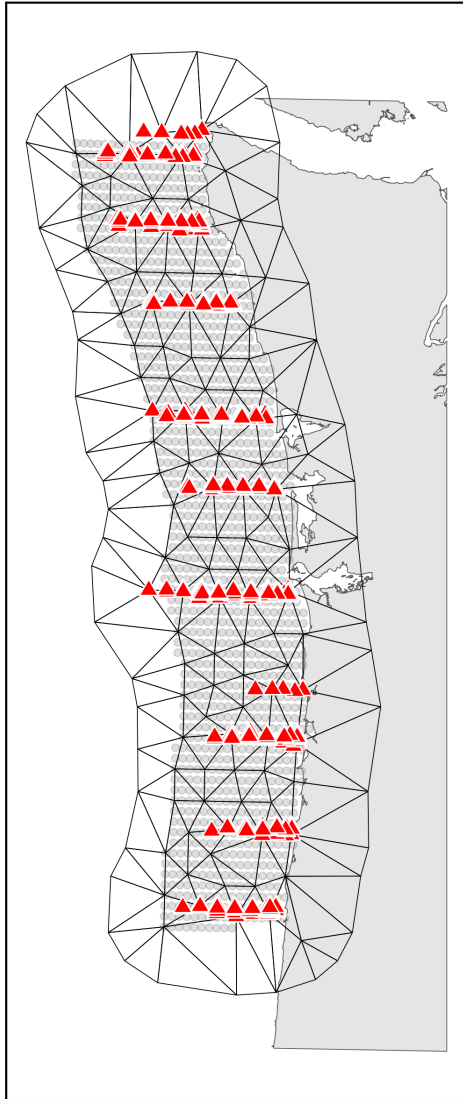


Figure 1. JSOES midwater trawl samples (red triangles), mesh (black lines), and the projection grid (gray circles).

Appendix C.2. JSOES Bongo Net

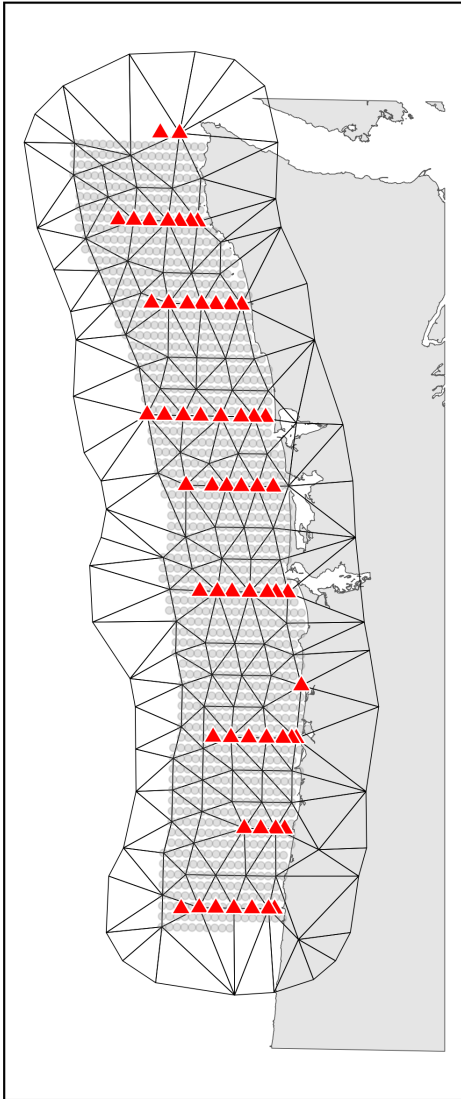


Figure 2. JSOES bongo net samples (red triangles), mesh (black lines), and the projection grid (gray circles).

Appendix C.3. JSOES Seabird Observations

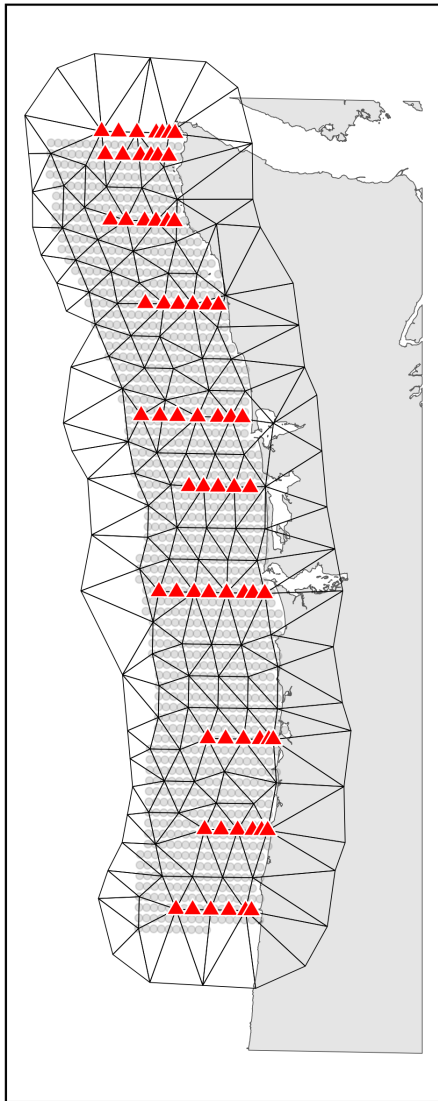


Figure 3. JSOES seabird observations (red triangles), mesh (black lines), and the projection grid (gray circles).

Appendix C.4. PRS/PWCC

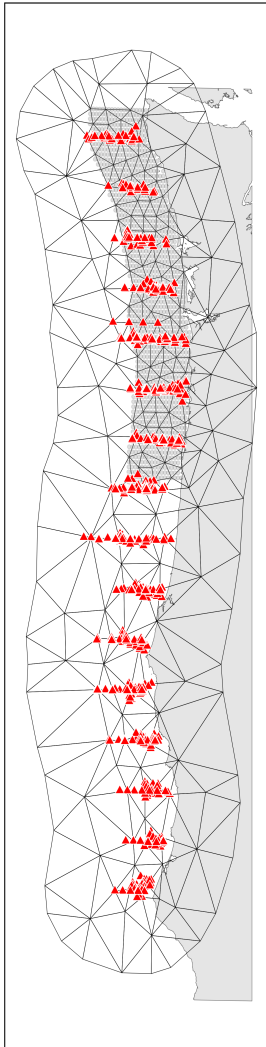


Figure 4. PRS/PWCC samples (red triangles), mesh (black lines), and the projection grid (gray circles).

Appendix C.5. Hake Survey

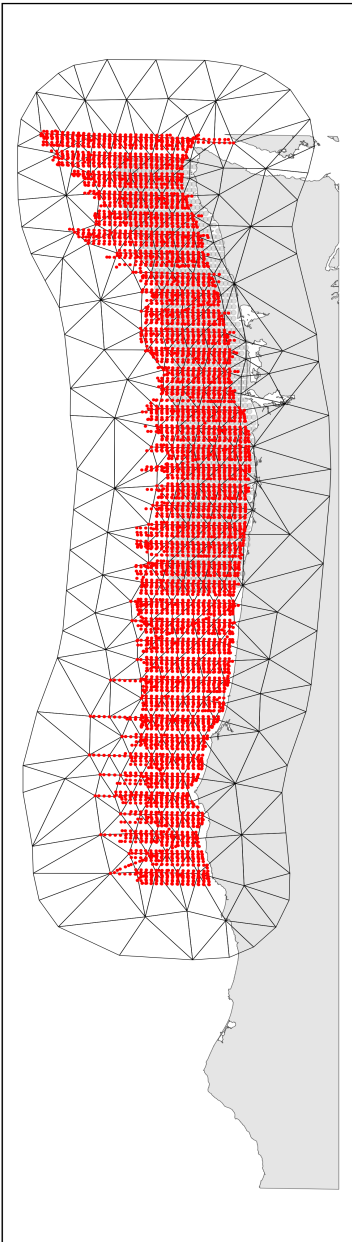


Figure 5. Hake survey samples (red circles), mesh (black lines), and the projection grid (gray circles).

Appendix D. Sample-based approach for estimating uncertainty in derived quantities

This approach estimates the uncertainty in a derived quantity by taking samples of both fixed and random effects, re-computing the derived quantity, and using the sampling distribution of the derived quantity to approximate uncertainty (Thorson and Kristensen, 2024). In this approach, samples are generated by assuming that fixed and random effects are normally distributed with their mean given by their maximum likelihood estimates (for fixed effects) or their empirical Bayes estimates (for random effects), and their variance given by the inverse of their inverse joint precision matrix, $\mathbf{Q}_{joint}$. For each sample drawn from this distribution, the values of fixed and random effects are plugged into the fitted TMB model, which then generates a new value of the derived quantity. We conducted this sampling approach with 500 samples to estimate the uncertainty in our overlap metrics.

Appendix E. PIT-Tag Data Filtering

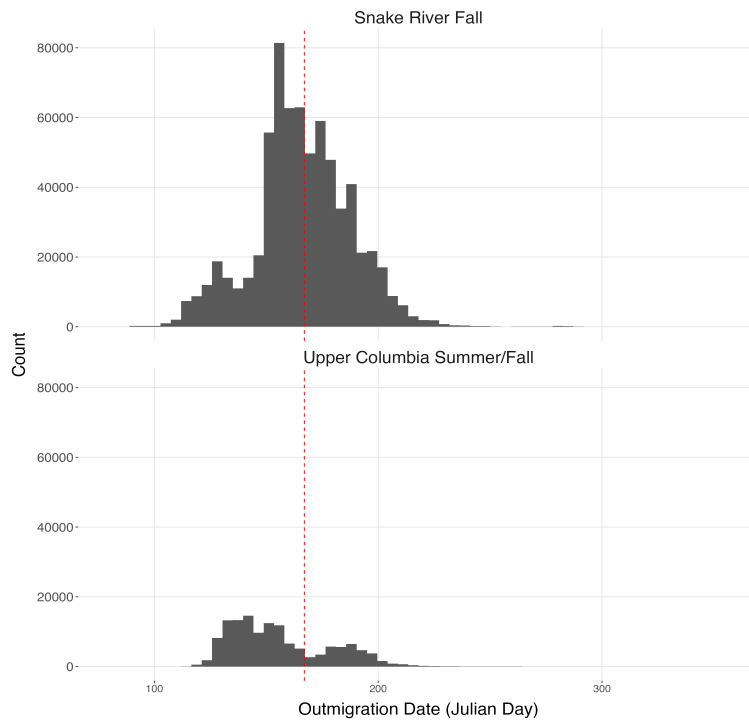


Figure 1. Outmigration timing (detection at Bonneville Dam or transport below Bonneville Dam as juveniles) for the two focal stocks, Snake River Fall and Upper Columbia Summer/Fall Chinook. The red dotted line represents June 15, which is the cutoff for inclusion in our dataset (only fish to the left of the dotted line were retained).

Appendix F. Survey Data



Figure 1. Subyearling Interior Fall Chinook catches in the JSOES Midwater Trawl.



Figure 2. Yearling Interior Fall Chinook catches in the JSOES Midwater Trawl.

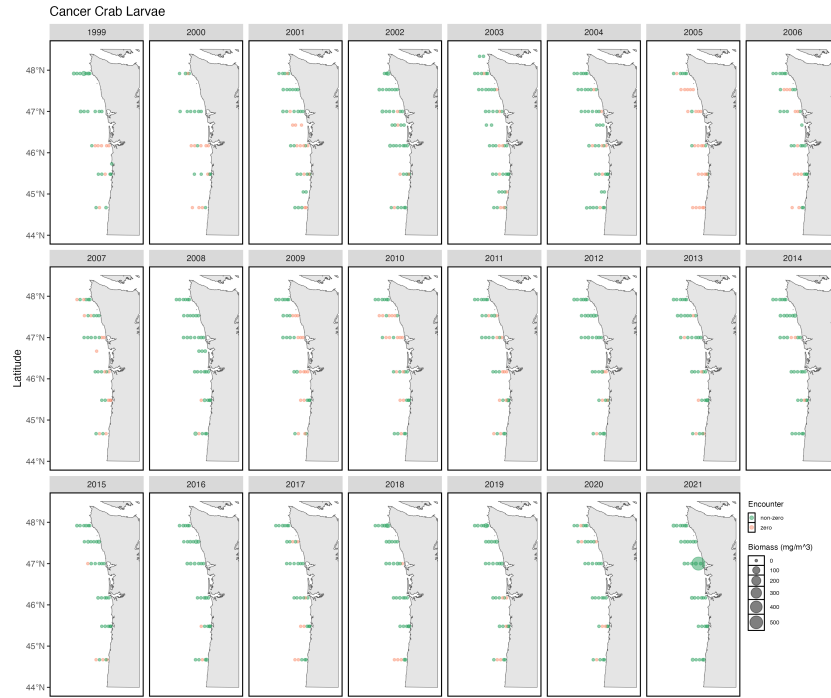


Figure 3. Cancer Crab Larvae catches in the JSOES Bongo net.

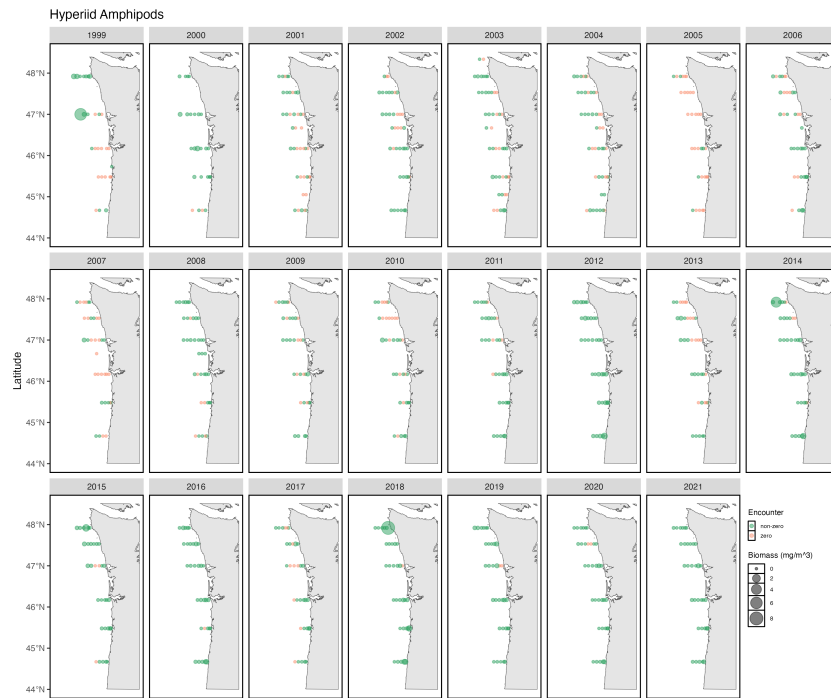


Figure 4. Hyperiid amphipod catches in the JSOES Bongo net.

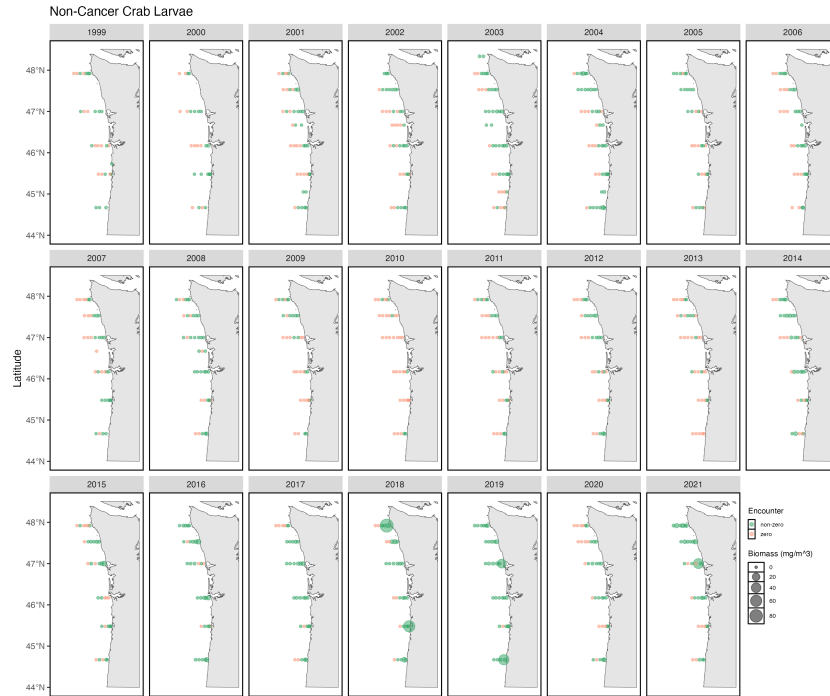


Figure 5. Non-Cancer Crab Larvae catches in the JSOES Bongo net.

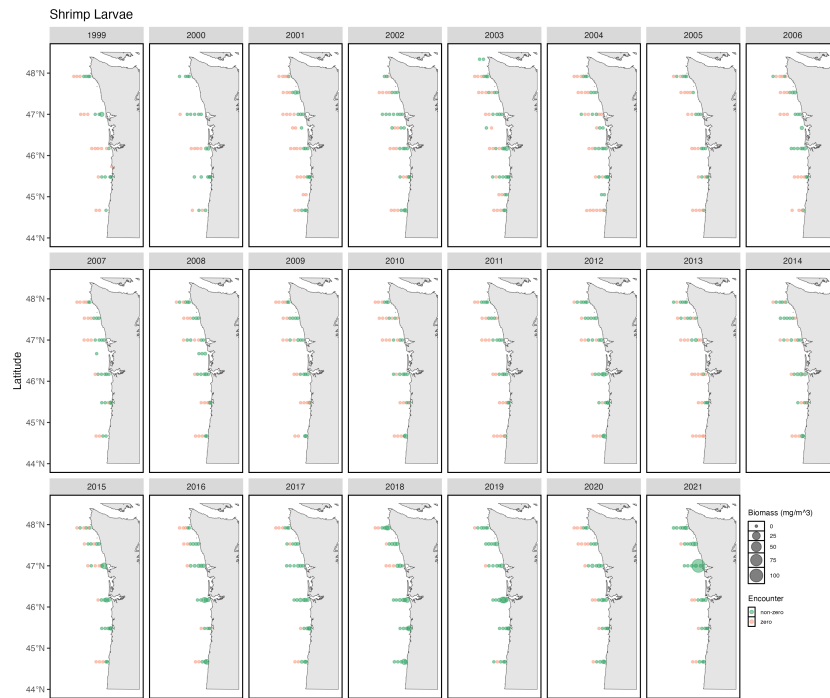


Figure 6. Shrimp Larvae catches in the JSOES Bongo net.

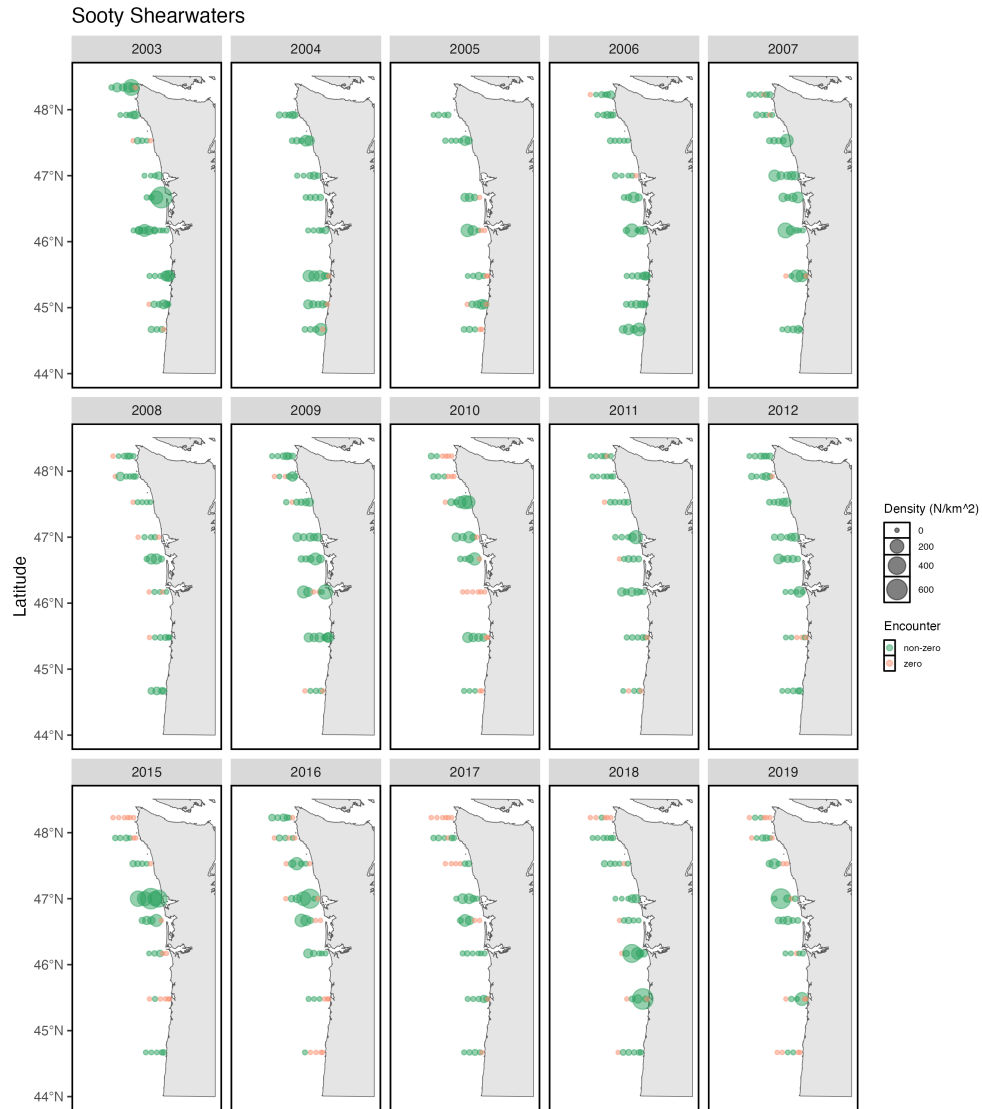


Figure 7. Sooty Shearwater observations during JSOES.

