IMPACT OF INCREASED BIGG'S KILLER WHALE (*ORCINUS ORCA RECTIPINNUS*) PRESENCE ON HARBOR SEAL (*PHOCA VITULINA*) HAUL-OUT USAGE

By

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ABSTRACT

Predators can influence prey not only through direct consumption but also through the behavioral responses they induce. In the Salish Sea, harbor seals (*Phoca vitulina*) are a primary prey of Bigg's killer whales (*Orcinus orca rectipinnus*), whose regional presence in inland waters has increased in recent decades. I evaluated whether killer whale presence was associated with changes in harbor seal haul-out usage across inland Washington management stocks using long-term monitoring data from 1990–2022. Haul-out usage exhibited substantial spatial and temporal variation, with modest increases through time but strong and persistent differences among haul-out sites. Across inland waters, killer whale presence was consistently associated with reduced haul-out counts, although the magnitude of these effects varied regionally. Rather than producing broad-scale redistribution away from predators, predator presence was associated with localized and heterogeneous changes in haul-out usage among sites. Haul-out counts also varied with in-water distance to salmon-bearing waterways, although predator presence did not produce consistent directional shifts toward or away from salmon-associated areas. Short-term responses to predator presence were highly variable and not statistically supported. Overall, results suggest that predator presence increased spatial variability in harbor seal haul-out behavior through localized and context-dependent responses rather than coordinated displacement across the landscape.

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TABLE OF CONTENTS

ABSTRACT……………………………………………………………………………...iv

ACKNOWLEDGEMENTS……………………………………………………………..v

LIST OF FIGURES……………………………………………………………………..ix

LIST OF TABLES……………………………………………………………………....xi

LIST OF SUPPLEMENTARY FIGURES AND TABLES……………………………….xii

GENERAL BACKGROUND…………………………………………………………...1

Study Area: Current, Historical, and Cultural Use………………………………………..1

Climate and Oceanographic Change in the Salish Sea……………………………………4

Species of Interest…………………………………………………………………………7

Harbor Seals……………………………………………………………………………….7

Bigg's Killer Whales………………………………………………………………………9

Pacific Salmon……………………………………………………………………...12

Harbor Seal Haul-Out Behavior…………………………………………………………16

Predator-Prey Theory and Non-Consumptive Effects…………………………………...19

Human Disturbance and Habitat Modification…………………………………………..22

Salmon Recovery and Predator Interactions……………………………………………..25

Relevance……………………………………………………………………………...27

INTRODUCTION……………………………………………………………………...31

METHODS……………………………………………………………………………...37

Study Site………………………………………………………………………………...38

First Stage: Determining Harbor Seal Haul-Out Usage Across Washington State Waters……………………………………………………………………………39