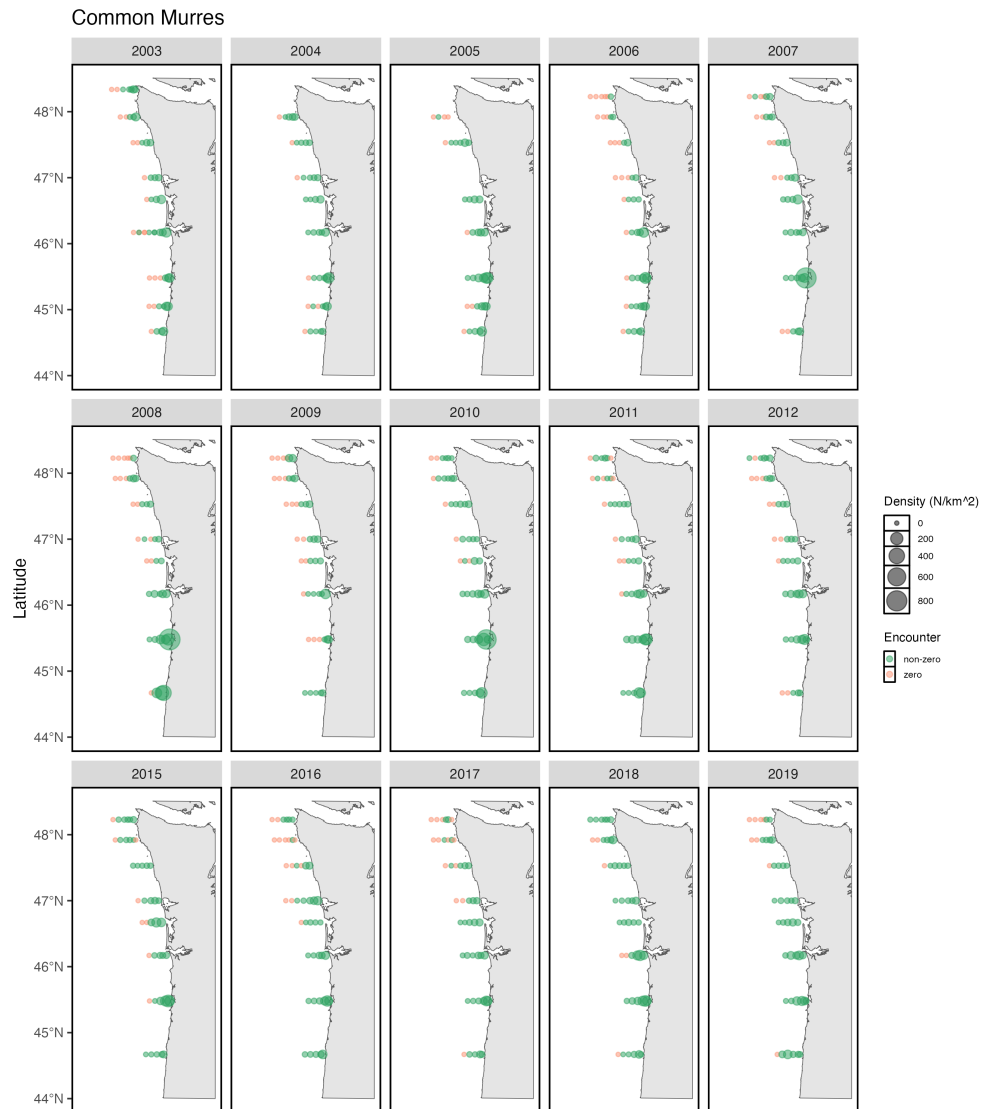


Figure 8. Common Murre observations during JSOES.

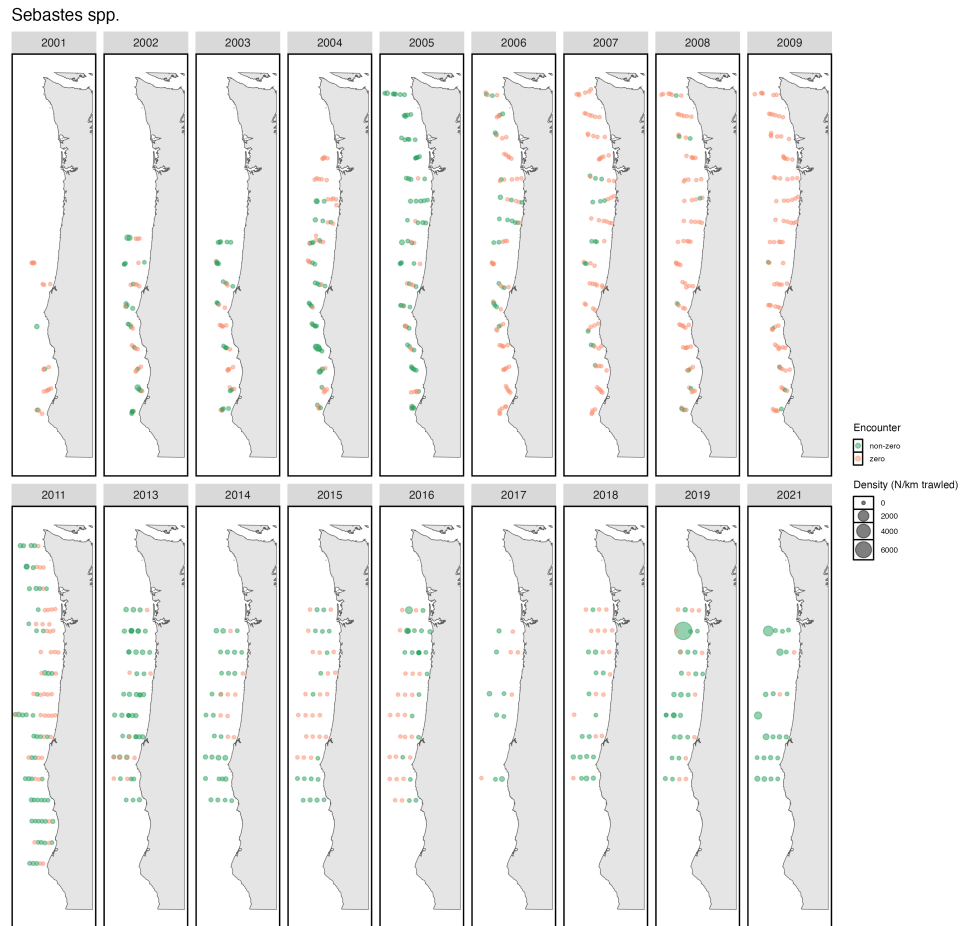


Figure 9. YOY Rockfish (*Sebastes* spp.) catches from the PWCC survey (2001-2009) and PRS (2011-2021).

Pacific Hake

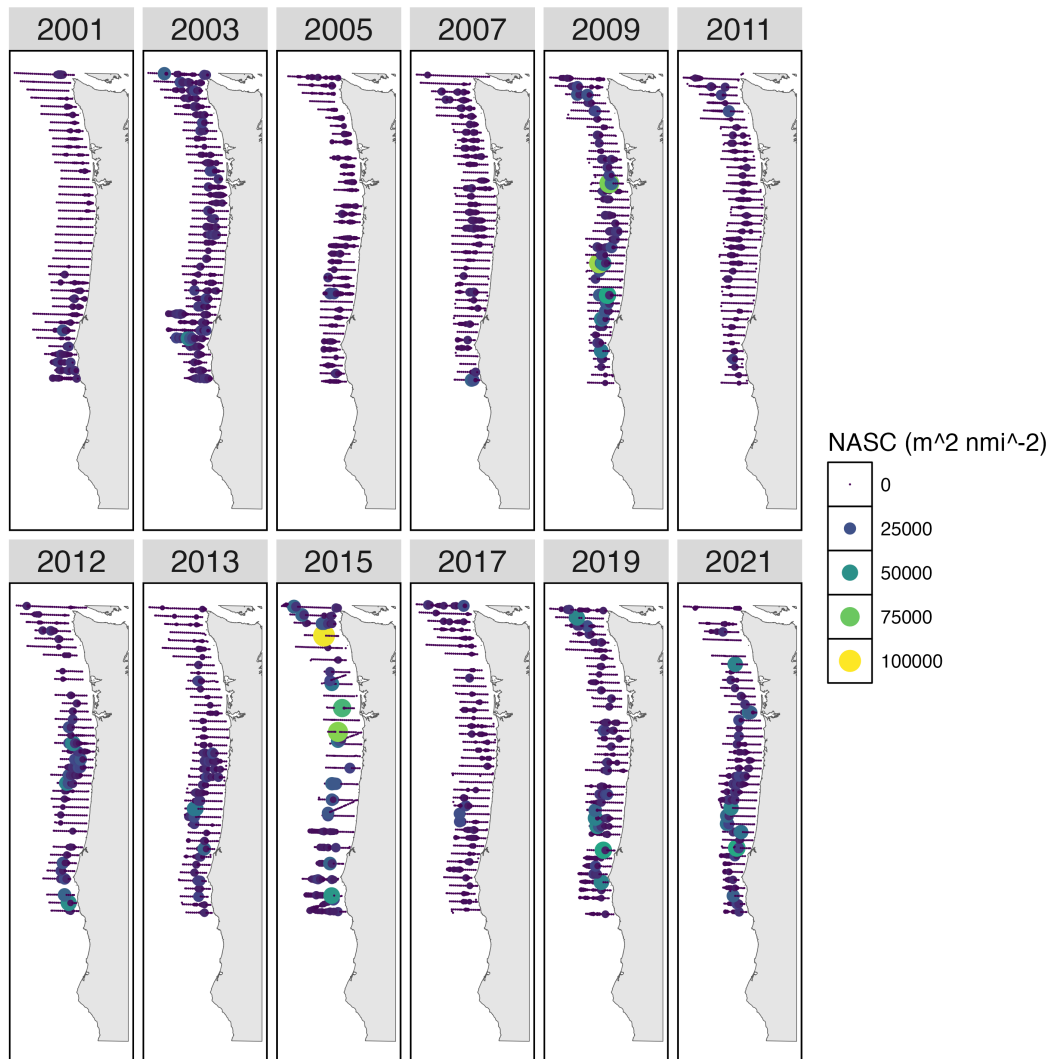


Figure 10. Hake observations from the Hake Survey.

Appendix G. SDM model selection process

Appendix G.1. Subyearling Interior Fall Chinook

The best fit model for Subyearling Interior Fall Chinook had the following model structure:

Spatial ON + Spatiotemporal IID + temp + s(dist)

- Where both the spatial and spatiotemporal random fields are anisotropic, the effect of temperature is linear, and the effect of distance from shore is a smooth spline.

Table 1. Random effects structure model comparison for Subyearling Interior Fall Chinook, using a saturated fixed effects structure.

Random Effects Structure	ΔAIC	ΔcAIC
Spatial ON + Spatiotemporal IID (anisotropic)	0.00	0.00
Spatial ON + Spatiotemporal AR1 (anisotropic)	2.00	2.00
Spatial ON + Spatiotemporal AR1 (isotropic)	2.41	4.04
Spatial OFF + Spatiotemporal AR1 (isotropic)	28.33	31.98
Spatial OFF + Spatiotemporal AR1 (anisotropic)	32.56	35.17
Spatial OFF + Spatiotemporal IID (anisotropic)	115.81	55.70
Spatial OFF + Spatiotemporal IID (isotropic)	119.88	55.91
Spatial ON + Spatiotemporal OFF (isotropic)	70.13	169.61
Spatial ON + Spatiotemporal IID (isotropic)	72.13	171.61
Spatial ON + Spatiotemporal OFF (anisotropic)	74.53	173.78
Spatial OFF + Spatiotemporal OFF	459.64	NA

Table 2. Fixed effects structure model comparison for Subyearling Interior Fall Chinook using the best fit random effects structure identified above.

Fixed Effects Structure	ΔAIC	ΔcAIC
temp + s(dist)	1.26	0.00
temp	1.60	1.36
s(temp) + s(dist)	3.26	2.00
s(dist)	3.12	3.14

Table 2. Fixed effects structure model comparison for Subyearling Interior Fall Chinook using the best fit random effects structure identified above.

Fixed Effects Structure	ΔAIC	$\Delta cAIC$
s(temp)	3.60	3.36
temp + dist	0.27	3.62
s(temp) + dist	2.27	5.62
no fixed effects	4.72	6.06
dist	2.24	7.35
as.factor(year) + temp	2.45	26.98
as.factor(year) + temp + dist	0.00	28.13
as.factor(year) + temp + s(dist)	1.92	28.13
as.factor(year) + s(temp)	4.45	28.98
as.factor(year) + s(temp) + s(dist)	3.92	30.13
as.factor(year) + s(temp) + dist	2.00	30.13
as.factor(year) + s(dist)	5.03	32.80
as.factor(year) + dist	3.12	33.04
as.factor(year)	8.13	33.84

Appendix G.2. Yearling Interior Fall Chinook.

The best fit model for Yearling Interior Fall Chinook had the following model structure:

Spatial ON + Spatiotemporal AR1 + temp

- Where both the spatial and spatiotemporal random fields are anisotropic, and the effect of temperature is linear.

Table 1. Random effects structure model comparison for Yearling Interior Fall Chinook, using a saturated fixed effects structure.

Random Effects Structure	ΔAIC	ΔcAIC
Spatial ON + Spatiotemporal AR1 (anisotropic)	0.00	0.00
Spatial ON + Spatiotemporal IID (anisotropic)	5.70	2.69
Spatial ON + Spatiotemporal AR1 (isotropic)	2.49	5.99
Spatial OFF + Spatiotemporal AR1 (anisotropic)	17.72	24.62
Spatial OFF + Spatiotemporal AR1 (isotropic)	19.16	32.54
Spatial OFF + Spatiotemporal IID (anisotropic)	99.85	48.77
Spatial OFF + Spatiotemporal IID (isotropic)	111.46	56.11
Spatial ON + Spatiotemporal OFF (isotropic)	88.84	183.85
Spatial ON + Spatiotemporal IID (isotropic)	90.84	185.85
Spatial ON + Spatiotemporal OFF (anisotropic)	93.20	187.86
Spatial OFF + Spatiotemporal OFF	346.66	NA

Table 2. Fixed effects structure model comparison for Yearling Interior Fall Chinook using the best fit random effects structure identified above.

Fixed Effects Structure	ΔAIC	ΔcAIC
temp	15.47	0.00
no fixed effects	18.51	1.47
temp + dist	12.64	1.66
s(temp)	17.47	2.00
temp + s(dist)	14.48	2.12
dist	15.01	2.96

Table 2. Fixed effects structure model comparison for Yearling Interior Fall Chinook using the best fit random effects structure identified above.

Fixed Effects Structure	ΔAIC	ΔcAIC
s(temp) + dist	14.64	3.66
s(dist)	16.91	3.68
s(temp) + s(dist)	16.48	4.12
as.factor(year) + temp	6.54	23.40
as.factor(year)	8.50	24.10
as.factor(year) + temp + dist	0.00	25.28
as.factor(year) + s(temp)	8.54	25.39
as.factor(year) + dist	0.62	25.69
as.factor(year) + s(temp) + dist	2.00	27.28
as.factor(year) + temp + s(dist)	2.00	27.28
as.factor(year) + s(dist)	2.62	27.69
as.factor(year) + s(temp) + s(dist)	4.00	29.28

Appendix G.3. Shrimp Larvae

The best fit model for shrimp larvae had the following model structure:

Spatial ON + Spatiotemporal AR1 + s(dist)

- Where both the spatial and spatiotemporal random fields are isotropic and the effect of distance from shore is a smooth spline.

Table 1. Random effects structure model comparison for Shrimp Larvae, using a saturated fixed effects structure.

Random Effects Structure	ΔAIC	ΔcAIC
Spatial ON + Spatiotemporal AR1 (isotropic)	0.00	0.00
Spatial ON + Spatiotemporal IID (anisotropic)	2.74	0.80
Spatial ON + Spatiotemporal AR1 (anisotropic)	4.74	2.80
Spatial OFF + Spatiotemporal AR1 (isotropic)	30.19	21.90
Spatial OFF + Spatiotemporal AR1 (anisotropic)	34.89	23.03
Spatial OFF + Spatiotemporal IID (isotropic)	78.08	65.01
Spatial OFF + Spatiotemporal IID (anisotropic)	82.92	68.24
Spatial ON + Spatiotemporal OFF (isotropic)	114.75	190.60
Spatial ON + Spatiotemporal IID (isotropic)	116.75	192.60
Spatial ON + Spatiotemporal OFF (anisotropic)	119.64	194.55
Spatial OFF + Spatiotemporal OFF	302.27	NA

Table 2. Fixed effects structure model comparison for Shrimp Larvae using the best fit random effects structure identified above.

Fixed Effects Structure	ΔAIC	ΔcAIC
s(dist)	55.12	0.00
temp + s(dist)	56.73	1.81
s(temp) + s(dist)	58.73	3.81
as.factor(year) + s(dist)	0.00	14.82
as.factor(year) + temp + s(dist)	1.78	17.31
dist	54.86	17.98

Table 2. Fixed effects structure model comparison for Shrimp Larvae using the best fit random effects structure identified above.

Fixed Effects Structure	ΔAIC	ΔcAIC
temp + dist	56.36	19.29
as.factor(year) + s(temp) + s(dist)	3.78	19.31
s(temp) + dist	58.36	21.29
no fixed effects	67.32	26.73
temp	68.49	27.74
s(temp)	70.49	29.74
as.factor(year) + dist	4.10	38.41
as.factor(year) + s(temp) + dist	8.05	42.73
as.factor(year) + temp + dist	10.79	43.53
as.factor(year)	29.21	43.76
as.factor(year) + temp	31.13	45.42
as.factor(year) + s(temp)	33.13	47.42

Appendix G.4. *Cancer* spp. Crab Larvae

The best fit model for Cancer crab larvae had the following model structure:

Spatial ON + Spatiotemporal AR1

- Where both the spatial and spatiotemporal random fields are anisotropic

Table 1. Random effects structure model comparison for Cancer Crab Larvae, using a saturated fixed effects structure.

Random Effects Structure	ΔAIC	$\Delta cAIC$
Spatial ON + Spatiotemporal AR1 (isotropic)	0.00	0.00
Spatial ON + Spatiotemporal AR1 (anisotropic)	4.49	1.54
Spatial ON + Spatiotemporal IID (anisotropic)	5.90	2.50
Spatial OFF + Spatiotemporal AR1 (isotropic)	11.87	20.15
Spatial OFF + Spatiotemporal AR1 (anisotropic)	16.64	22.85
Spatial OFF + Spatiotemporal IID (isotropic)	32.14	46.85
Spatial OFF + Spatiotemporal IID (anisotropic)	36.11	47.56
Spatial ON + Spatiotemporal OFF (isotropic)	217.96	303.96
Spatial ON + Spatiotemporal IID (isotropic)	219.96	305.96
Spatial ON + Spatiotemporal OFF (anisotropic)	222.85	307.92
Spatial OFF + Spatiotemporal OFF	299.36	NA

Table 2. Fixed effects structure model comparison for Cancer Crab Larvae using the best fit random effects structure identified above.

Fixed Effects Structure	ΔAIC	$\Delta cAIC$
no fixed effects	101.34	0.00
as.factor(year)	3.64	1.27
as.factor(year) + dist	3.87	1.57
as.factor(year) + s(dist)	0.00	1.67
temp	103.26	1.86
dist	103.34	2.00

Table 2. Fixed effects structure model comparison for Cancer Crab Larvae using the best fit random effects structure identified above.

Fixed Effects Structure	ΔAIC	$\Delta cAIC$
as.factor(year) + temp	5.64	3.20
s(temp)	105.26	3.86
as.factor(year) + temp + s(dist)	1.85	3.86
temp + dist	105.26	3.87
s(dist)	103.69	4.49
as.factor(year) + s(temp)	7.64	5.20
as.factor(year) + s(temp) + dist	7.83	5.81
as.factor(year) + s(temp) + s(dist)	3.85	5.86
s(temp) + dist	107.26	5.86
as.factor(year) + temp + dist	11.73	6.31
temp + s(dist)	105.63	6.35
s(temp) + s(dist)	107.63	8.35

Appendix G.5. Non-Cancer spp. Crab Larvae

The best fit model for non-Cancer crab larvae had the following model structure:

Spatial ON + Spatiotemporal ARI + as.factor(year) + dist

- Where both the spatial and spatiotemporal random fields are isotropic, there is a different intercept term for each year, and the effect of distance from shore is linear.

Table 1. Random effects structure model comparison for Non-Cancer Crab Larvae, using a saturated fixed effects structure.

Random Effects Structure	ΔAIC	ΔcAIC
Spatial ON + Spatiotemporal AR1 (isotropic)	0.00	0.00
Spatial ON + Spatiotemporal IID (anisotropic)	2.90	2.00
Spatial ON + Spatiotemporal AR1 (anisotropic)	4.90	4.00
Spatial OFF + Spatiotemporal AR1 (isotropic)	15.77	13.49
Spatial OFF + Spatiotemporal AR1 (anisotropic)	20.67	17.49
Spatial OFF + Spatiotemporal IID (isotropic)	17.32	18.92
Spatial OFF + Spatiotemporal IID (anisotropic)	22.22	22.82
Spatial ON + Spatiotemporal OFF (isotropic)	126.02	197.12
Spatial ON + Spatiotemporal IID (isotropic)	128.02	199.12
Spatial ON + Spatiotemporal OFF (anisotropic)	130.92	201.11
Spatial OFF + Spatiotemporal OFF	175.57	NA

Table 2. Fixed effects structure model comparison for Non-Cancer Crab Larvae using the best fit random effects structure identified above.

Fixed Effects Structure	ΔAIC	ΔcAIC
as.factor(year) + dist	0.46	0.00
as.factor(year) + temp + dist	0.00	1.98
as.factor(year) + s(dist)	2.46	2.00
as.factor(year) + s(temp) + dist	2.00	3.98
as.factor(year) + temp + s(dist)	2.00	3.98
as.factor(year) + s(temp) + s(dist)	4.00	5.98

Table 2. Fixed effects structure model comparison for Non-Cancer Crab Larvae using the best fit random effects structure identified above.

Fixed Effects Structure	ΔAIC	ΔcAIC
as.factor(year)	42.27	11.27
as.factor(year) + temp	41.04	13.84
as.factor(year) + s(temp)	43.04	15.84
s(temp)	109.21	21.64
no fixed effects	111.46	23.29
s(temp) + dist	93.69	24.23
dist	96.07	25.48
temp	112.23	25.96
s(temp) + s(dist)	95.69	26.23
s(dist)	98.07	27.48
temp + dist	97.16	28.67
temp + s(dist)	99.16	30.67

Appendix G.6. Hyperiid amphipods

The best fit model for hyperiid amphipods had the following model structure:

Spatial ON + Spatiotemporal IID

- Where both the spatiotemporal random fields are anisotropic

Table 1. Random effects structure model comparison for Hyperiid Amphipods, using a saturated fixed effects structure.

Random Effects Structure	ΔAIC	ΔcAIC
Spatial ON + Spatiotemporal IID (anisotropic)	0.96	0.00
Spatial ON + Spatiotemporal AR1 (anisotropic)	2.54	1.43
Spatial ON + Spatiotemporal AR1 (isotropic)	0.00	2.19
Spatial OFF + Spatiotemporal AR1 (anisotropic)	19.12	9.57
Spatial OFF + Spatiotemporal IID (anisotropic)	26.68	10.72
Spatial OFF + Spatiotemporal AR1 (isotropic)	20.16	13.73
Spatial OFF + Spatiotemporal IID (isotropic)	30.79	25.25
Spatial ON + Spatiotemporal OFF (isotropic)	194.74	323.36
Spatial ON + Spatiotemporal IID (isotropic)	196.74	325.36
Spatial ON + Spatiotemporal OFF (anisotropic)	199.51	327.34
Spatial OFF + Spatiotemporal OFF	298.11	NA

Table 2. Fixed effects structure model comparison for Hyperiid Amphipods using the best fit random effects structure identified above.

Fixed Effects Structure	ΔAIC	ΔcAIC
no fixed effects	53.54	0.00
temp	54.12	0.30
dist	55.24	0.97
temp + dist	55.91	1.50
s(temp)	56.12	2.30
s(dist)	57.24	2.97

Table 2. Fixed effects structure model comparison for Hyperiid Amphipods using the best fit random effects structure identified above.

Fixed Effects Structure	ΔAIC	ΔcAIC
temp + s(dist)	57.91	3.50
s(temp) + dist	57.91	3.50
s(temp) + s(dist)	59.91	5.50
as.factor(year)	5.16	37.64
as.factor(year) + temp	6.72	38.76
as.factor(year) + dist	3.96	40.11
as.factor(year) + s(temp)	8.72	40.77
as.factor(year) + s(temp) + dist	6.98	42.87
as.factor(year) + temp + dist	28.70	49.59
as.factor(year) + s(dist)	0.00	52.18
as.factor(year) + temp + s(dist)	1.15	52.88
as.factor(year) + s(temp) + s(dist)	3.15	54.88

Appendix G.7. Common Murres

The best fit model for Common Murres had the following model structure:

Spatiotemporal IID + dist

- Where the spatial random fields are anisotropic and the effect of distance from shore is linear.