Second Stage: Identifying Factors Associated with Haul-Out Usage…………………...42

Bigg's Killer Whale Presence…………………………………………………42

Pacific Salmon Runs…………………………………………………………..45

Confounding Variables………………………………………………………..47

Third Stage: Evaluating Spatial and Temporal Dynamics in Haul-Out Usage…………49

Distributional Assessment…………………………………………………….50

Stock-Level Temporal Trends………………………………………………...52

Hierarchical Modeling of Site-Level Variation……………………………….53

Environmental Covariates and Predator Presence……………………………55

Model Diagnostics………………………………………………………………….58

Short-Term Responses to Predator Presence…………………………………………59

Predator Temporal Dynamics………………………………………………………60

Spatial Patterns in Haul-Out Usage…………………………………………………...61

RESULTS…..……………………………………………………………………...65

Stock-Level Temporal Trends in Haul-Out Usage……………………………………65

Regional Patterns in Mean Haul-Out Counts……………...……………………………..67

Site-Level Temporal Trends from Hierarchical Mixed-Effects Models…………………69

Predator Occurrence and Haul-Out Usage……………………………………………71

Temporal Dynamics of Predator Effects……………………………………75

Regional Variation in Predator Effects………………………………………..76

Habitat Context of Predator Effects…………………………………………...79

Environmental and Prey Covariates Associated with Haul-Out Usage………………….81

Habitat Composition……………………………………………………………81

Spatial Position..……………………………………………………………...82

Salmon Distance and Predator Interaction………………………………………86

Combined Effects of Predators, Habitat and Prey Accessibility………………...88

Short-Term Responses to Predator Presence……………………………………………89

Spatial Redistribution in Haul-Out Use…………………………………………………91

DISCUSSION…………………………………………………………………………...96

Regional Trends in Haul-Out Usage……………………………………………………..97

Site-Level Heterogeneity………………………………………………………………...99

Predator Presence……………………..………………………………………………...102

Spatial Redistribution in Haul-Out Use………………………………………………...105

Salmon Accessibility…………………………………………………………………...107

Habitat Characteristics…………………………………………………………………111

Implications for Predator-Prey Dynamics……………………………………………...114

Study Limitations and Future Directions………………………………………………117

Conclusion……………………………………………………………………………...121

REFERENCES……………………………………………………………………….....124

APPENDIX……………………………………………………………………………..133

LIST OF FIGURES

Figure 1. Distribution of harbor seal (*Phoca vitulina*) haul-out sites included in predator analyses across inland Washington State management stocks from 1990–2022. Points represent haul-out locations retained following exclusion of Outer Coast and western Northern Inland edge-effect sites.

Figure 2. Mean annual harbor seal (*Phoca vitulina*) haul-out counts per site across Washington State from 1990 to 2022 with annual survey coverage. Points in the upper panel show yearly mean site-level haul-out counts, with point size proportional to the number of haul-out sites surveyed each year. The solid line represents a LOESS-smoothed temporal trend with 95% confidence intervals (shaded). The lower panel shows the number of haul-out sites surveyed annually.

Figure 3. Site-level harbor seal (*Phoca vitulina*) haul-out counts across inland Washington State stocks from 1990–2022. Gray lines represent individual haul-out site trajectories, and blue lines represent LOESS-smoothed stock-level temporal trends. Y-axes are scaled independently among stocks to improve visualization of within-stock temporal variation.

Figure 4. Harbor seal (*Phoca vitulina*) haul-out sites retained for predator analyses and Bigg's killer whale (*Orcinus orca rectipinnus*) sightings across inland Washington waters and adjacent transboundary marine areas, 1990–2022. Harbor seal haul-out sites are shown in black, and Bigg's killer whale sightings are shown in blue. Outer Coast haul-out sites and western Northern Inland edge sites excluded from the final inland predator analysis are not shown. Canadian killer whale sightings are included because all sightings within 50 km of retained haul-out sites were used to define predator exposure.

Figure 5. Distribution of minimum in-water distances between inland harbor seal (*Phoca vitulina*) haul-out sites and Bigg's killer whale (*Orcinus orca rectipinnus*) sightings from 1990–2022. Dashed line indicates the 50-km threshold used to define predator presence.

Figure 6. Predicted harbor seal (*Phoca vitulina*) haul-out counts under predator absence (>50 km) and presence (≤50 km) across inland Washington State management stocks from 1990–2022. Lines represent predicted values from the hierarchical negative binomial mixed-effects model, and shaded areas indicate 95% confidence intervals.

Figure 7. Estimated percent change in mean harbor seal (*Phoca vitulina*) haul-out counts under different temporal formulations of Bigg's killer whale (*Orcinus orca rectipinnus*) exposure. Error bars represent 95% confidence intervals.

Figure 8. Percent change in predicted harbor seal (*Phoca vitulina*) haul-out counts associated with Bigg's killer whale (*Orcinus orca rectipinnus*) presence (≤50 km) across inland Washington State management stocks from 1990–2022. Points represent estimated percent change and horizontal error bars indicate 95% confidence intervals. Hood Canal exhibited the strongest reduction in haul-out counts, Northern Inland showed a more moderate reduction, and Southern Puget Sound showed no statistically significant predator-associated effect.

Figure 9. Distance from each harbor seal (*Phoca vitulina*) haul-out site to the mainland shoreline. Distances were calculated as minimum water-constrained paths and may differ from straight-line proximity due to complex coastline geometry. Most haul-out sites occurred within a few kilometers of the mainland shoreline, with larger distances primarily associated with island-associated haul-out sites.

Figure 10. Percent change in predicted harbor seal (*Phoca vitulina*) haul-out counts associated with Bigg's killer whale (*Orcinus orca rectipinnus*) presence (≤50 km) across nearshore and offshore haul-out sites. Points represent estimated percent change and horizontal error bars indicate 95% confidence intervals. Predator-associated reductions in haul-out usage were similar across site positions, indicating no evidence that predator responses differed consistently between offshore and nearshore haul-out sites.

Figure 11. Predicted harbor seal (*Phoca vitulina*) haul-out counts as a function of distance to the nearest river mouth. Predicted counts tended to decline with increasing distance from riverine inputs, although uncertainty surrounding this relationship was high. Shaded regions represent 95% confidence intervals.

Figure 12. Predicted harbor seal (*Phoca vitulina*) haul-out counts as a function of in-water distance to salmon-bearing waterways under predator-absent (>50 km) and predator-present (≤50 km) conditions. Shaded ribbons represent 95% confidence intervals. Relationships between salmon proximity and haul-out usage were weak and highly uncertain across predator conditions.

Figure 13. Proportion of pairwise site-level changes in harbor seal (*Phoca vitulina*) haul-out counts across Hood Canal that occurred in the same versus opposite directions. Raw changes more frequently occurred in the same direction, reflecting shared temporal trends across sites. After centering changes within year to account for stock-wide temporal variation, opposite-direction changes became more common, indicating localized redistribution among haul-out sites.

Figure 14. Pairwise comparison of centered year-to-year changes in harbor seal (*Phoca vitulina*) haul-out counts across Hood Canal sites. Each point represents a pair of sites within the same year. The weak negative relationship indicates localized compensatory changes consistent with limited redistribution among haul-out sites.

LIST OF TABLES

Table 1. Stock-level negative binomial GLM estimates of annual trends in harbor seal (*Phoca vitulina*) haul-out counts (1990–2022) in Washington State. Percent change calculated as ($e^{\beta} - 1$) × 100.

Table 2. Fixed-effect estimates from the hierarchical negative binomial model relating haul-out counts to killer whale (*Orcinus orca rectipinnus*) presence (≤50-km) across inland Washington State management stocks (Outer Coast excluded). Coefficients are on the log scale.

Table 3. Fixed-effect estimates from the negative binomial mixed-effects model evaluating shoreline type associated with harbor seal (*Phoca vitulina*) haul-out counts across inland Washington State. Rocky shoreline was used as the reference category.

Table 4. Progression of hierarchical negative binomial mixed-effects models evaluating associations between predator presence, prey accessibility, and environmental covariates and harbor seal (*Phoca vitulina*) haul-out counts across inland Washington State waters. Values represent fixed-effect coefficients (β ± SE) on the log scale.

Table 5. Summary of pairwise directional patterns in year-to-year changes in harbor seal (*Phoca vitulina*) haul-out counts across Hood Canal sites before and after centering within year.

LIST OF SUPPLEMENTARY FIGURES AND TABLES

Table S1. Poisson GLM diagnostics showing overdispersion in harbor seal (*Phoca vitulina*) haul-out count data in Washington State (1990-2022).

Table S2. Fixed-effect estimates from the hierarchical negative binomial model of harbor seal (*Phoca vitulina*) haul-out counts across Washington State. Percent change is shown for the year effect.

Table S3. Full fixed-effect estimates from hierarchical negative binomial mixed-effects models used in the model progression analysis evaluating predator, prey, and environmental influences on harbor seal (*Phoca vitulina*) haul-out counts across inland Washington State waters. Model 1 included predator presence only, Model 2 added prey accessibility, and Model 3 incorporated environmental covariates. Values are presented on the log scale.

Table S4. Comparison of temporal predator exposure metrics used to evaluate associations between Bigg's killer whale (*Orcinus orca rectipinnus*) occurrence and harbor seal (*Phoca vitulina*) haul-out counts across inland Washington State. Lower AIC values indicate better model support; ΔAIC values represent differences relative to the best-supported model.

Table S5. Comparison of final negative binomial mixed-effects models evaluating predator occurrence, environmental covariates, and salmon accessibility associated with harbor seal (*Phoca vitulina*) haul-out counts across inland Washington State.

Table S6. Fixed-effect estimates from the inland-only negative binomial mixed-effects model evaluating associations between predator occurrence, environmental covariates, and in-water distance to salmon-bearing waterways on harbor seal (*Phoca vitulina*) haul-out counts. Outer Coast sites were excluded due to limited killer whale sighting coverage. Values are shown on the log scale.