Table 1. Random effects structure model comparison for Common Murres, using a saturated fixed effects structure.

Random Effects Structure	ΔAIC	ΔcAIC
Spatial OFF + Spatiotemporal IID (anisotropic)	0.00	0.00
Spatial OFF + Spatiotemporal AR1 (anisotropic)	2.00	2.00
Spatial ON + Spatiotemporal IID (anisotropic)	1.47	2.89
Spatial ON + Spatiotemporal AR1 (anisotropic)	3.47	4.89
Spatial OFF + Spatiotemporal IID (isotropic)	2.17	5.62
Spatial OFF + Spatiotemporal AR1 (isotropic)	4.17	7.69
Spatial ON + Spatiotemporal OFF (isotropic)	144.88	234.37
Spatial ON + Spatiotemporal OFF (anisotropic)	148.62	236.08
Spatial ON + Spatiotemporal IID (isotropic)	146.88	236.37
Spatial ON + Spatiotemporal AR1 (isotropic)	146.88	236.37
Spatial OFF + Spatiotemporal OFF	186.17	NA

Table 2. Fixed effects structure model comparison for Common Murres using the best fit random effects structure identified above.

Fixed Effects Structure	ΔAIC	ΔcAIC
dist	11.71	0.00
temp + dist	8.96	1.10
s(dist)	13.71	2.00
temp + s(dist)	10.96	3.10
s(temp) + dist	10.96	3.10
s(temp) + s(dist)	12.96	5.10

Table 2. Fixed effects structure model comparison for Common Murres using the best fit random effects structure identified above.

Fixed Effects Structure	ΔAIC	ΔcAIC
as.factor(year) + dist	7.98	36.29
as.factor(year) + s(dist)	9.98	38.29
as.factor(year) + s(temp) + dist	0.00	41.10
as.factor(year) + temp + s(dist)	0.00	41.10
as.factor(year) + s(temp) + s(dist)	2.00	43.10
no fixed effects	138.78	53.95
s(temp)	139.53	55.52
temp	138.02	58.28
as.factor(year)	166.54	86.42
as.factor(year) + s(temp)	166.92	87.63
as.factor(year) + temp	165.51	90.73
as.factor(year) + temp + dist	63.41	153.34

Appendix G.8. Sooty Shearwaters

The best fit model for Sooty Shearwaters had the following model structure:

Spatiotemporal AR1 + s(dist)

- Where the spatiotemporal random fields are anisotropic and the effect of distance from shore is a smooth spline.

Table 1. Random effects structure model comparison for Sooty Shearwaters, using a saturated fixed effects structure.

Random Effects Structure	ΔAIC	ΔcAIC
Spatial OFF + Spatiotemporal AR1 (isotropic)	0.00	0.00
Spatial OFF + Spatiotemporal AR1 (anisotropic)	2.89	1.19
Spatial ON + Spatiotemporal IID (anisotropic)	1.84	2.14
Spatial OFF + Spatiotemporal IID (isotropic)	2.72	2.60
Spatial ON + Spatiotemporal AR1 (anisotropic)	3.05	2.67
Spatial OFF + Spatiotemporal IID (anisotropic)	5.49	3.75
Spatial ON + Spatiotemporal OFF (isotropic)	114.97	201.85
Spatial ON + Spatiotemporal IID (isotropic)	116.97	203.85
Spatial ON + Spatiotemporal AR1 (isotropic)	116.97	203.85
Spatial ON + Spatiotemporal OFF (anisotropic)	119.07	204.26
Spatial OFF + Spatiotemporal OFF	173.61	NA

Table 2. Fixed effects structure model comparison for Sooty Shearwaters using the best fit random effects structure identified above.

Fixed Effects Structure	ΔAIC	ΔcAIC
s(dist)	20.91	0.00
temp + s(dist)	22.59	1.66
s(temp) + s(dist)	24.59	3.66
as.factor(year) + s(dist)	0.00	36.74
as.factor(year) + temp + s(dist)	1.07	39.12
as.factor(year) + s(temp) + s(dist)	3.07	41.12

Table 2. Fixed effects structure model comparison for Sooty Shearwaters using the best fit random effects structure identified above.

Fixed Effects Structure	ΔAIC	$\Delta cAIC$
no fixed effects	50.61	111.44
dist	52.52	113.63
temp	52.58	113.68
s(temp)	54.58	115.69
temp + dist	54.45	116.01
s(temp) + dist	56.45	118.02
as.factor(year)	29.26	141.19
as.factor(year) + dist	30.56	143.29
as.factor(year) + temp	31.22	143.54
as.factor(year) + s(temp)	33.22	145.54
as.factor(year) + s(temp) + dist	34.28	148.17
as.factor(year) + temp + dist	146.30	347.88

Appendix G.9. YOY Rockfishes

The best fit model for YOY rockfishes had the following model structure:

Spatial ON + Spatiotemporal IID

- Where both the spatial and spatiotemporal random fields are anisotropic

Table 1. Random effects structure model comparison for YOY Rockfishes, using a saturated fixed effects structure.

Random Effects Structure	ΔAIC	ΔcAIC
Spatial ON + Spatiotemporal IID (anisotropic)	0.00	0.00
Spatial OFF + Spatiotemporal AR1 (anisotropic)	2.17	1.43
Spatial ON + Spatiotemporal AR1 (anisotropic)	1.91	1.65
Spatial OFF + Spatiotemporal IID (anisotropic)	1.47	2.05
Spatial OFF + Spatiotemporal IID (isotropic)	14.37	18.69
Spatial OFF + Spatiotemporal AR1 (isotropic)	15.56	18.79
Spatial ON + Spatiotemporal OFF (isotropic)	361.54	596.07
Spatial ON + Spatiotemporal IID (isotropic)	363.54	598.07
Spatial ON + Spatiotemporal AR1 (isotropic)	363.54	598.07
Spatial ON + Spatiotemporal OFF (anisotropic)	366.44	600.09
Spatial OFF + Spatiotemporal OFF	448.41	NA

Table 2. Fixed effects structure model comparison for YOY Rockfishes using the best fit random effects structure identified above.

Fixed Effects Structure	ΔAIC	ΔcAIC
no fixed effects	49.26	0.00
temp	46.70	2.35
s(dist)	47.97	2.48
temp + s(dist)	48.49	2.96
s(temp)	48.70	4.36
s(temp) + s(dist)	50.49	4.96

Table 2. Fixed effects structure model comparison for YOY Rockfishes using the best fit random effects structure identified above.

Fixed Effects Structure	ΔAIC	ΔcAIC
temp + dist	47.18	9.48
dist	47.35	10.71
as.factor(year)	4.08	10.88
s(temp) + dist	49.18	11.48
as.factor(year) + temp	4.65	13.28
as.factor(year) + s(dist)	1.20	14.86
as.factor(year) + s(temp)	6.65	15.30
as.factor(year) + temp + s(dist)	2.92	17.09
as.factor(year) + s(temp) + s(dist)	4.92	19.09
as.factor(year) + dist	0.00	19.58
as.factor(year) + temp + dist	1.94	21.99
as.factor(year) + s(temp) + dist	3.94	24.01

Appendix G.10. Pacific Hake

The best fit model for Pacific Hake had the following model structure:

Spatiotemporal AR1 + s(dist)

- Where the spatiotemporal random fields are isotropic and the effect of distance from shore is a smooth spline.

Table 1. Random effects structure model comparison for Pacific Hake, using a saturated fixed effects structure.

Random Effects Structure	ΔAIC	ΔcAIC
Spatial OFF + Spatiotemporal AR1 (isotropic)	113.45	0.00
Spatial ON + Spatiotemporal AR1 (anisotropic)	0.00	0.79
Spatial ON + Spatiotemporal IID (anisotropic)	41.39	30.82
Spatial OFF + Spatiotemporal AR1 (anisotropic)	48.96	34.22
Spatial OFF + Spatiotemporal IID (anisotropic)	621.49	314.84
Spatial OFF + Spatiotemporal IID (isotropic)	833.57	384.14
Spatial ON + Spatiotemporal OFF (isotropic)	1441.65	2349.91
Spatial ON + Spatiotemporal IID (isotropic)	1443.65	2351.91
Spatial ON + Spatiotemporal AR1 (isotropic)	1443.65	2351.91
Spatial ON + Spatiotemporal OFF (anisotropic)	1417.77	2364.26
Spatial OFF + Spatiotemporal OFF	3133.11	NA

Table 2. Fixed effects structure model comparison for Pacific Hake using the best fit random effects structure identified above.

Fixed Effects Structure	ΔAIC	ΔcAIC
s(dist)	0.00	0.00
temp + s(dist)	1.38	0.58
s(temp) + s(dist)	3.38	2.57
as.factor(year) + s(dist)	2.45	58.79
as.factor(year) + temp + s(dist)	3.22	59.18
as.factor(year) + s(temp) + s(dist)	5.22	61.16

Table 2. Fixed effects structure model comparison for Pacific Hake using the best fit random effects structure identified above.

Fixed Effects Structure	ΔAIC	ΔcAIC
temp	178.48	269.93
s(temp)	180.48	271.83
temp + dist	180.46	271.89
no fixed effects	178.46	273.52
s(temp) + dist	182.46	273.80
dist	180.45	275.49
as.factor(year) + temp	185.16	291.35
as.factor(year) + s(temp)	187.16	293.26
as.factor(year)	186.69	294.73
as.factor(year) + s(temp) + dist	189.10	295.29
as.factor(year) + dist	188.68	296.69
as.factor(year) + temp + dist	115.04	324.19

Appendix H. SDM model projections

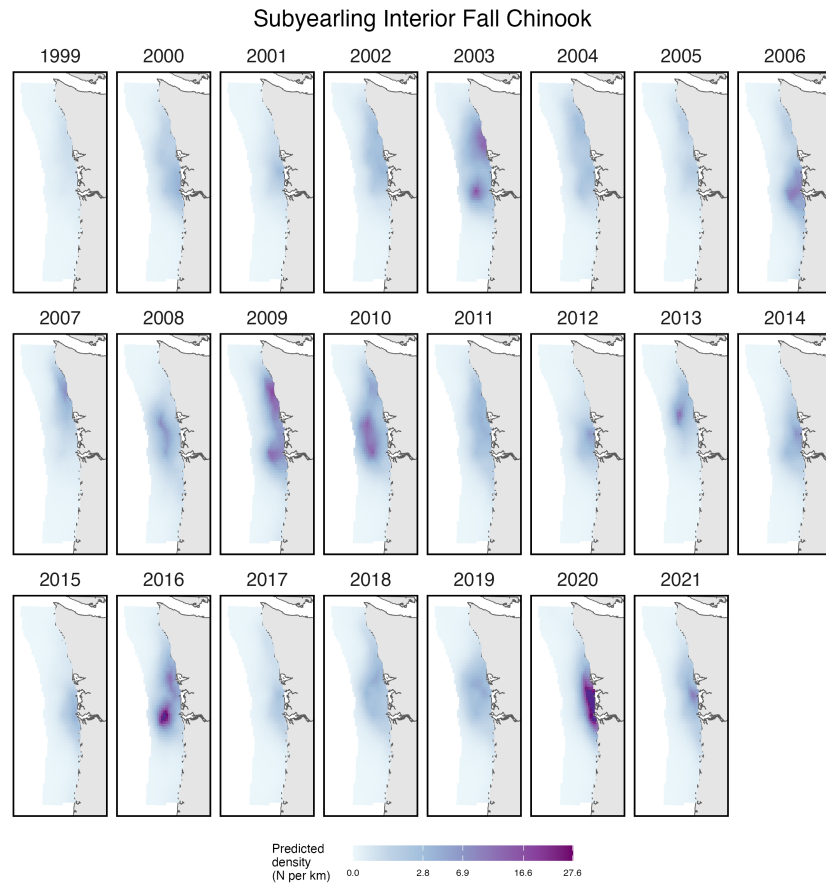


Figure 1. SDM predictions for Subyearling Interior Fall Chinook.

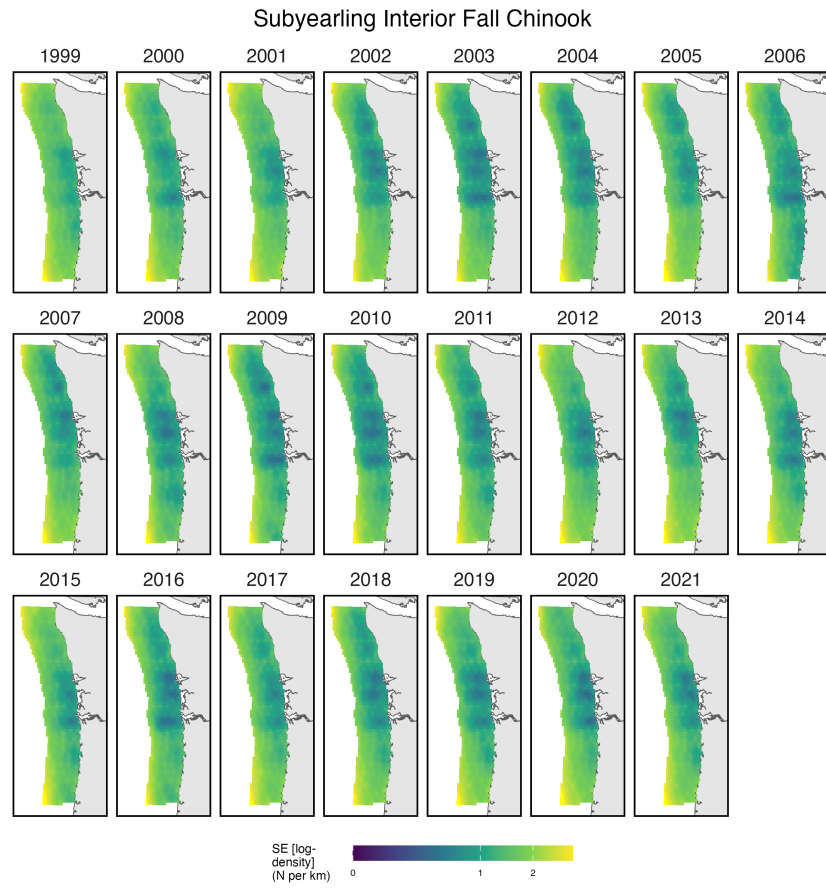


Figure 2. Standard error for SDM predictions for Subyearling Interior Fall Chinook.

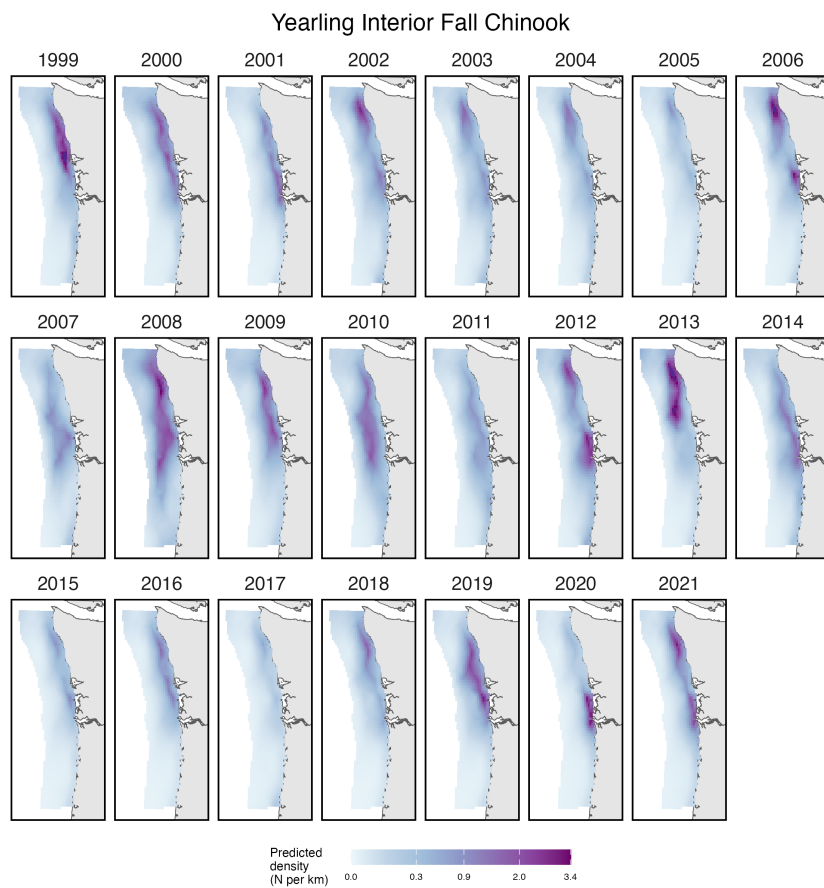


Figure 3. SDM predictions for Yearling Interior Fall Chinook.

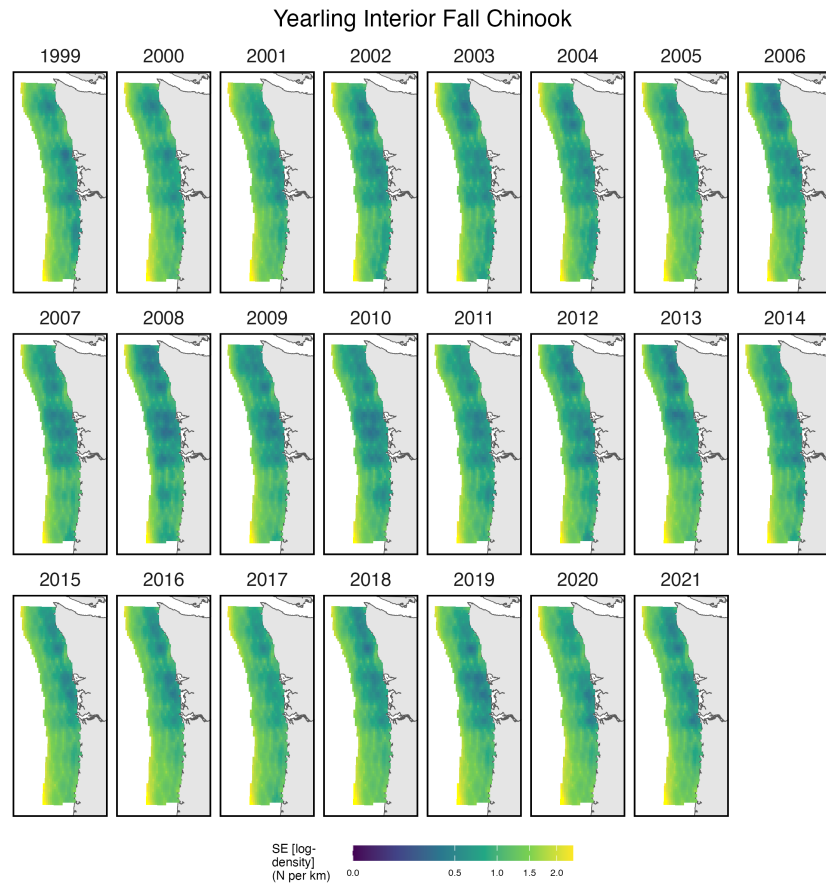


Figure 4. Standard error for SDM predictions for Yearling Interior Fall Chinook.

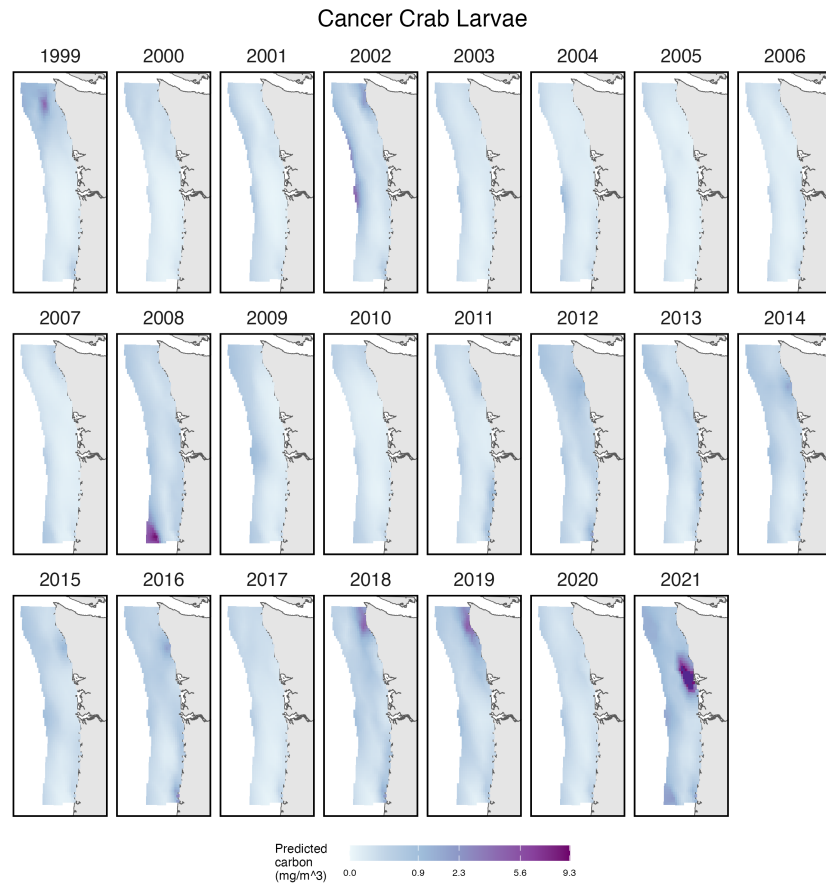


Figure 5. SDM predictions for *Cancer* spp. Crab Larvae.

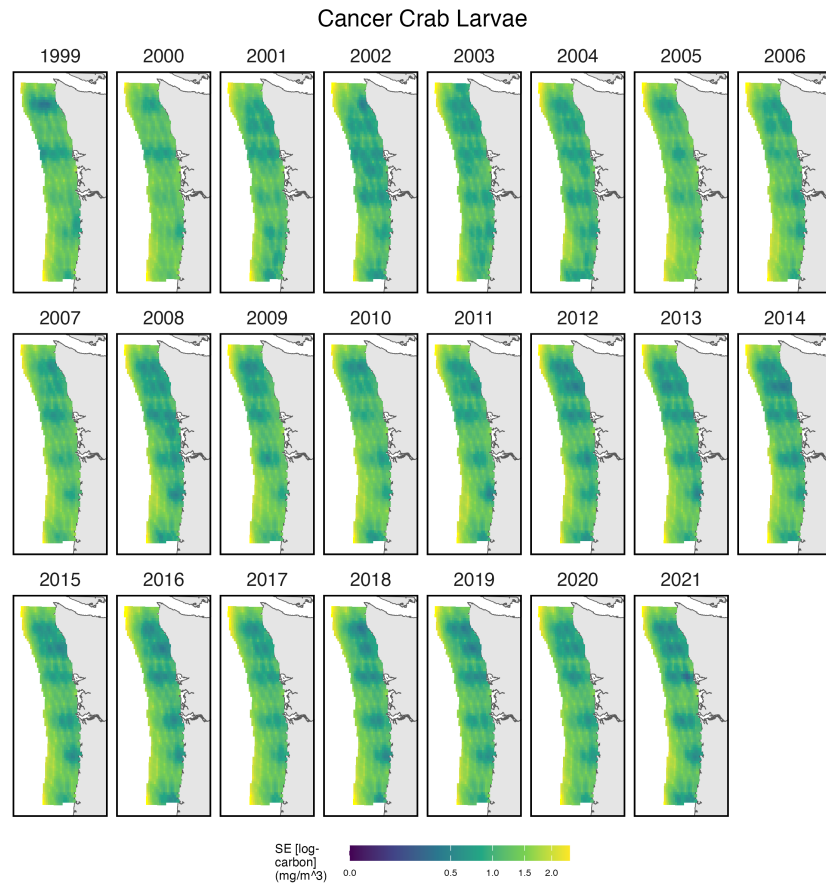


Figure 6. Standard error for SDM predictions for *Cancer* spp. Crab Larvae.

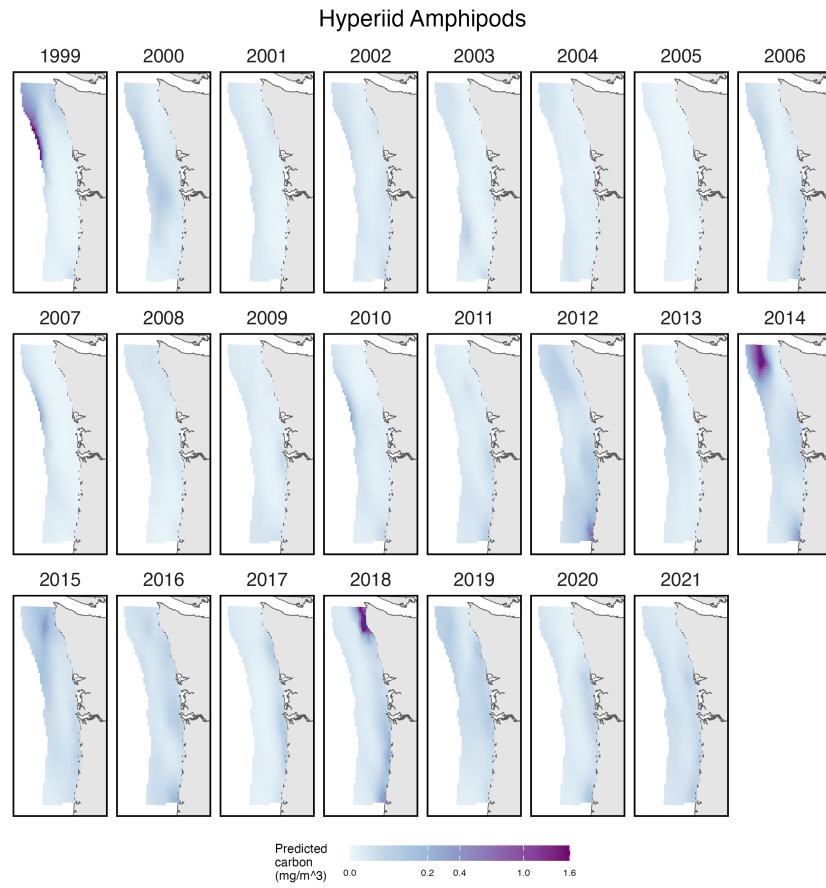


Figure 7. SDM predictions for Hyperiid Amphipods.

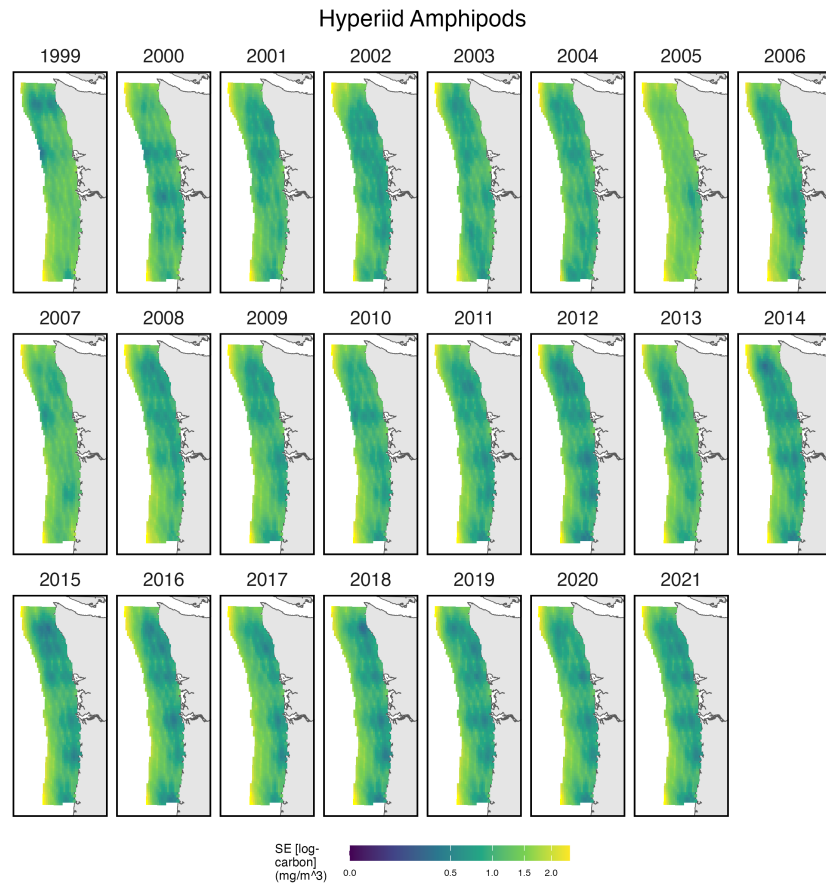


Figure 8. Standard error for SDM predictions for Hyperiid Amphipods.

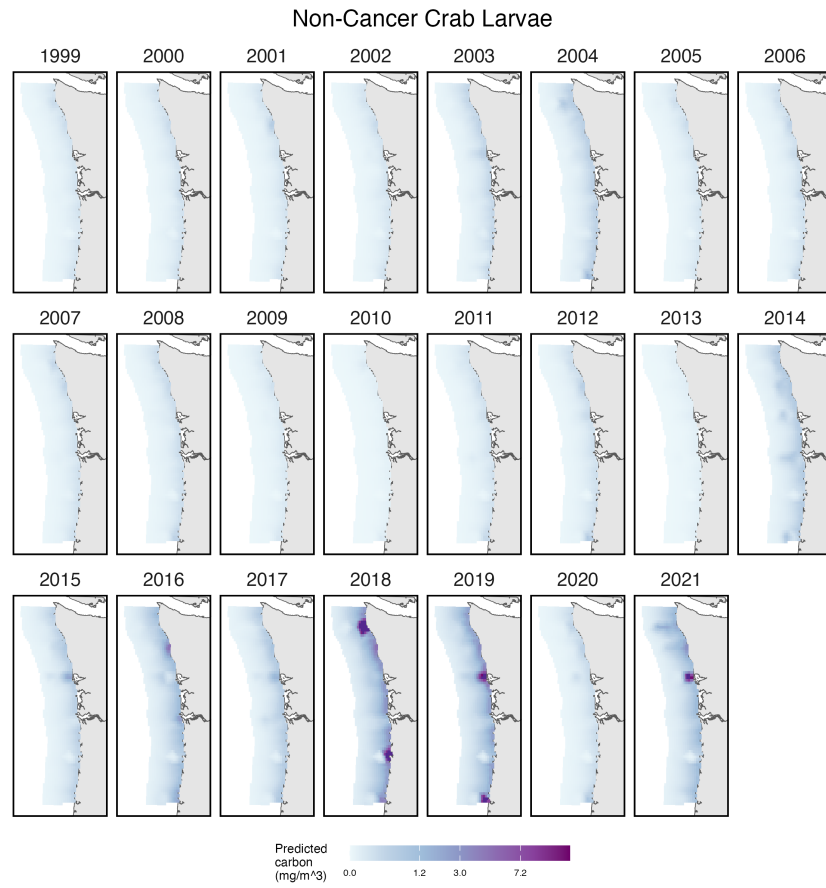


Figure 9. SDM predictions for Non-*Cancer* spp. Crab Larvae.

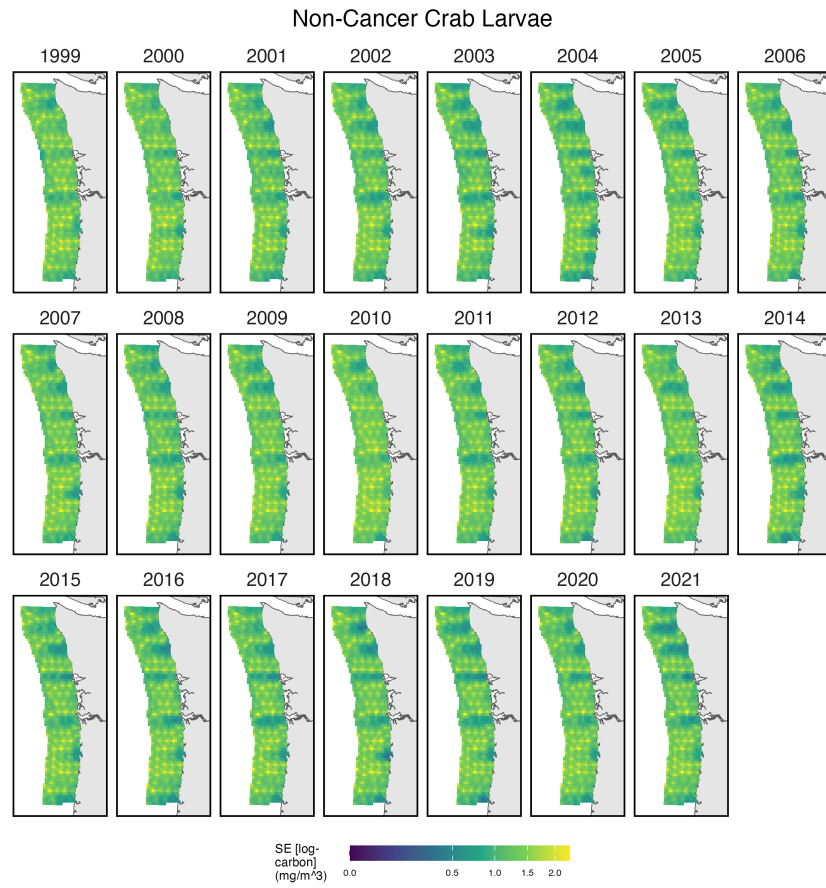


Figure 10. Standard error for SDM predictions for Non-*Cancer* spp. Crab Larvae.

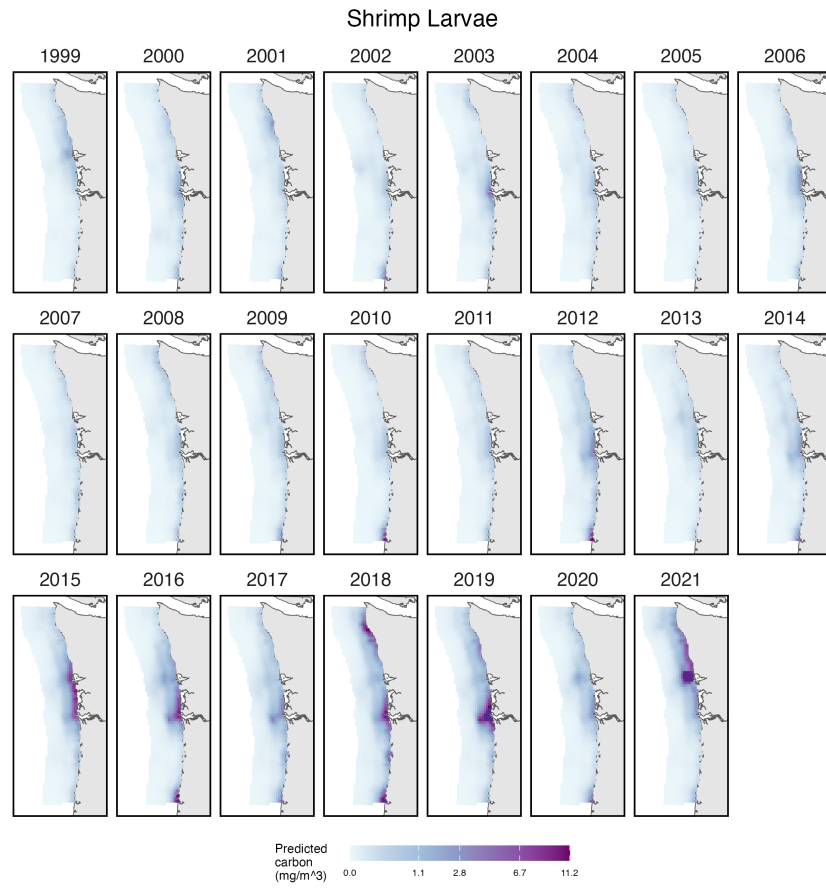


Figure 11. SDM predictions for Shrimp Larvae.

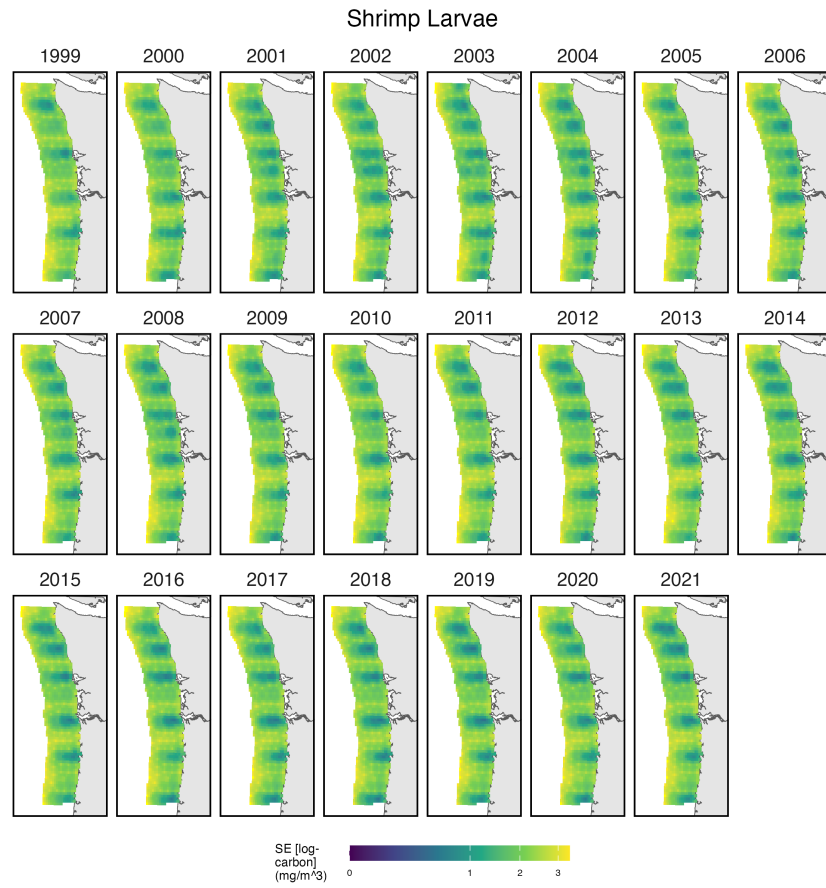


Figure 12. Standard error for SDM predictions for Shrimp Larvae.

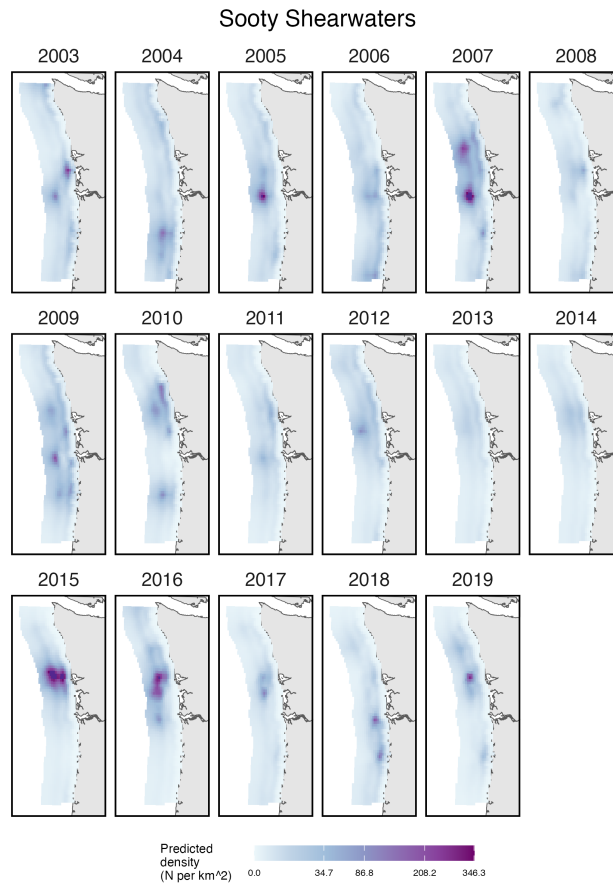


Figure 13. SDM predictions for Sooty Shearwaters.

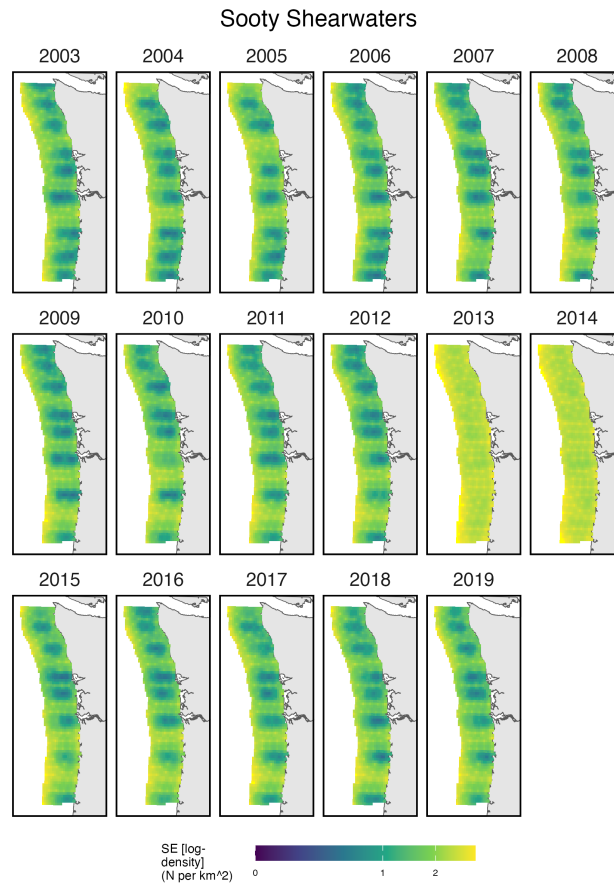


Figure 14. Standard error for SDM predictions for Sooty Shearwaters.

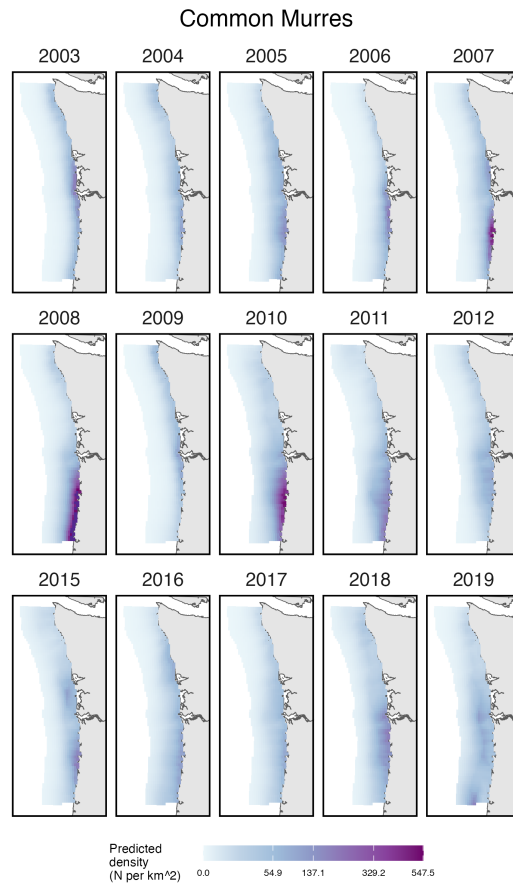


Figure 15. SDM predictions for Common Murres.

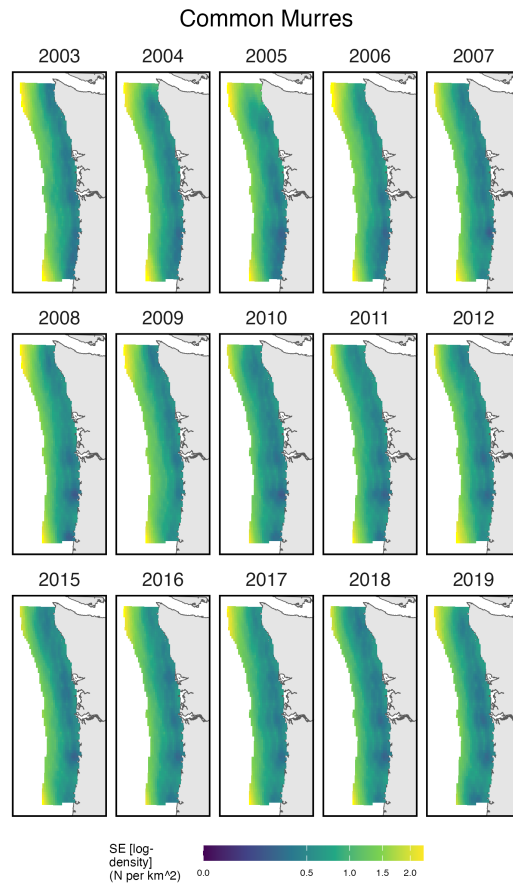


Figure 16. Standard error for SDM predictions for Common Murres.

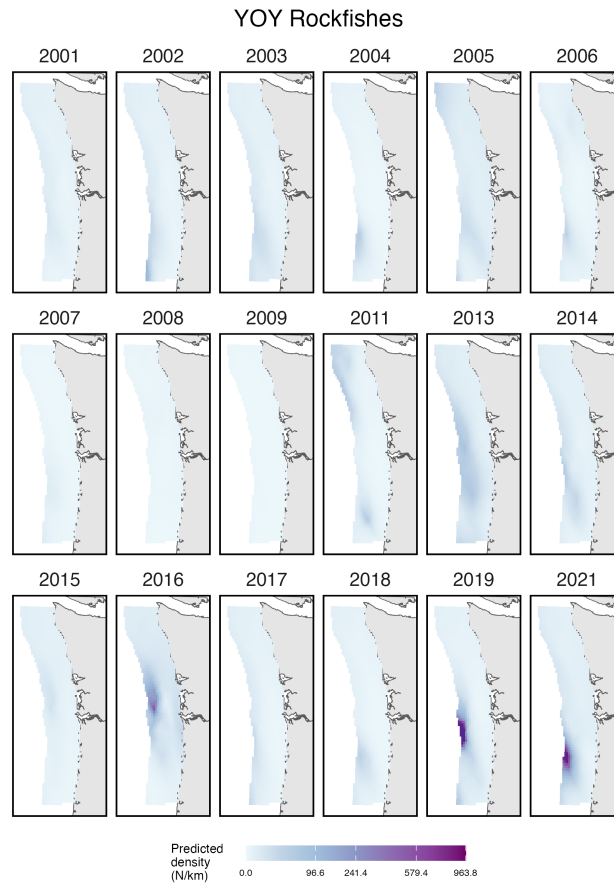


Figure 17. SDM predictions for YOY Rockfishes (*Sebastes* spp.).