Table S7. Comparison of negative binomial mixed-effects models evaluating associations between predator occurrence, salmon accessibility, and harbor seal (*Phoca vitulina*) haul-out counts across inland Washington State.

Figure S1. Diagnostic plots of DHARMa residuals for the final inland negative binomial mixed-effects model of harbor seal (*Phoca vitulina*) haul-out counts. The QQ plot (left) indicated significant deviation from the expected uniform distribution (Kolmogorov–Smirnov test, $p < 0.001$), although no evidence of overdispersion was detected (dispersion test, $p = 0.074$). The residuals versus predicted plot (right) showed slight structure across fitted values, and the outlier test was significant ($p < 0.001$), suggesting minor residual deviation likely associated with unmodeled site-level heterogeneity. Overall, diagnostics indicated acceptable model performance for ecological inference despite some deviation from ideal residual behavior.

Figure S2. Predator exposure at inland harbor seal (*Phoca vitulina*) haul-out sites exhibiting divergent temporal trajectories relative to the population-level trend after exclusion of potential edge-effect sites. Points show the proportion of years in which Bigg's killer whales (*Orcinus* *orca rectipinnus*) were observed within 50 km of each haul-out site. Divergent site-level trajectories occurred across a broad range of predator exposure values, indicating that localized temporal variation in haul-out usage was not consistently structured by predator exposure alone.

Figure S3. Percent change in predicted harbor seal (*Phoca vitulina*) haul-out counts associated with Bigg's killer whale (*Orcinus orca rectipinnus*) presence (≤50 km) across nearshore and offshore haul-out sites. Points represent estimated percent change and horizontal error bars indicate 95% confidence intervals. Predator-associated reductions in haul-out usage were similar across site positions, with no significant interaction between predator presence and site position.

Figure S4. Mean harbor seal (*Phoca vitulina*) haul-out counts within 7 days before and after independent Bigg's killer whale (*Orcinus orca rectipinnus*) sighting events within 50 km. Points represent paired site-event means, with gray lines connecting before and after observations. The blue line shows the overall mean response.

GENERAL BACKGROUND

Study Area: Current, Historical, and Cultural Use

The Salish Sea comprises the inland marine waters of Washington State, USA and the Province of British Columbia, Canada, including Puget Sound, the Strait of Juan de Fuca, and the Strait of Georgia. Its physical structure is shaped by the interaction of Pacific Ocean waters with river systems draining the western slopes of the Cascade Range and coastal British Columbia (Thomson 1994, Babson et al. 2006). These interactions generate strong gradients in salinity and temperature that drive mixing and contribute to the estuarine character of the system (Moore et al. 2008, Khangaonkar et al. 2019). These physical conditions structure diverse communities of plankton, forage fishes, seabirds, and marine mammals (Sobocinski 2021). The Strait of Juan de Fuca is the primary connection between the outer coast and inland basins, transporting water, nutrients, and organisms and forming a dynamic transition zone where oceanographic processes influence seasonal and long-term patterns in species distribution. Although this thesis is centered on inland Salish Sea ecosystems, some analyses are aligned with Washington State harbor seal management stocks, which include inland Salish Sea units and the adjacent outer coast.

At the western entrance of the Strait of Juan de Fuca, inland estuarine outflow interacts with coastal ocean processes from the northern California Current System. Along the outer coast, seasonal upwelling during spring and summer brings nutrient-rich deep water onto the continental shelf, supporting high phytoplankton productivity and coastal food webs. As this nutrient-rich water interacts with estuarine outflow at the entrance to the Strait of Juan de Fuca, it contributes to the formation of the Juan de Fuca eddy, a semi-persistent feature that retains nutrients and promotes elevated primary production (Raphael et al. 2015, Sobocinski 2021). During summer, the eddy supports dense concentrations of plankton, krill, and forage fish, creating predictable foraging habitat for marine birds, pinnipeds, and salmonids. Seasonal peaks in Pacific herring (*Clupea pallasii*), salmonids, and pinniped abundance in this transition zone highlight the role of coastal oceanography in shaping predator distributions near the boundary between the outer coast and inland Salish Sea waters (Chasco et al. 2017).