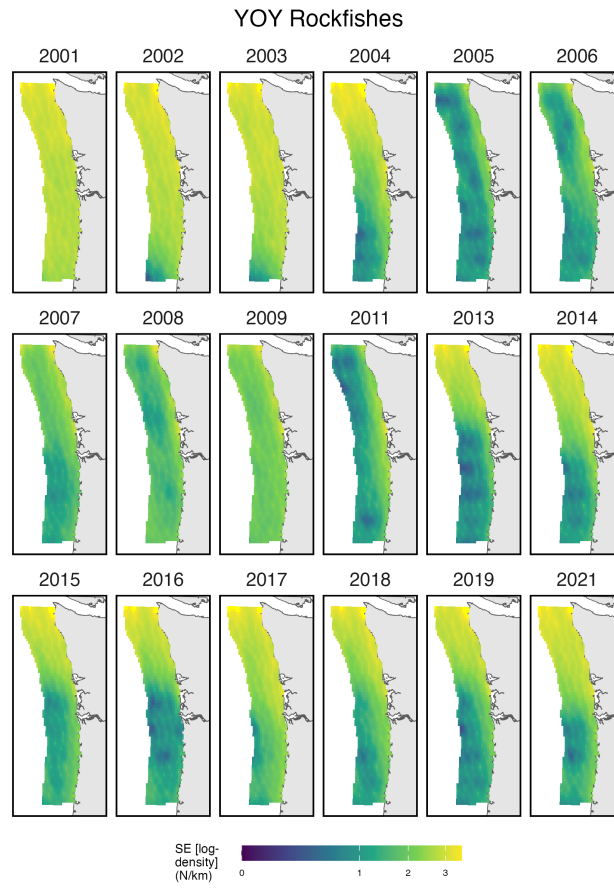


Figure 18. Standard error for SDM predictions for YOY Rockfishes (*Sebastes* spp.).

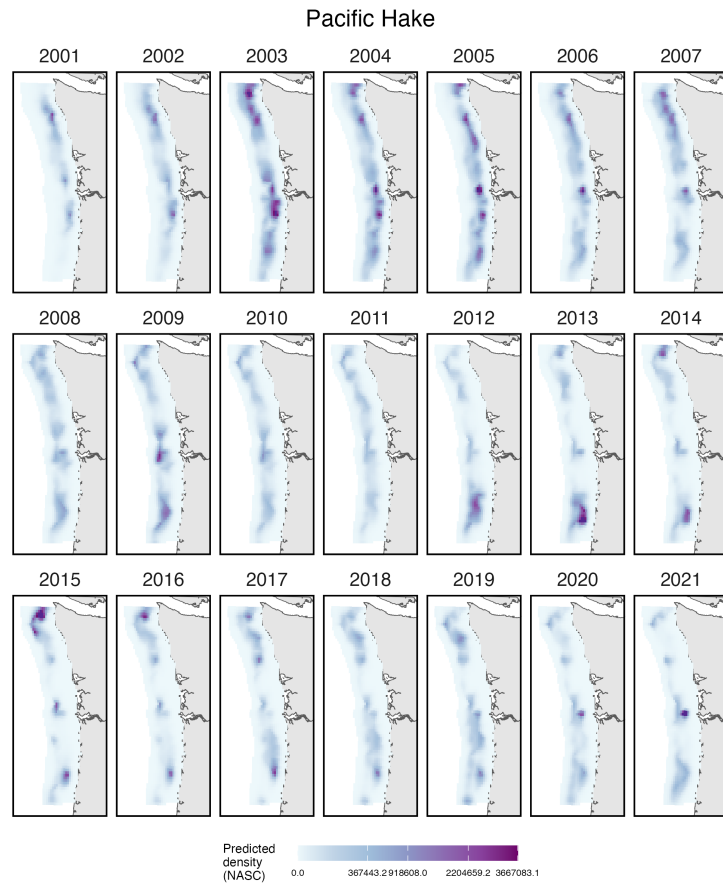


Figure 19. SDM predictions for Hake.

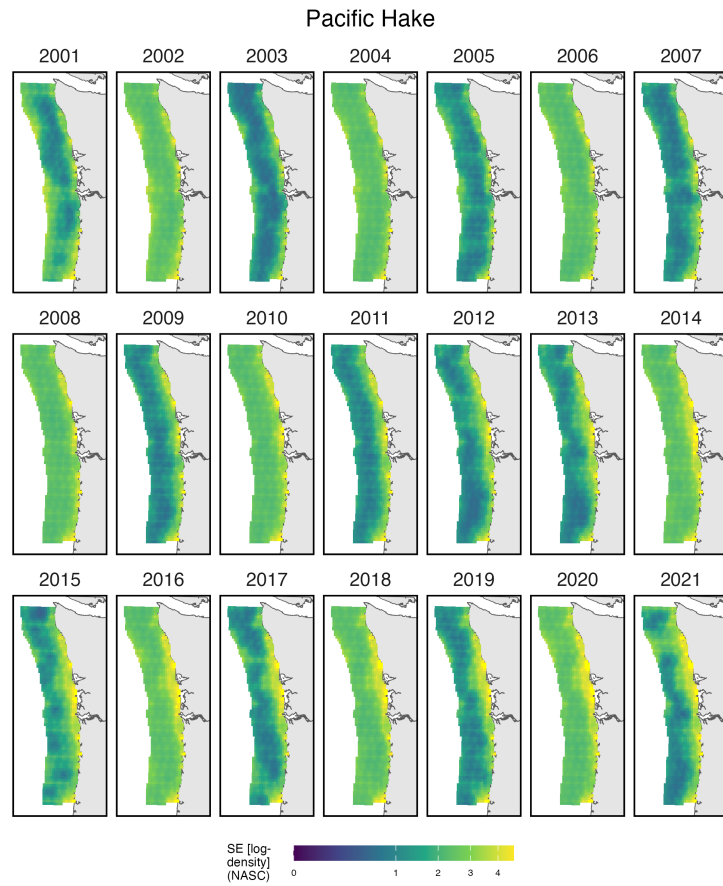


Figure 20. Standard error for SDM predictions for Hake.

Appendix I. SDM-derived marine survival covariates

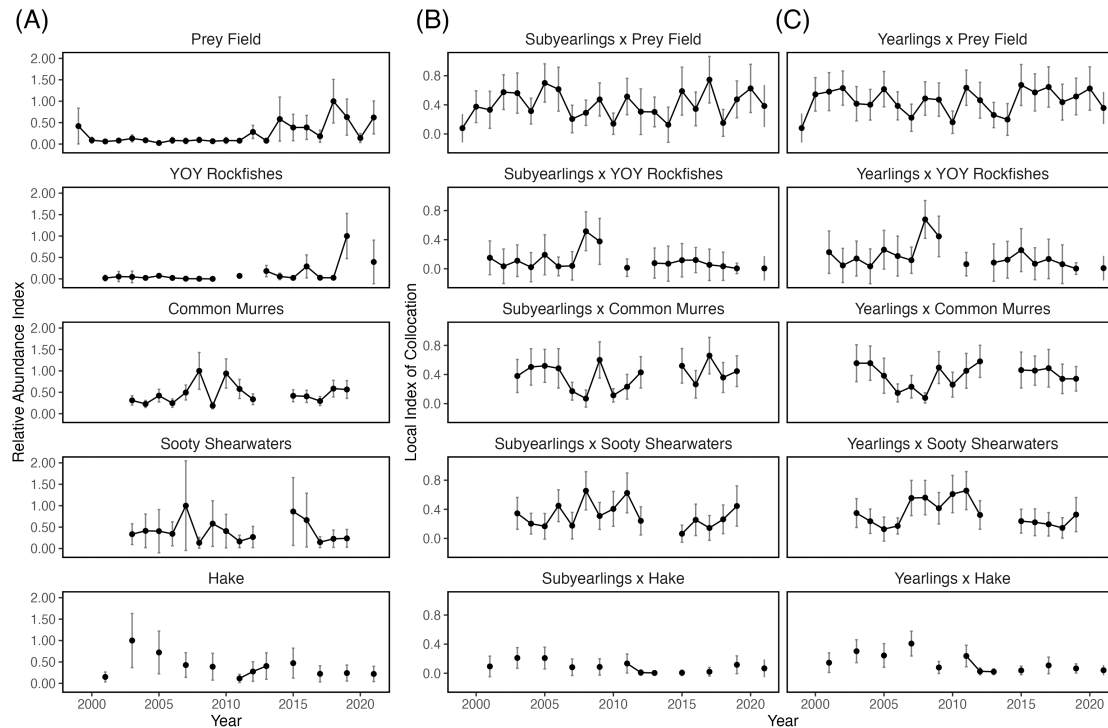


Figure 1. SDM-derived inputs for the survival model. Relative abundance indices for the study region (each time series is scaled relative to the maximum value in the time series) for each covariate taxon in the study region are shown in panel (A), the local index of collocation for the overlap between subyearling interior Fall Chinook Salmon and each of the predator or prey taxa is shown in panel (B), and the local index of collocation for the overlap between yearling interior Fall Chinook Salmon and each of the predator or prey taxa is shown in panel (C). Points are the maximum likelihood estimates for the value in each year while the bars show the 95% confidence interval.

The relative abundance of both the Bongo net aggregate prey field and the YOY rockfishes increased towards the end of the time series, driven by a handful of tows with very high catches of some of the component prey species (Appendix F). The abundance of Pacific Hake was less variable than that of the two seabirds, and the variance of the estimates was generally lower. Overlap between both subyearling and yearling Chinook Salmon was lowest with Pacific Hake, due to Pacific Hake having a more offshore distribution than juvenile Chinook Salmon (Appendix H). Overlap between both subyearling and yearling Chinook Salmon and the other four taxa (prey field, YOY rockfishes, Common Murres, and Sooty Shearwaters) was variable throughout the time series and was estimated with greater variance.

Appendix J. Fit between latent state estimated in the survival model (stage two model) and the SDM-estimated value (stage one model)

Appendix J.1. Seabirds x Subyearlings

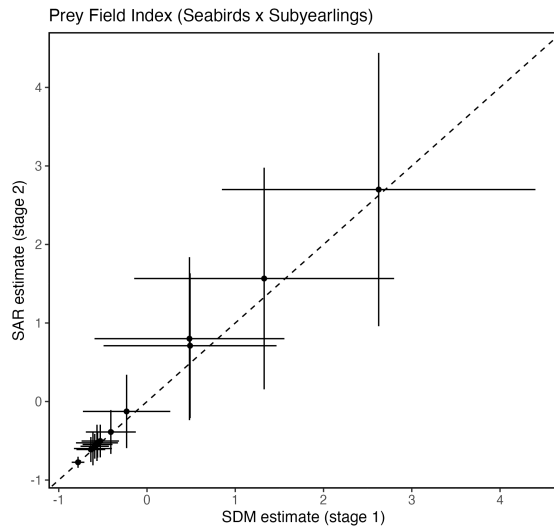


Figure 1. Fit to prey field index. Points show the maximum likelihood estimates for each parameter, while the bars show the 95% confidence intervals.

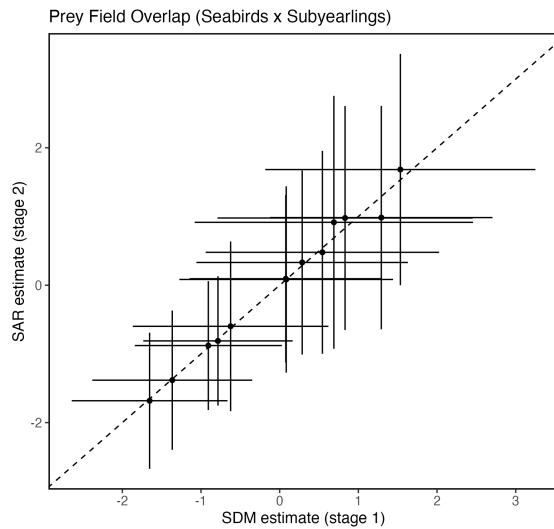


Figure 2. Fit to prey field overlap. Points show the maximum likelihood estimates for each parameter, while the bars show the 95% confidence intervals.

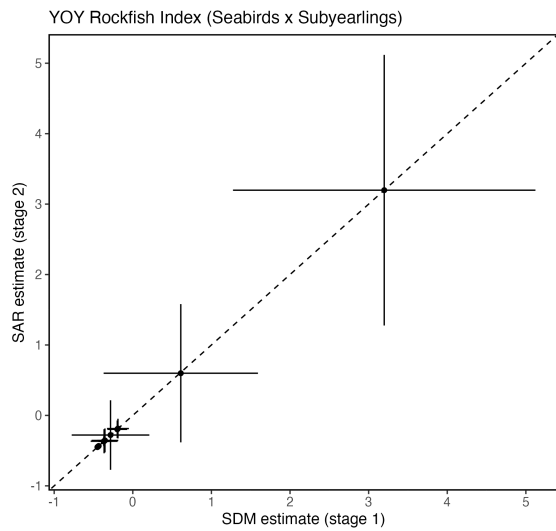


Figure 3. Fit to YOY rockfishes index. Points show the maximum likelihood estimates for each parameter, while the bars show the 95% confidence intervals.

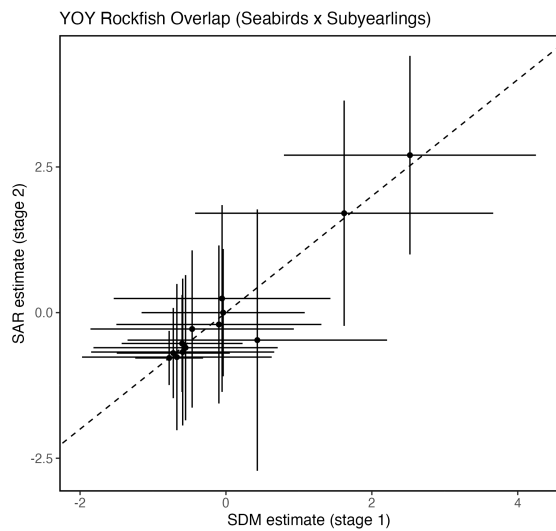


Figure 4. Fit to YOY rockfishes overlap. Points show the maximum likelihood estimates for each parameter, while the bars show the 95% confidence intervals.

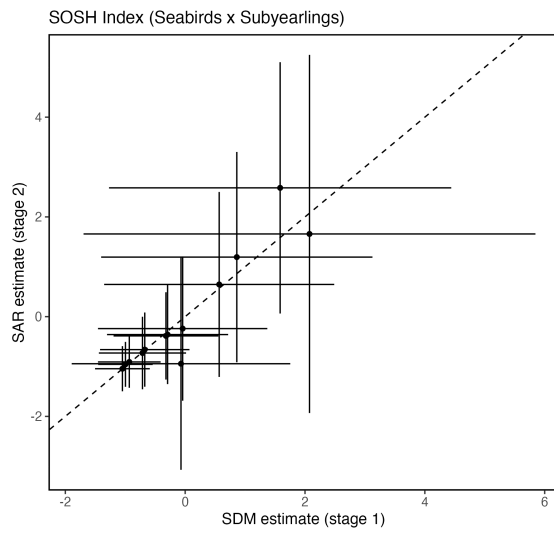


Figure 5. Fit to Sooty Shearwaters index. Points show the maximum likelihood estimates for each parameter, while the bars show the 95% confidence intervals.

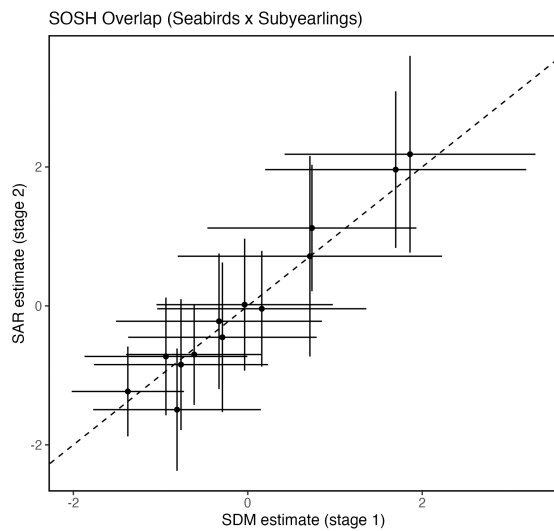


Figure 6. Fit to Sooty Shearwaters overlap. Points show the maximum likelihood estimates for each parameter, while the bars show the 95% confidence intervals.

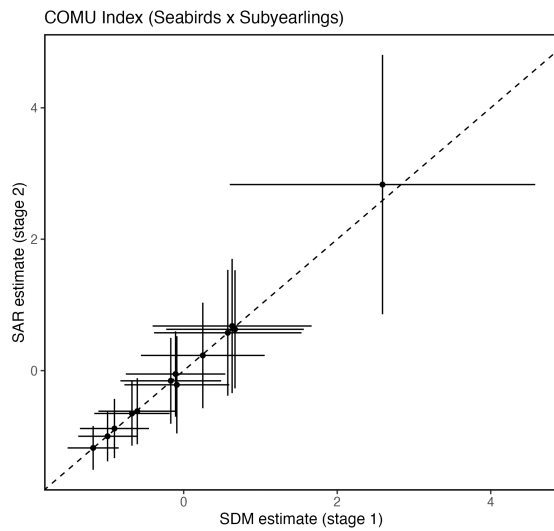


Figure 7. Fit to Common Murres index. Points show the maximum likelihood estimates for each parameter, while the bars show the 95% confidence intervals.

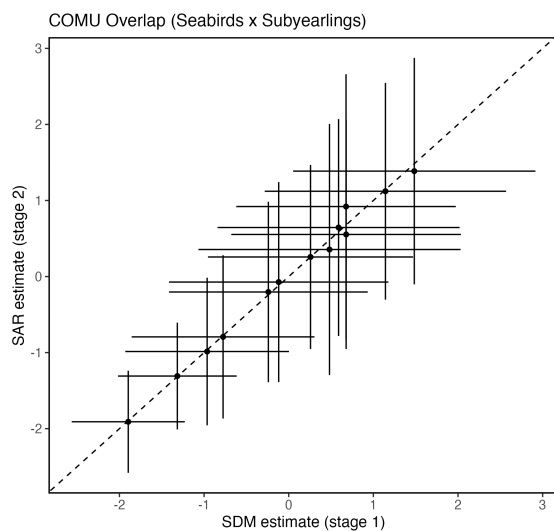


Figure 8. Fit to Common Murres overlap. Points show the maximum likelihood estimates for each parameter, while the bars show the 95% confidence intervals.

Appendix J.2. Seabirds x Yearlings

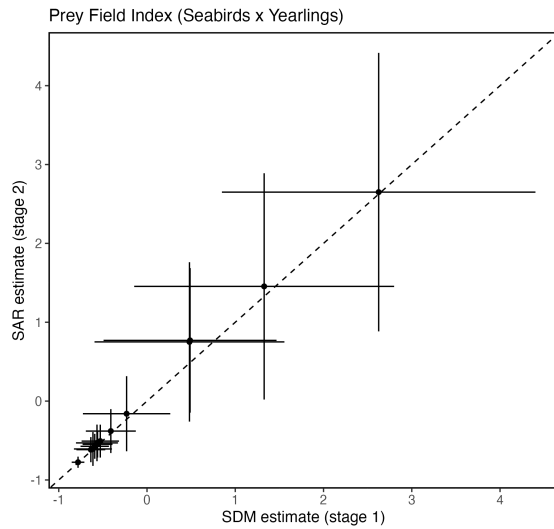


Figure 1. Fit to prey field index. Points show the maximum likelihood estimates for each parameter, while the bars show the 95% confidence intervals.

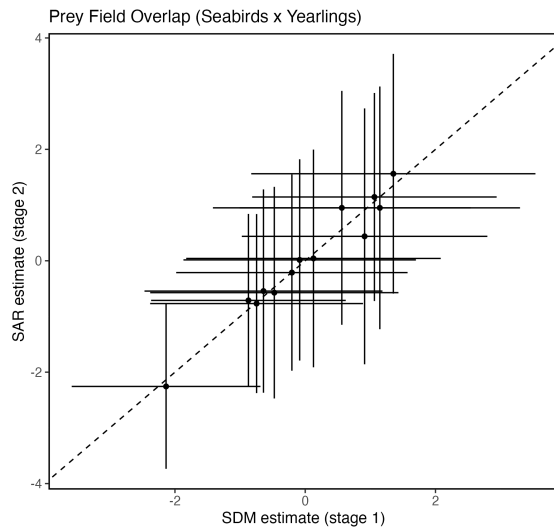


Figure 2. Fit to prey field overlap. Points show the maximum likelihood estimates for each parameter, while the bars show the 95% confidence intervals.

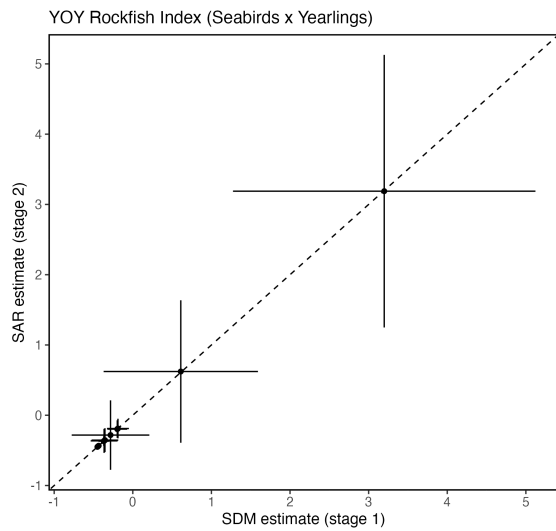


Figure 3. Fit to YOY rockfishes index. Points show the maximum likelihood estimates for each parameter, while the bars show the 95% confidence intervals.

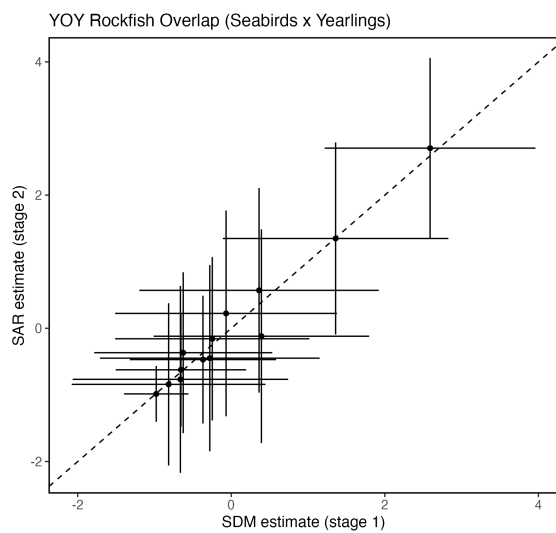


Figure 4. Fit to YOY rockfishes overlap. Points show the maximum likelihood estimates for each parameter, while the bars show the 95% confidence intervals.

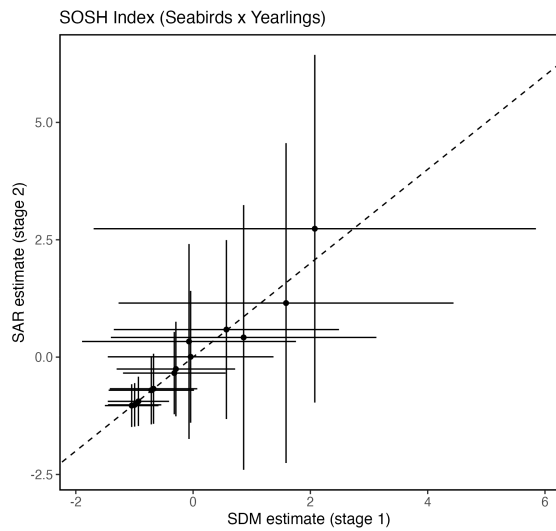


Figure 5. Fit to Sooty Shearwaters index. Points show the maximum likelihood estimates for each parameter, while the bars show the 95% confidence intervals.

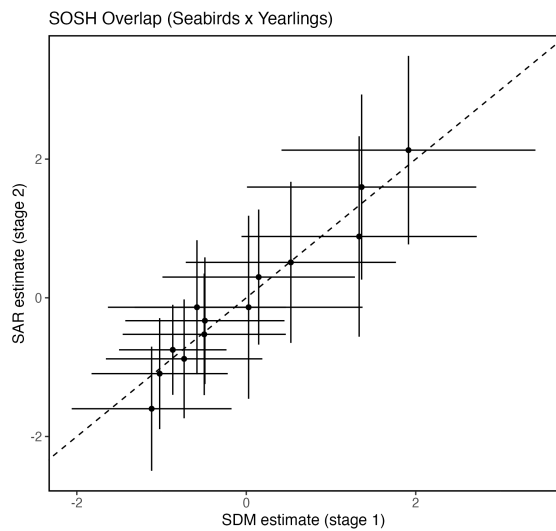


Figure 6. Fit to Sooty Shearwaters overlap. Points show the maximum likelihood estimates for each parameter, while the bars show the 95% confidence intervals.

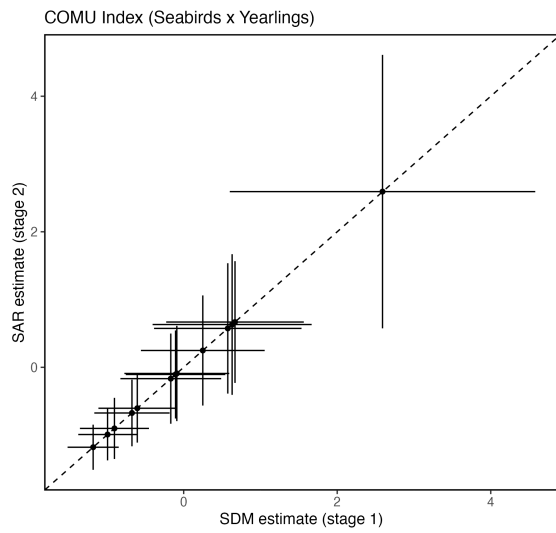


Figure 7. Fit to Common Murres index. Points show the maximum likelihood estimates for each parameter, while the bars show the 95% confidence intervals.

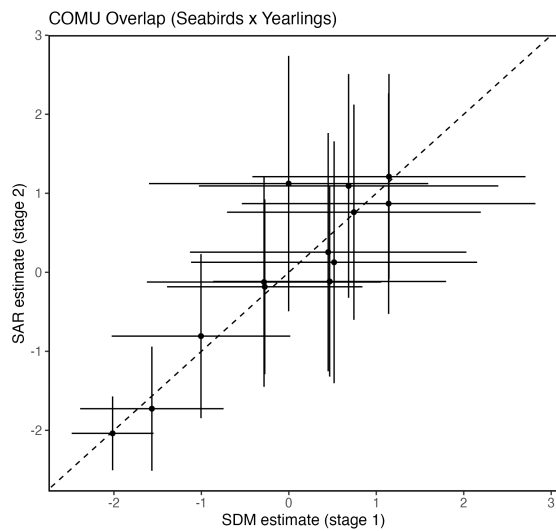


Figure 8. Fit to Common Murres overlap. Points show the maximum likelihood estimates for each parameter, while the bars show the 95% confidence intervals.

Appendix J.3. Hake x Subyearlings

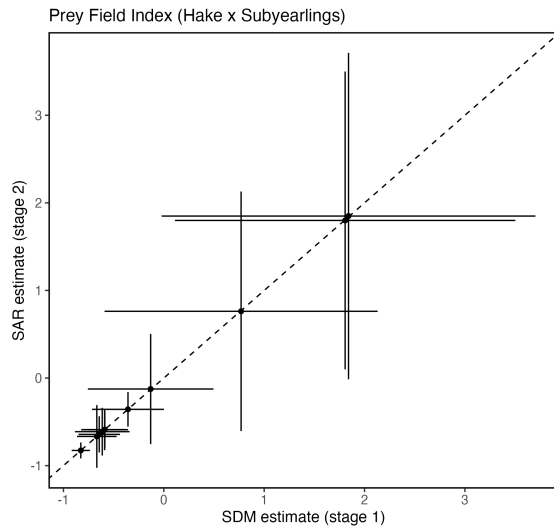


Figure 1. Fit to prey field index. Points show the maximum likelihood estimates for each parameter, while the bars show the 95% confidence intervals.

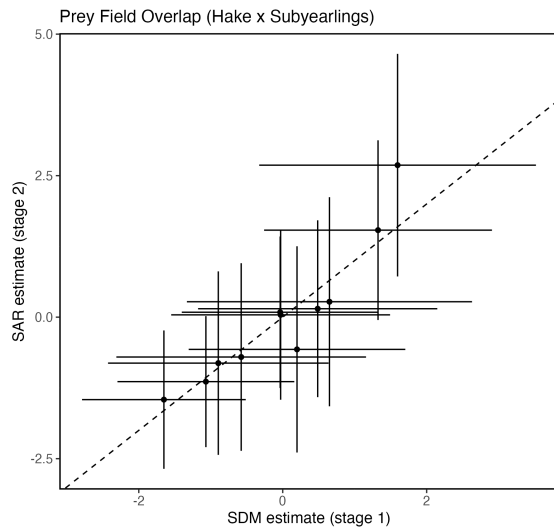


Figure 2. Fit to prey field overlap. Points show the maximum likelihood estimates for each parameter, while the bars show the 95% confidence intervals.

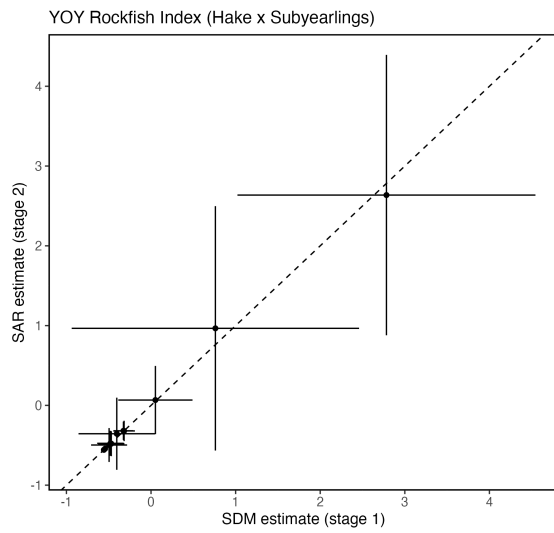


Figure 3. Fit to YOY rockfishes index. Points show the maximum likelihood estimates for each parameter, while the bars show the 95% confidence intervals.

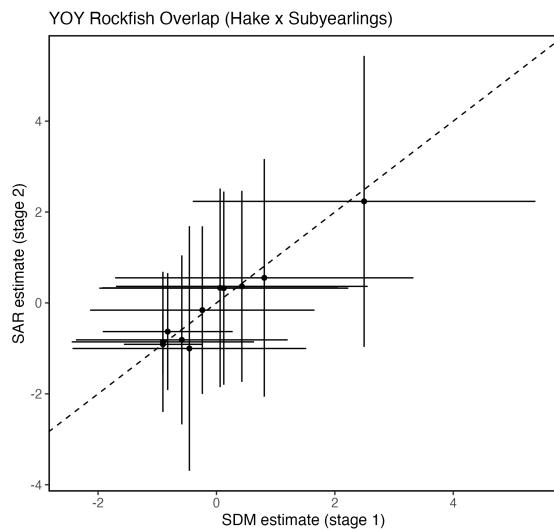


Figure 4. Fit to YOY rockfishes overlap. Points show the maximum likelihood estimates for each parameter, while the bars show the 95% confidence intervals.

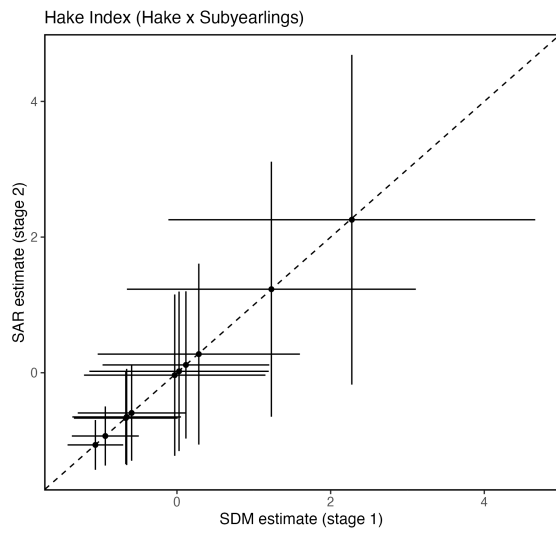


Figure 5. Fit to Hake index. Points show the maximum likelihood estimates for each parameter, while the bars show the 95% confidence intervals.

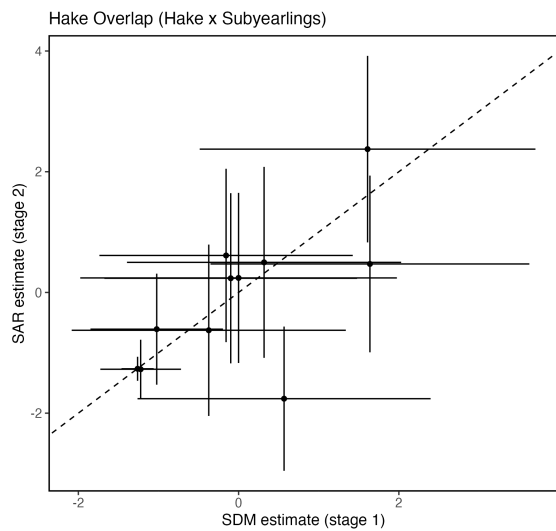


Figure 6. Fit to Hake overlap. Points show the maximum likelihood estimates for each parameter, while the bars show the 95% confidence intervals.

Appendix J.4. Hake x Yearlings

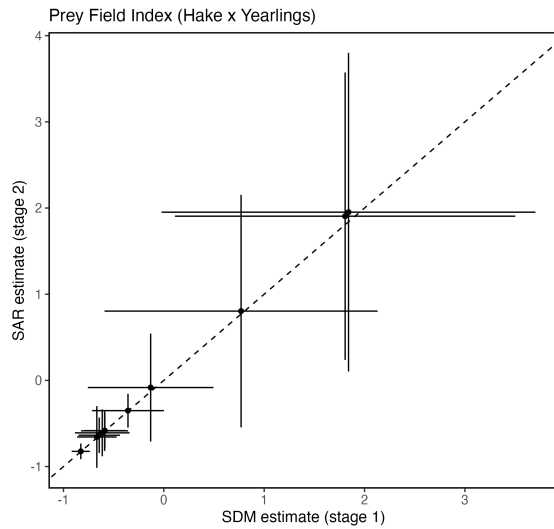


Figure 1 Fit to prey field index. Points show the maximum likelihood estimates for each parameter, while the bars show the 95% confidence intervals.

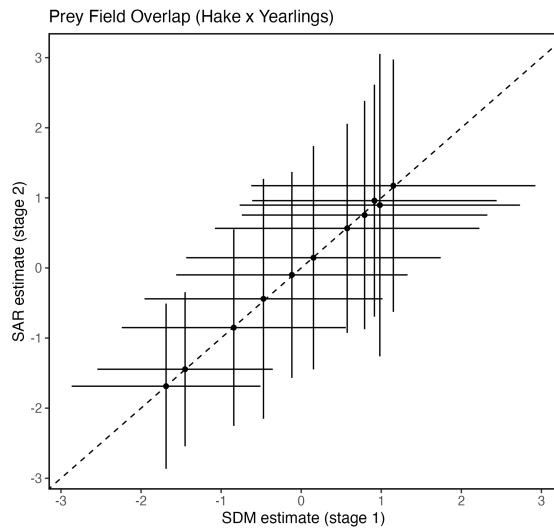


Figure 2. Fit to prey field overlap. Points show the maximum likelihood estimates for each parameter, while the bars show the 95% confidence intervals.

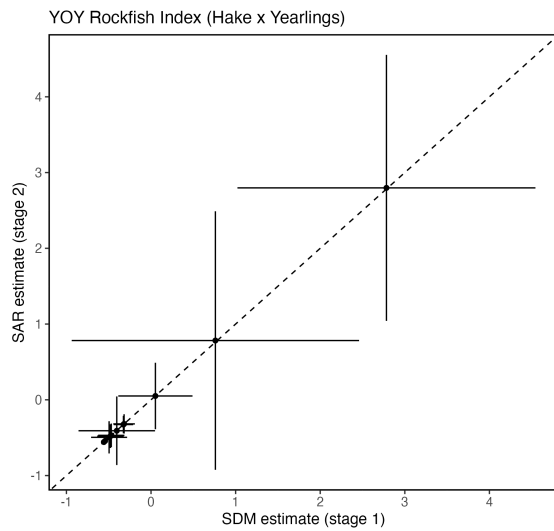


Figure 3. Fit to YOY rockfishes index. Points show the maximum likelihood estimates for each parameter, while the bars show the 95% confidence intervals.

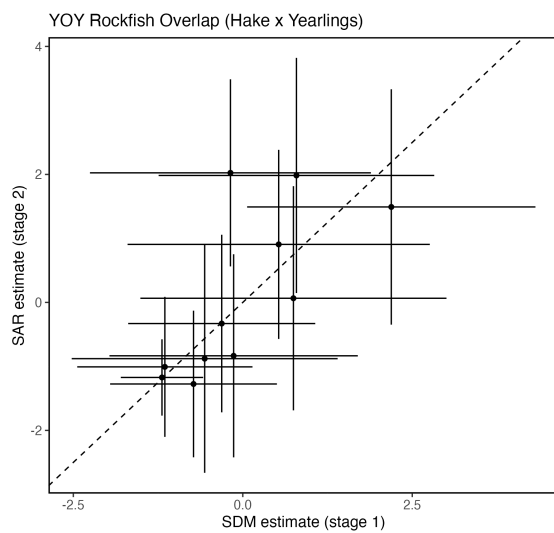


Figure 4. Fit to YOY rockfishes overlap. Points show the maximum likelihood estimates for each parameter, while the bars show the 95% confidence intervals.

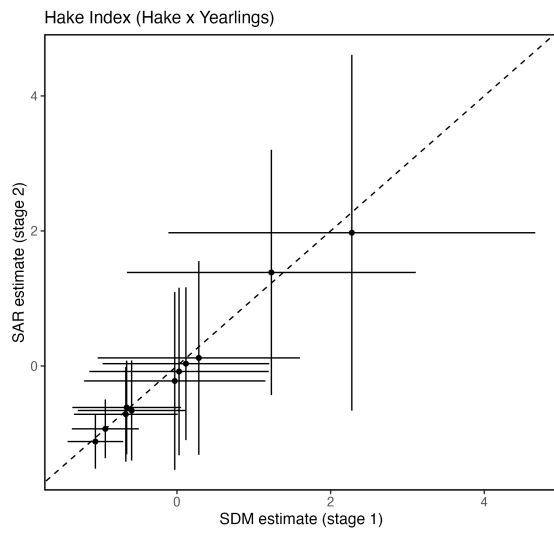


Figure 5. Fit to Hake index. Points show the maximum likelihood estimates for each parameter, while the bars show the 95% confidence intervals.

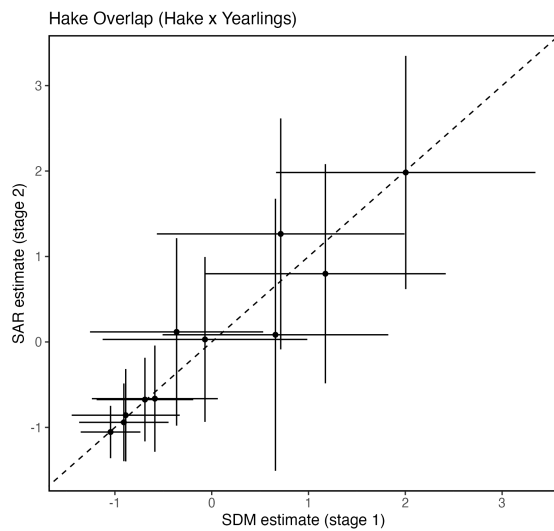


Figure 6. Fit to Hake overlap. Points show the maximum likelihood estimates for each parameter, while the bars show the 95% confidence intervals.

Appendix K. No Errors-in-Variables Sensitivity Analysis

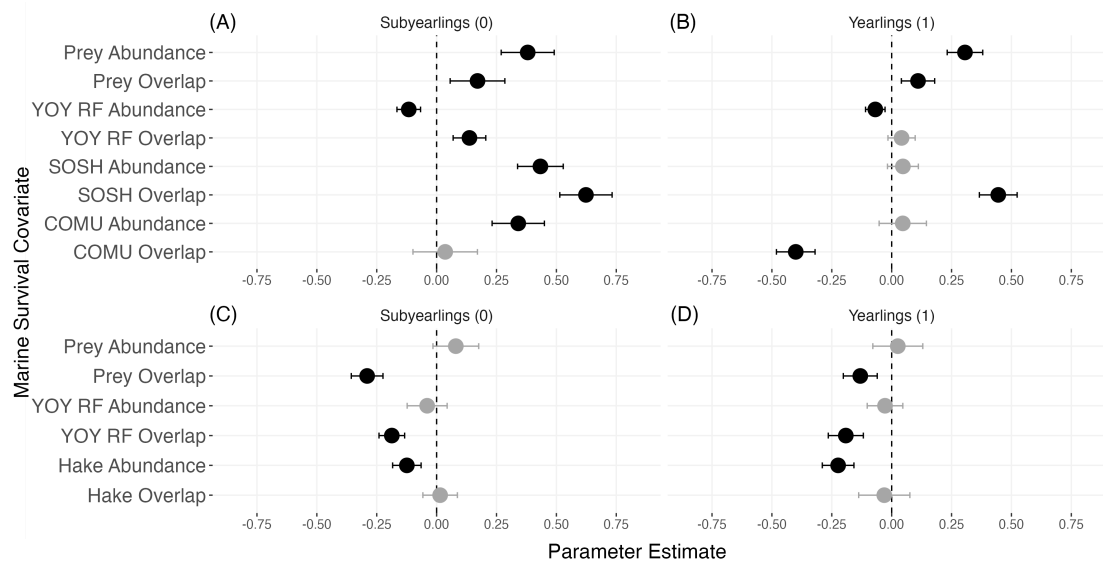


Figure 1. Figure 3 from the main text reproduced with a model where the SDM-derived marine survival covariates are treated as known, without the uncertainty accounted for using the errors-in-variables approach. Regression coefficients for the SDM-derived survival covariates in the survival models with seabirds as the focal predators (A, B) and Pacific Hake as the focal predator (C, D). In panels (A) and (C), the parameter estimates are shown for the effect of overlap with subyearling (0) interior Chinook Salmon; in panels (B) and (D), the parameter estimates are shown for the effect of overlap with yearling (1) interior Chinook Salmon. Regression coefficients are defined in Table 2. Points show the maximum likelihood estimates for each parameter, while the bars show the 95% confidence intervals. Parameters where the 95% confidence interval does not cross zero are shown in black and are interpreted as statistically significant.

Appendix L. Additional marine survival covariates

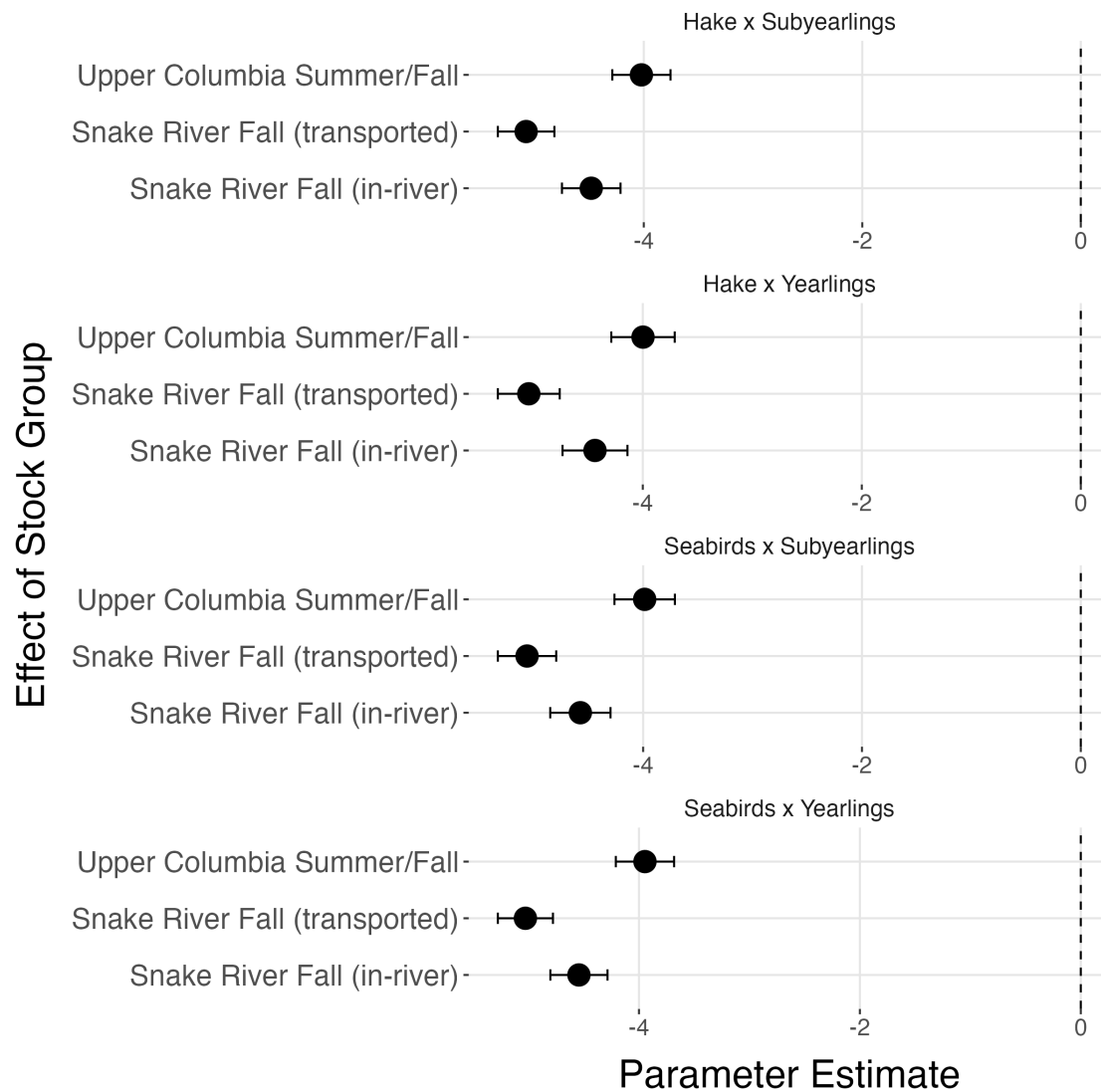


Figure 1. Effect of stock group/transport status on marine survival.