The coastline and inland waters of the Salish Sea have supported Indigenous communities for many generations. Coast Salish Nations and the Makah Tribe at the western entrance of the Strait of Juan de Fuca have long relied on salmon, shellfish, kelp, seabirds, and marine mammals for subsistence, cultural practices, and community well-being (Sobocinski 2021). Species such as harbor seals (*Phoca vitulina*), Steller sea lions (*Eumetopias jubatus*), and salmonids remain important components of these ecosystems and have been utilized by Indigenous hunters and fishers for many generations (Gaydos and Pearson 2011, Quinn and Losee 2022). These harvesting traditions were guided by detailed ecological understanding and stewardship systems that emphasized balance, sustainability, and reciprocity, with archaeological and ecological evidence demonstrating long-term enhancement and persistence of marine resources under Indigenous management (Groesbeck et al. 2014, Lepofsky et al. 2015, Efford et al. 2023). Regional evaluations further show that these systems supported the long-term resilience of salmon populations and continue to shape present-day relationships with the Salish Sea (Atlas et al. 2020, Sobocinski 2021).

European colonization, commercial harvest, and large-scale environmental change significantly altered the ecological and cultural landscape of the region. Intensive commercial exploitation of marine mammals during the eighteenth and nineteenth centuries caused sharp declines in multiple pinniped species, and government-directed removal programs in the mid twentieth century further reduced harbor seal numbers in Washington (Jeffries et al. 2003). Steller sea lions and other marine mammals experienced similar declines throughout the North Pacific (Wade et al. 2007, Muto et al. 2021). Salmon populations declined due to overfishing, habitat alteration, and migration barriers (Gustafson et al. 1997, Quinn and Losee 2022), while shoreline armoring, dredging, and vessel traffic reshaped estuarine habitats (Simenstad et al. 2011, Moore et al. 2008). Following passage of the Marine Mammal Protection Act in 1972 and similar protections in Canada, pinniped populations recovered substantially. Harbor seals increased and stabilized at high abundance (Jeffries et al. 2003, Jefferson et al. 2021, Pearson et al. 2025), and Steller and California (*Zalophus californianus)* sea lions expanded in range and number (Wade et al. 2007, Muto et al. 2021, Allyn and Scordino 2020). These recoveries have contributed to restructuring of marine food webs and predator–prey interactions across the region.

Management of the Salish Sea today involves collaboration among federal and state agencies, scientific institutions, and sovereign tribal nations that co-manage fisheries and habitat stewardship. Tribal nations continue to exercise treaty-reserved rights and contribute leadership in conservation and management. Current strategies increasingly integrate traditional ecological knowledge with scientific research to promote sustainable harvest and ecological resilience (Sobocinski 2021). The continued ecological and cultural importance of the Salish Sea underscores the need to understand species interactions, environmental change, and the ecological roles of recovering marine predators (Gaydos and Pearson 2011, Sobocinski 2021).

Climate and Oceanographic Change in the Salish Sea

The Salish Sea is experiencing ongoing environmental change associated with climate variability, ocean warming, and broader shifts in the northeastern Pacific Ocean (Moore et al. 2008, Mantua et al. 2010). These changes are altering regional circulation, stratification, and nutrient dynamics, which influence the biological communities that support the base and middle levels of marine food webs (Thomson 1994, Khangaonkar et al. 2019). Variation in water temperature, freshwater inputs, and coastal ocean processes affects the availability and distribution of prey for many marine species within inland waters, including harbor seals, salmonids, and killer whales (*Orcinus orca*) (Duffy et al. 2005, Beamish et al. 2010, Quinn and Losee 2022). As these foundational physical conditions become more variable, ecological responses across trophic levels are also becoming increasingly dynamic (Moore et al. 2008, Khangaonkar et al. 2019). Although this study focuses on inland Salish Sea ecosystems, those inland basins remain strongly influenced by oceanographic forcing at the outer coast. Seasonal upwelling along the Washington outer coast delivers nutrients that ultimately enter the Strait of Juan de Fuca and shape productivity within inland waters (Thomson 1994, Khangaonkar et al. 2019). Variability in upwelling intensity, stratification, and freshwater inputs influences nutrient transport and primary production, which in turn affects zooplankton communities and forage fishes that support higher predators such as salmon, pinnipeds, and killer whales (Duffy et al. 2005, Quinn and Losee 2022). Climate-related shifts in coastal ocean conditions have increased variability in these nutrient pathways, contributing to fluctuations in biological productivity that influence the timing and availability of prey within the Salish Sea (Moore et al. 2008, Beamish et al. 2010). Periods of reduced productivity can limit energy transfer into inland ecosystems, affecting juvenile salmon growth and survival, altering foraging opportunities for harbor seals and sea lions, and influencing predator distributions that track prey aggregations (Duffy et al. 2005, Beamish et al. 2010, Gaydos and Pearson 2011). These bottom-up effects can propagate across trophic levels, reshaping when and where predators concentrate and altering use of nearshore habitats throughout inland waters (Raphael et al. 2015, Quinn and Losee 2022).