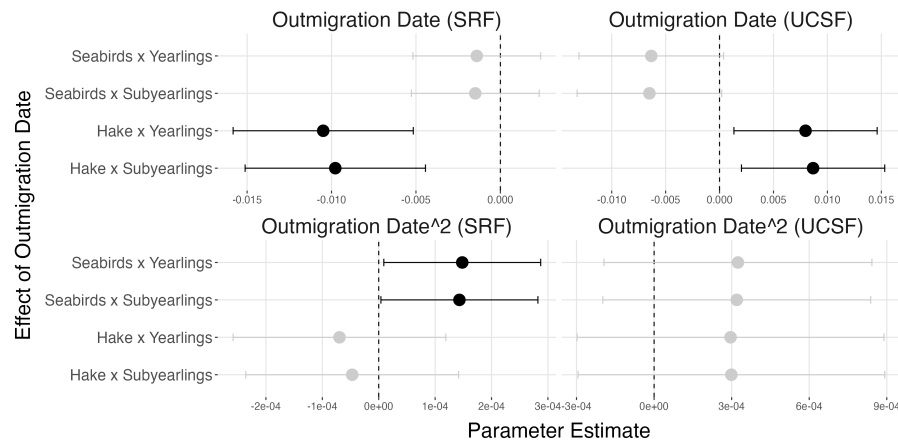


Figure 2. Effect of outmigration timing (outmigration date and outmigration date²), relative to mean outmigration date, for Snake River Fall and Upper Columbia Summer/Fall fish, relative to mean migration date. Note that this is relative to the mean migration date of the fish included in the model, and therefore does not include the later migrants for either stock.

Appendix M. Model fitted values

Model fitted values had consistently wide confidence intervals, although the Pacific Hake models were more precise than the seabird models. Confidence intervals were generally higher for years with higher marine survival.

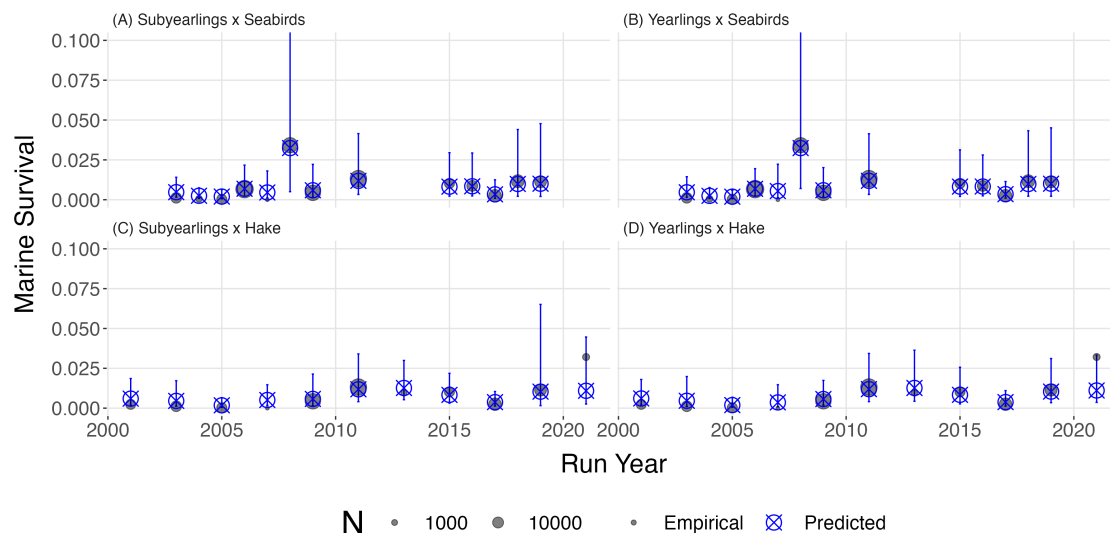


Figure 1. Empirical marine survival data (points) and predicted marine survival for each juvenile run year for Snake River Fall transported fish, with the maximum likelihood estimates shown as crossed circles and the 95% confidence intervals shown as bars. The predicted values for the four models are shown in panels A-D. Note that in many years, these confidence intervals extend beyond the plot boundaries.

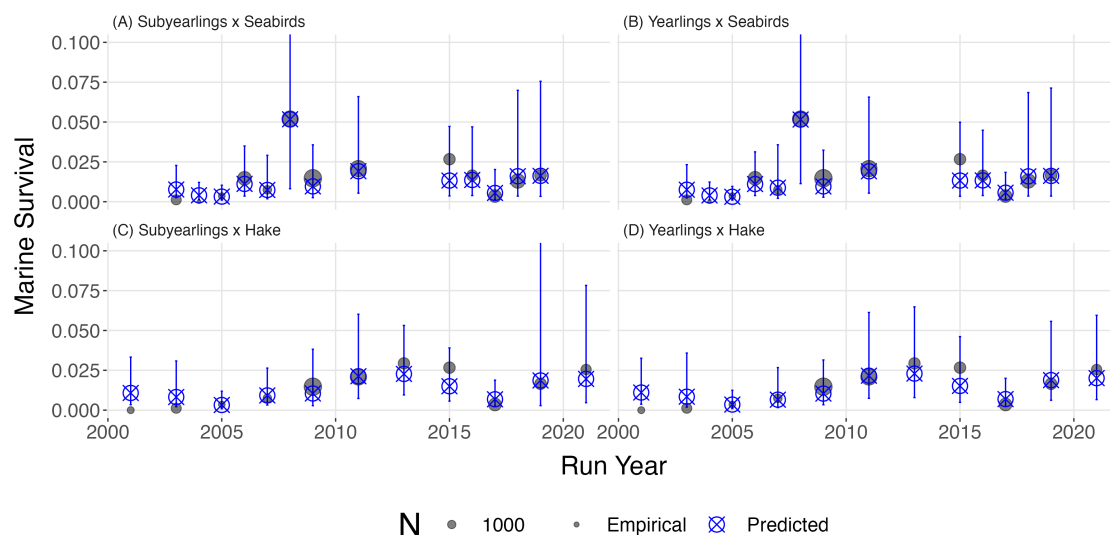


Figure 2. Empirical marine survival data (points) and predicted marine survival for each juvenile run year for Snake River Fall in-river fish, with the maximum likelihood estimates shown as crossed circles and the 95% confidence intervals shown as bars. The predicted values for the four models are shown in panels A-D. Note that in many years, these confidence intervals extend beyond the plot boundaries.

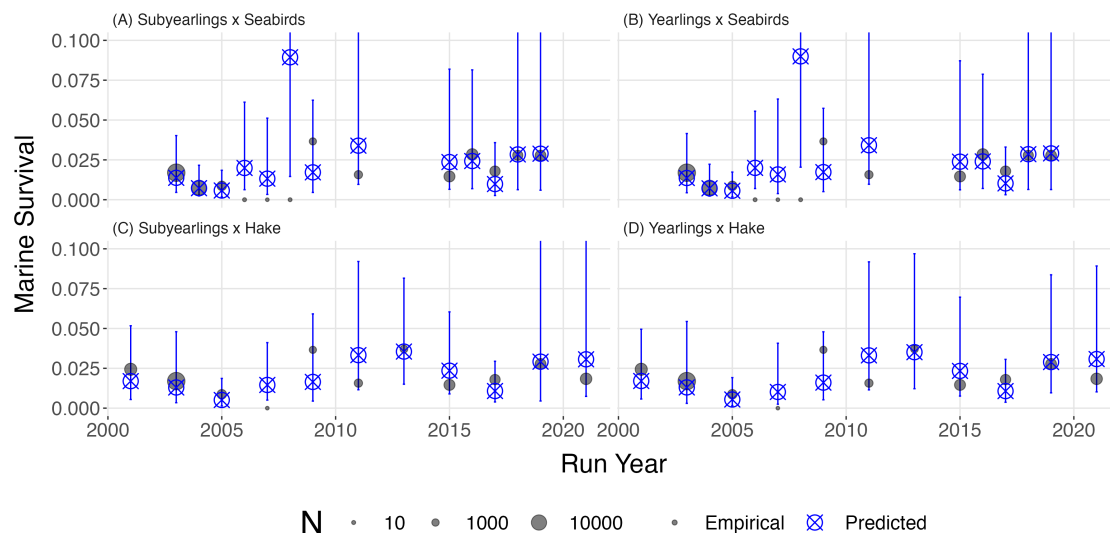


Figure 3. Empirical marine survival data (points) and predicted marine survival for each juvenile run year for Upper Columbia Summer/Fall fish, with the maximum likelihood estimates shown as crossed circles and the 95% confidence intervals shown as bars. The predicted values for the four models are shown in panels A-D. Note that in many years, these confidence intervals extend beyond the plot boundaries.

Chapter 3 Appendix References

- Daly, E. A., R. D. Brodeur, and T. D. Auth. 2017. Anomalous ocean conditions in 2015: Impacts on spring Chinook salmon and their prey field. *Marine Ecology Progress Series* 566:168–182.
- Daly, E. A., R. D. Brodeur, and L. A. Weitkamp. 2009. Ontogenetic Shifts in Diets of Juvenile and Subadult Coho and Chinook Salmon in Coastal Marine Waters: Important for Marine Survival? *Transactions of the American Fisheries Society* 138:1420–1438.
- de Blois, S. 2020. The 2019 Joint U . S .– Canada Integrated Ecosystem and Pacific Hake Acoustic-Trawl Survey: Cruise Report SH-19-06. NOAA Processed Report NMFS-NWFSC-PR-2020-03:1–50.
- Friedman, W. R., J. A. Santora, I. D. Schroeder, D. D. Huff, R. D. Brodeur, J. C. Field, and B. K. Wells. 2018. Environmental and geographic relationships among salmon forage assemblages along the continental shelf of the California Current. *Marine Ecology Progress Series* 596:181–198.
- Hess, J. E., N. R. Campbell, A. P. Matala, D. J. Hasselman, and S. R. Narum. 2013. Genetic assessment of Columbia River stocks. Columbia River Inter-Tribal Fish Commission annual report.
- Kalinowski, S. T., K. R. Manlove, and M. L. Taper. 2007. ONCOR: A computer program for genetic stock identification. Montana State University, Bozeman.

- Morgan, C. A., A. D. Robertis, and R. W. Zabel. 2005. Columbia River plume fronts. I. Hydrography, zooplankton distribution, and community composition. *Mar Ecol Prog Ser.*
- Teel, D. J., B. J. Burke, D. R. Kuligowski, C. A. Morgan, and D. M. Van Doornik. 2015. Genetic identification of chinook salmon: Stock-specific distributions of juveniles along the Washington and Oregon coasts. *Marine and Coastal Fisheries* 7:274–300.
- Thorson, J. T., and K. Kristensen. 2024. *Spatio-Temporal Models for Ecologists.* Chapman and Hall/CRC.
- Van Doornik, D. M., D. R. Kuligowski, C. A. Morgan, B. J. Burke, and T. R. Seamons. 2019. Insights, from genetic analyses, into stock-specific distribution of juvenile steelhead (*Oncorhynchus mykiss*) from the Columbia River during early marine migration. *Fishery Bulletin* 117.

Chapter 4 Appendix

Appendix A. Length-based cutoffs for age-0 Sablefish recruits.

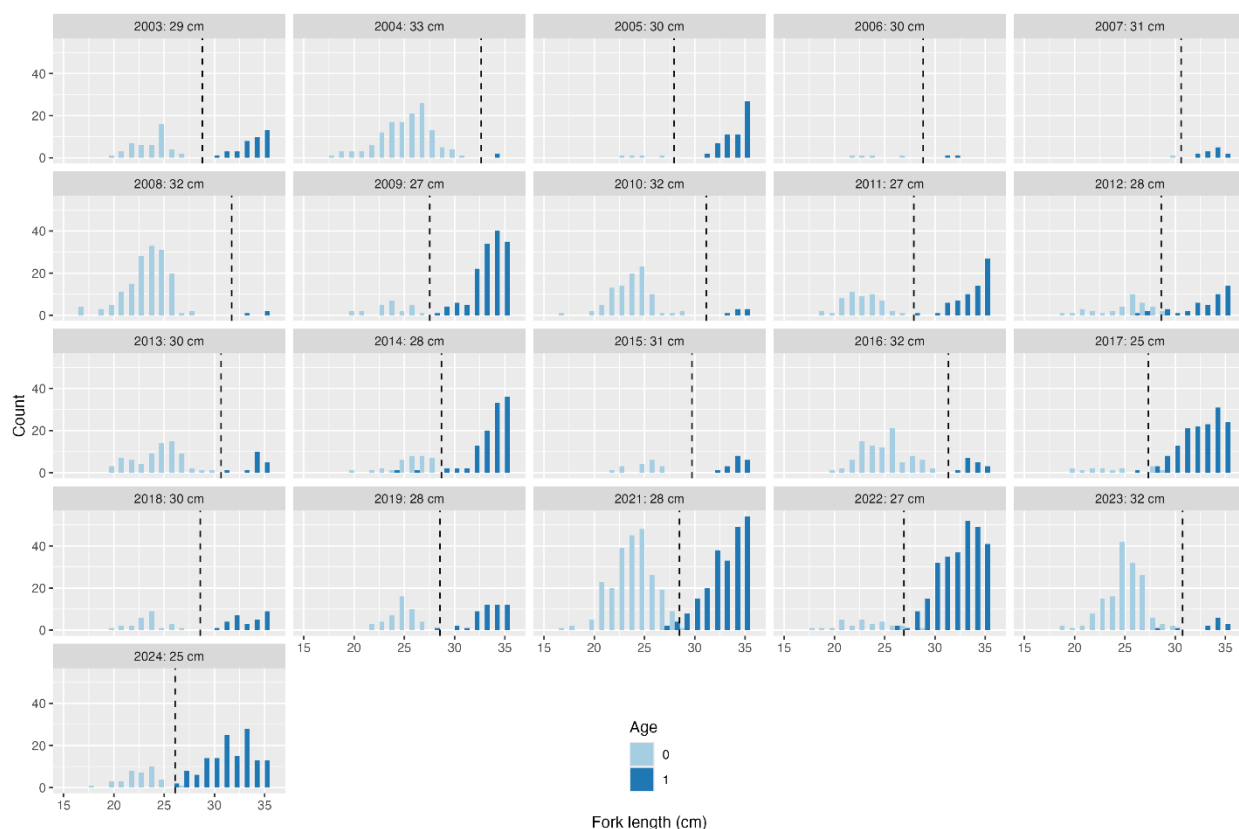


Figure 1. Length-based cutoffs estimated for each year for age-0 Sablefish recruits. Histograms depict the size distributions of age-0 and age-1 fish by year, with the dashed vertical line indicating the L_{50} estimated for each year. This L_{50} is also shown in the facet title and was used as the year-specific length cutoff for age-0 Sablefish from the length data.

Appendix B. Trawl survey catches

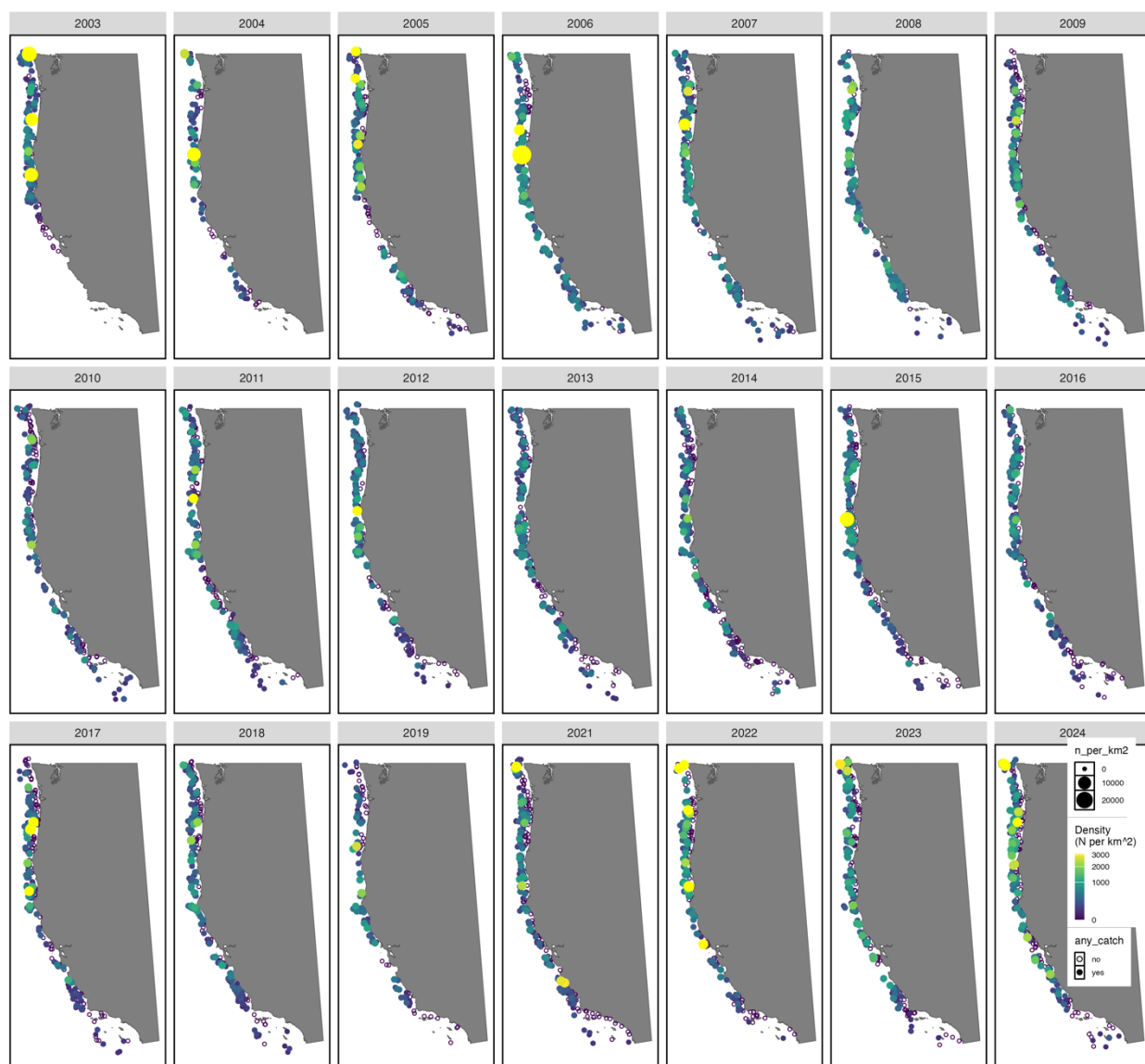


Figure 1. Catches of female spawners in pass 1 of the WCGBTS.

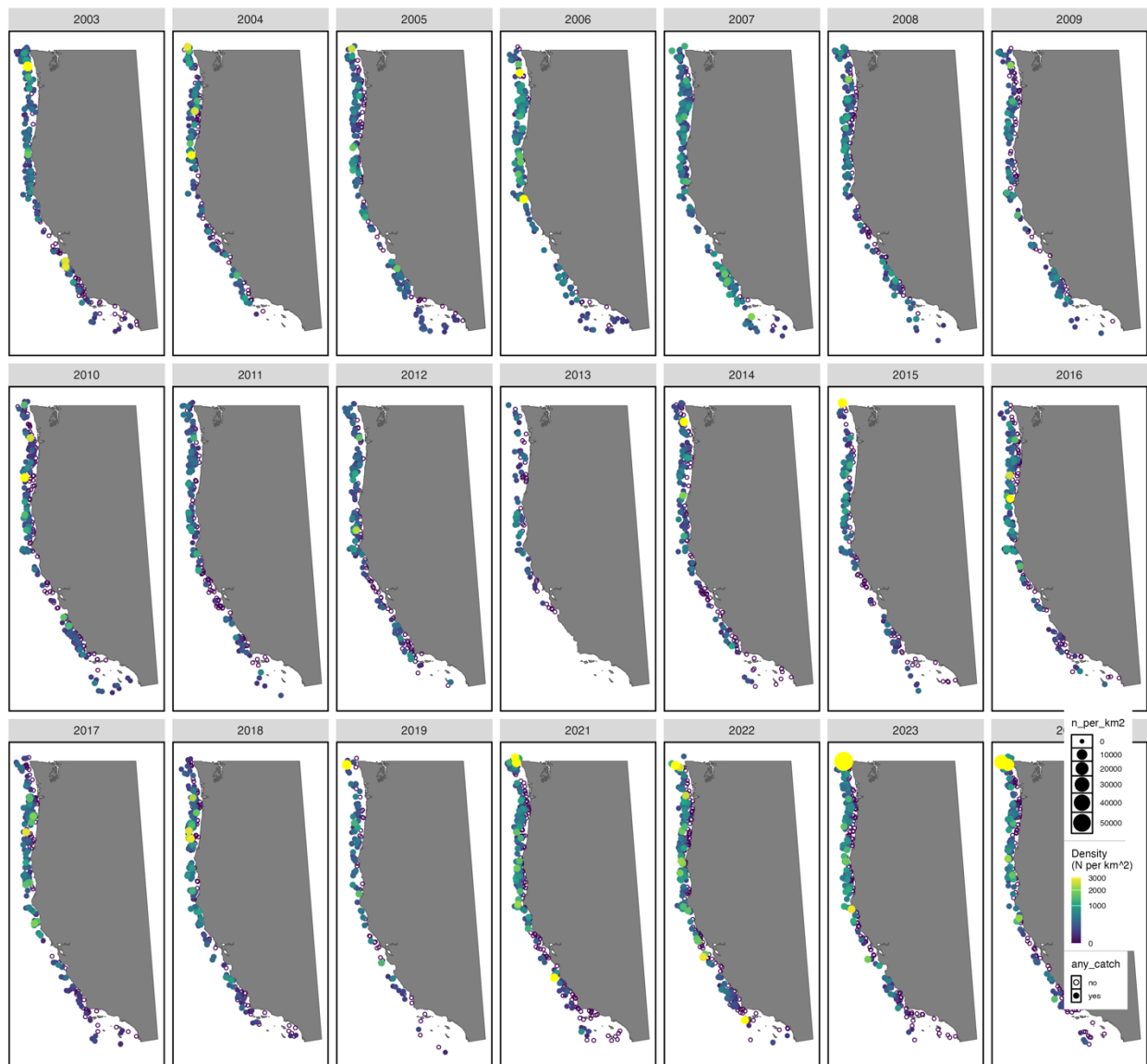


Figure 2. Catches of female spawners in pass 2 of the WCGBTS.