Marine heatwaves in the northeastern Pacific, including the pronounced warm anomaly from 2014 to 2016, further illustrate the connection between large-scale ocean conditions and ecological dynamics within the Salish Sea (Bond et al. 2015, Cavole et al. 2016). Elevated surface temperatures altered plankton community composition, reduced the availability of energy-rich zooplankton, and affected the distribution and survival of larval and juvenile fishes (Cavole et al. 2016, Peterson et al. 2017). These changes influenced species that depend on productive nearshore habitats during critical life stages, including Pacific salmon (*Oncorhynchus* spp., hereafter salmon), harbor seals, and other marine predators whose movements track prey availability (Gaydos and Pearson 2011, Quinn and Losee 2022). Declines in high-quality planktonic prey during marine heatwave conditions can reduce juvenile fish growth and survival, contributing to longer-term shifts in predator–prey interactions within inland Salish Sea waters (Beamish et al. 2010, Peterson et al. 2017). Climate change is also influencing the timing and spatial distribution of adult salmon returning to river systems. Altered freshwater flow regimes, warmer spawning streams, and shifts in snowmelt timing have increased interannual variability in salmon migration timing and residency within nearshore and estuarine habitats of the Salish Sea (Mantua et al. 2010, Quinn and Losee 2022). Changes in the timing and duration of salmon presence in coastal waters may influence when and where harbor seals encounter migrating salmon, potentially reshaping patterns of temporal and spatial overlap between predators and their prey (Nelson et al. 2019, Quinn and Losee 2022).

Environmental variability also affects predators. Bigg's killer whales (*O. o. rectipinnus*) respond to changes in the distribution and availability of marine mammal prey and tend to concentrate in areas where harbor seals, porpoises (*Phocoenidae*), or sea lions (*Otariidae*) are abundant (Ford et al. 1998, Houghton et al. 2015, Shields et al. 2018). The substantial increase in harbor seal abundance within inland waters over recent decades is thought to have contributed to increased occurrence and more frequent use of the Salish Sea by Bigg's killer whales (Ford et al. 1998, Houghton et al. 2015, Shields et al. 2018). Climate-driven variability in marine productivity and prey aggregation further influences how predictable prey are at river mouths, haul-out sites, and nearshore foraging areas, affecting spatial and temporal dynamics of predator–prey interactions within the Salish Sea (Moore et al. 2008, Beamish et al. 2010, Gaydos and Pearson 2011). As environmental conditions continue to evolve, interpreting long-term patterns in harbor seal haul-out usage and Bigg's killer whale occurrence requires explicit consideration of shifting productivity, prey availability, and habitat characteristics (Ford et al. 1998, Quinn and Losee 2022). Because these ecological responses unfold over decadal timescales, long-term datasets are essential for detecting meaningful trends in predator and prey behavior and for understanding the cumulative influence of climate variability and ecosystem change within inland Salish Sea ecosystems (Moore et al. 2008, Mantua et al. 2010)