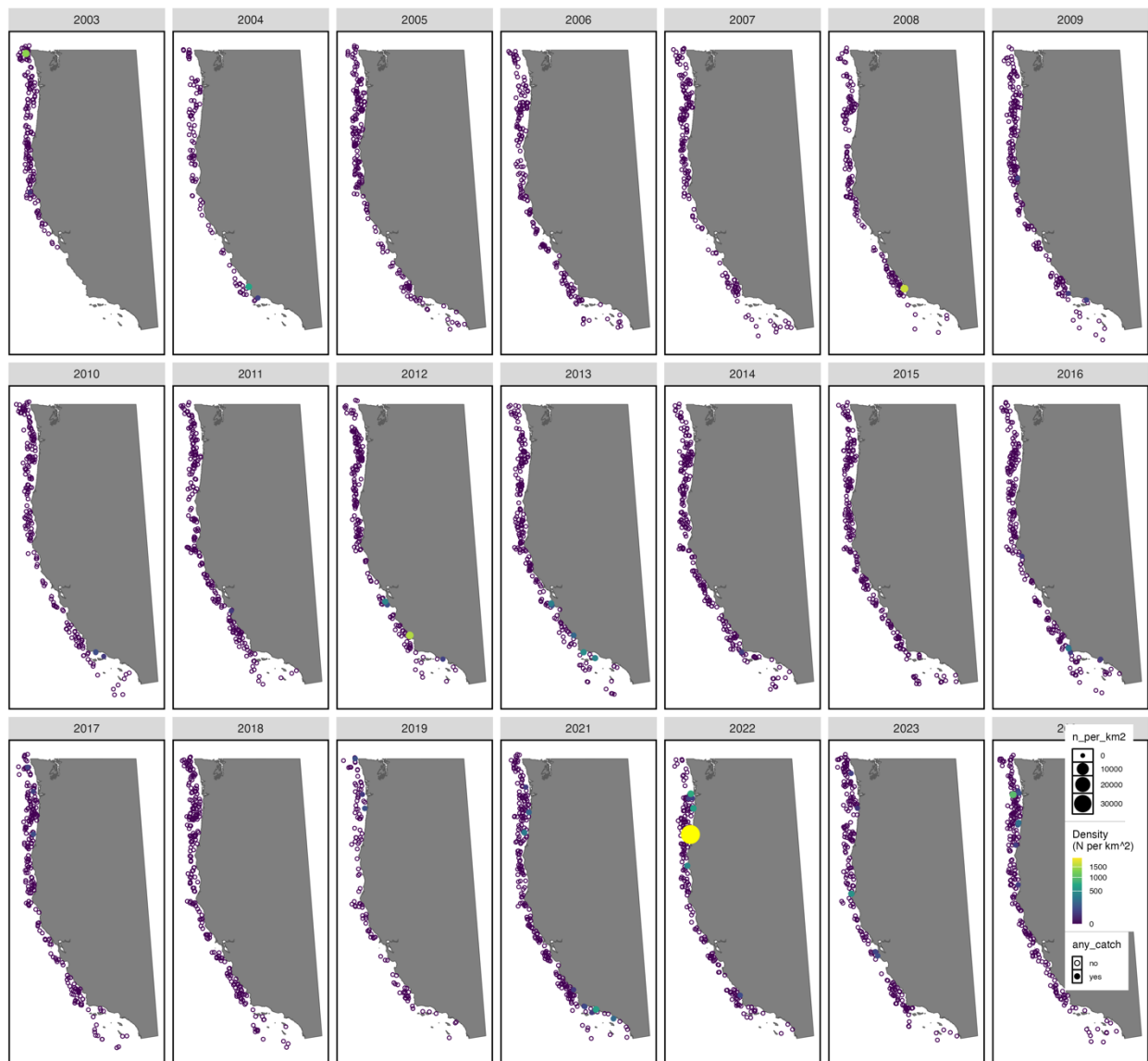


Figure 3. Catches of age-0 recruits in pass 1 of the WCGBTS.

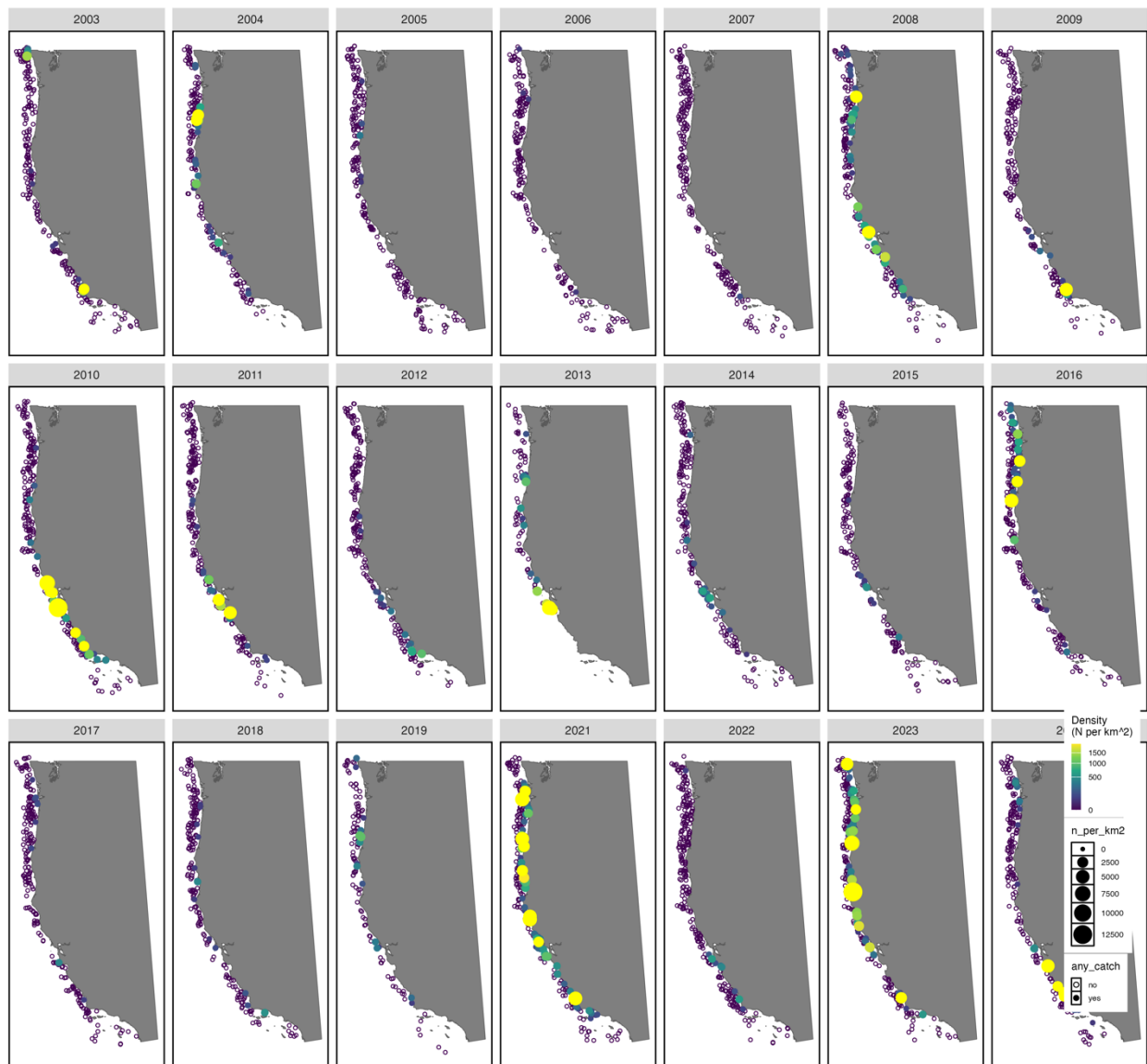


Figure 4. Catches of age-0 recruits in pass 2 of the WCGBTS.

Appendix C. Covariate correlations

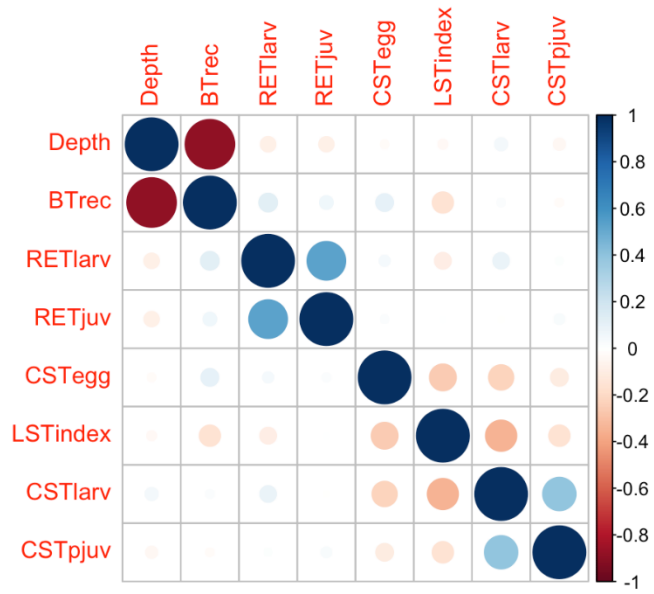


Figure 1. Correlations between predictors in the encounter probability model.

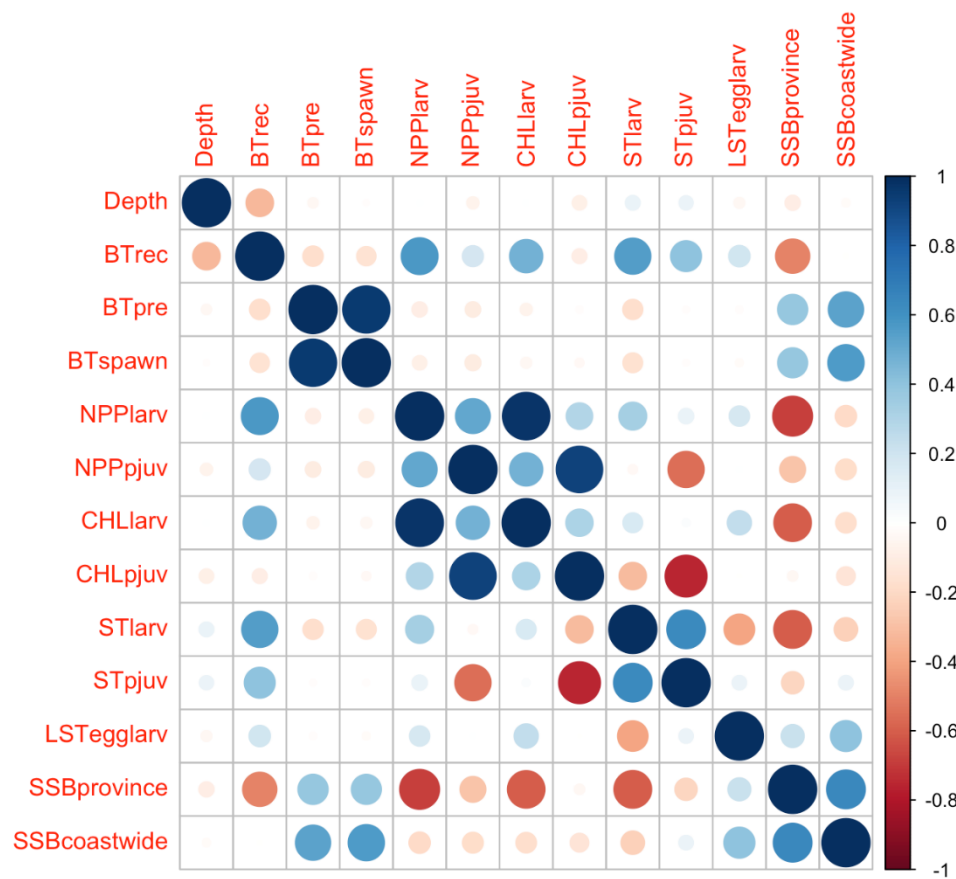


Figure 2. Correlations between predictors in the positive catch model.

Appendix D. Gamma distribution for positive catch model

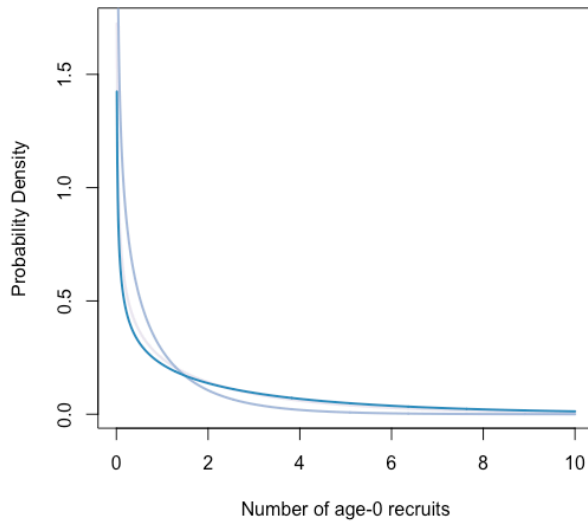


Figure 1. Gamma distribution parameterized using the maximum likelihood estimate of the ϕ term and with the three shades of blue showing the PDF for three values of the linear predictor μ , based on the 25th, 50th, and 75th percentiles of the predicted values.

Appendix E. Random effects selection for encounter probability and positive catch models

Table 1. AIC and cAIC scores for the candidate random effects structures for the encounter probability model.

Model	AIC	cAIC
Model 1: Spatial ON + Spatiotemporal iid (anisotropic)	1610.11817	1527.3854
Model 2: Spatial ON + Spatiotemporal AR1 (anisotropic)	1610.52753	1530.35284
Model 9: Spatial ON + Spatiotemporal iid (isotropic)	1633.82376	1535.14924
Model 3: Spatial ON + Spatiotemporal AR1 (isotropic)	1633.91225	1538.11142
Model 5: Spatial OFF + Spatiotemporal AR1 (anisotropic)	1644.28979	1576.42229
Model 6: Spatial OFF + Spatiotemporal iid (anisotropic)	1654.21729	1583.37069

Model 4: Spatial OFF + Spatiotemporal AR1 (isotropic)	1654.46838	1584.85321
Model 7: Spatial OFF + Spatiotemporal iid (isotropic)	1658.70349	1585.78249
Model 10: Spatial ON + Spatiotemporal OFF (anisotropic)	1816.68732	1774.18095
Model 8: Spatial ON + Spatiotemporal OFF (isotropic)	1840.8685	1795.82726
Model 11: Spatial OFF + Spatiotemporal OFF	2003.15083	NA

Table 2. AIC and cAIC scores for the candidate random effects structures for the positive catch model.

Model	AIC	cAIC
Model 7: Spatial OFF + Spatiotemporal iid (isotropic)	3373.02081	3220.06583
Model 4: Spatial OFF + Spatiotemporal AR1 (isotropic)	3374.71743	3221.67245
Model 3: Spatial ON + Spatiotemporal AR1 (isotropic)	3378.29445	3223.90706
Model 9: Spatial ON + Spatiotemporal iid (isotropic)	3377.02081	3224.06583
Model 6: Spatial OFF + Spatiotemporal iid (anisotropic)	3374.91522	3224.52421
Model 5: Spatial OFF + Spatiotemporal AR1 (anisotropic)	3376.47537	3226.3971
Model 1: Spatial ON + Spatiotemporal iid (anisotropic)	3378.91522	3228.52421
Model 2: Spatial ON + Spatiotemporal AR1 (anisotropic)	3380.47373	3230.38383
Model 8: Spatial ON + Spatiotemporal OFF (isotropic)	3483.67305	3431.81885
Model 10: Spatial ON + Spatiotemporal OFF (anisotropic)	3487.41576	3435.43634
Model 11: Spatial OFF + Spatiotemporal OFF	3570.21921	NA

Appendix F. Female spawner estimated distribution

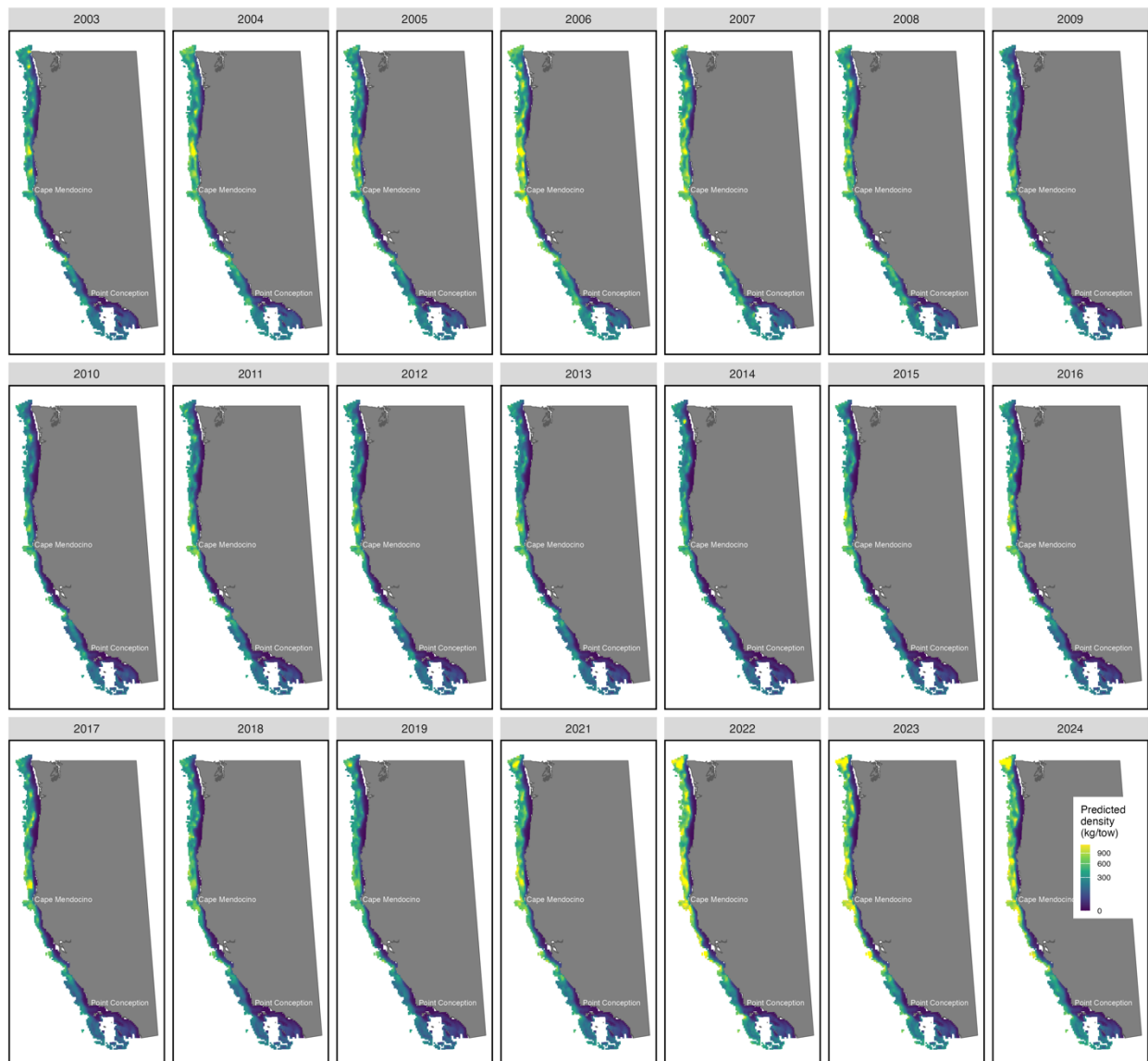


Figure 1. Combined encounter probability and positive catch predictions for female spawner biomass.

Appendix G. Spatial and spatiotemporal random fields for the encounter probability model

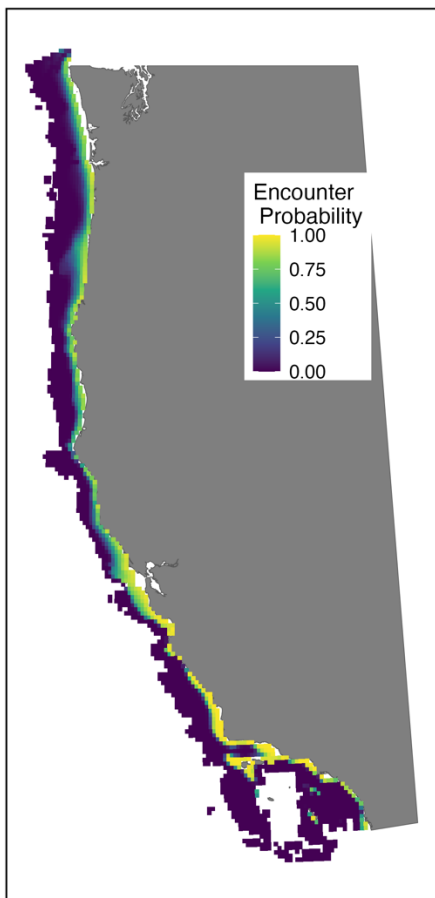


Figure 1. Estimated encounter probability of age-0 Sablefish recruits in pass 2, without spatiotemporal random effects, but including the spatial random field and the effect of depth. This therefore depicts the mean expected encounter probability across all years.

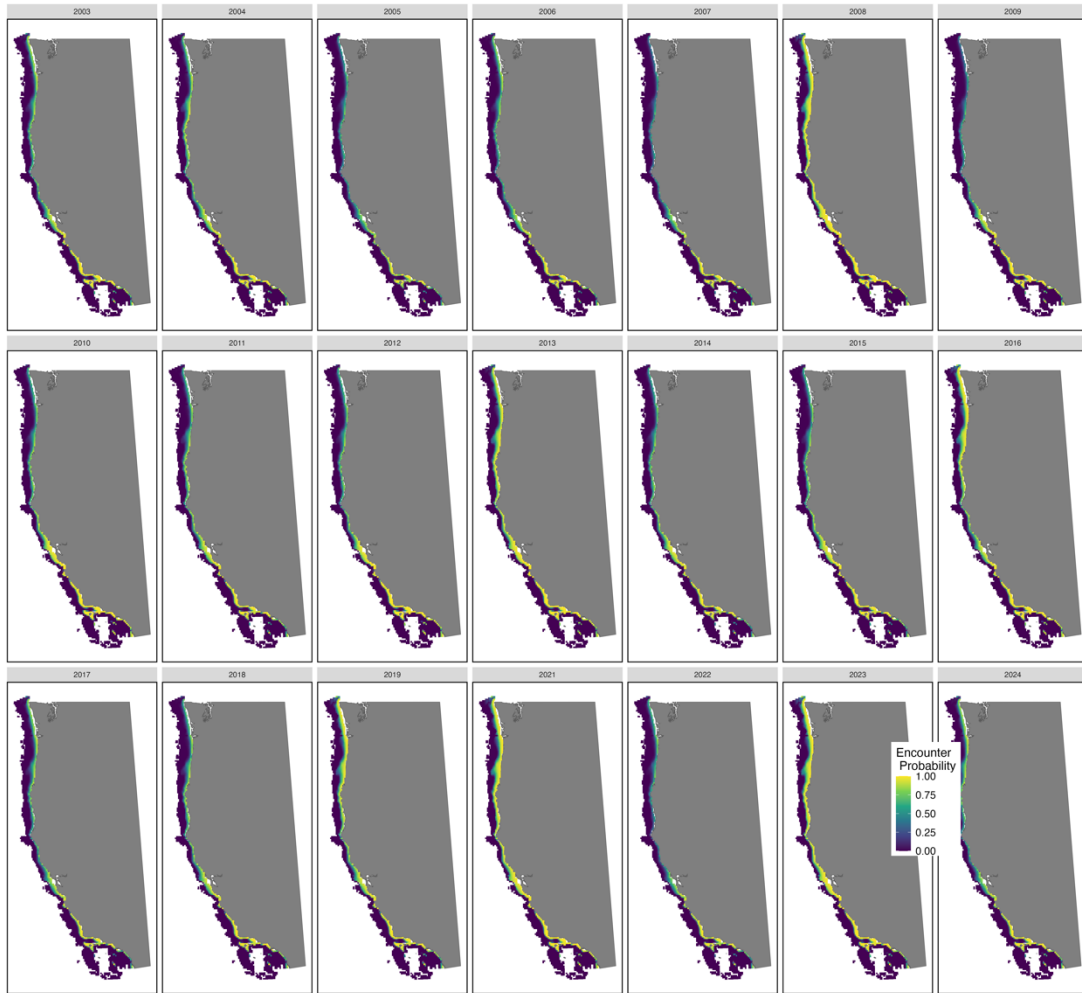


Figure 2. Estimated encounter probability of age-0 Sablefish recruits in pass 2 by year (including spatial and spatiotemporal random effects and the effect of depth).