Species of Interest

Harbor Seals

Harbor seals are the most abundant pinniped species in the Salish Sea and occupy a broad range of habitats throughout inland marine waters. They occur in sheltered bays, estuaries, rocky and sandy shorelines, tidal channels, river mouths, and nearshore coastal areas. This wide distribution reflects a flexible ecological strategy that allows harbor seals to use diverse haul-out substrates and exploit a broad range of prey species across their global range (Teilmann and Galatius 2018). Following the end of government-directed removal programs and other forms of harvest in the twentieth century, harbor seal populations recovered rapidly. In Washington's inland waters, abundance increased substantially from the 1970s through the early 2000s and later stabilized at levels thought to approximate regional carrying capacity (Jeffries et al. 2003). Recent assessments indicate that harbor seal stocks within Puget Sound, Hood Canal, the Strait of Juan de Fuca, and the San Juan Archipelago remain stable and occur at relatively high abundance across major inland basins (Pearson et al. 2025). Comparable patterns of high abundance and stable populations have also been documented for Pacific harbor seals in Canadian portions of the Salish Sea (Tucker et al. 2025).

Across their geographic range, harbor seals exhibit moderate fidelity to specific haul-out sites, repeatedly returning to locations that provide suitable substrate, proximity to foraging areas, and protection from wave exposure (Cunningham et al. 2009, Brusa et al. 2025). Within the Salish Sea, seals use a wide variety of natural and anthropogenic structures for hauling out, including rocky reefs, sandbars, mudflats, tidal ledges, floating logs, small nearshore islands, breakwaters, and navigational buoys (Allen et al. 1984, London et al. 2012). Haul-out usage varies seasonally in response to biological and environmental drivers (Jeffries et al. 2003, Cunningham et al. 2009). Use generally increases during the pupping season in late spring and early summer, when females give birth and nurse dependent pups, and again during the annual molt in midsummer (Huber et al. 2001, Jefferson et al. 2015). At finer temporal scales, haul-out behavior is influenced by tide height, time of day, air temperature, wind exposure, precipitation, and disturbance from humans or predators (Allen et al. 1984, London et al. 2012). Together, these factors shape spatial and temporal variation in haul-out use throughout inland Washington waters.

Harbor seals are generalist predators that adjust diet composition in response to prey availability, habitat, and season. Diet studies from the San Juan Islands indicate that clupeids, gadids, flatfishes, cephalopods, dogfish, and several salmon species contribute substantially to seal diets, with proportions varying across space and time (Lance et al. 2012). Salmon can become an important seasonal component, particularly during migration periods. Harbor seals frequently aggregate near river mouths and other migration bottlenecks where adult salmon stage prior to freshwater entry and where out-migrating juveniles transition into marine habitat (Springer et al. 2003, Heithaus et al. 2008). These seasonal concentrations are consistent with increased predation on salmon during migration periods, reflecting the importance of salmonids as a seasonal prey resource (Lance et al. 2012, Nelson et al. 2024). Demographic differences in diet have also been documented, with male harbor seals consuming adult salmon more frequently than females, likely reflecting differences in energetic demands, foraging strategy, and habitat use (Schwarz et al. 2018, Conwell et al. 2024).

Harbor seals occupy a central position within the Salish Sea food web as both mesopredators and primary prey of Bigg's killer whales. Mammal-eating killer whales routinely target harbor seals in coastal and inland waters, and seals represent one of the most consistently consumed prey items in their diet (Ford et al. 1998). This dual role positions harbor seals as key mediators of energy flow within inland ecosystems. They influence fish populations through direct predation while simultaneously responding to predation risk from apex predators. Changes in killer whale abundance, distribution, or hunting behavior therefore have the potential to influence seal movements, haul-out patterns, and foraging activity. These responses may alter spatial and temporal overlap between seals and prey species of ecological, commercial, and cultural importance. Understanding harbor seal ecology within inland Salish Sea waters is therefore essential for evaluating food web dynamics, predator recovery, and the potential for risk-mediated, non-consumptive processes to shape habitat use and species interactions.

Bigg's Killer Whales

Bigg's killer whales, often referred to as the mammal-eating ecotype, are one of the primary apex predators in the northeastern Pacific Ocean. Unlike the fish-eating Southern Resident ecotype (*Orcinus orca ater*), Bigg's killer whales specialize on marine mammals and consume a wide range of prey including harbor seals, harbor porpoises (*Phocoena phocoena*), Dall's porpoises (*Phocoenoides dalli*), and several species of sea lions (Ford et al. 1998, Murray et al.

2025). Their geographic range extends from central California north through British Columbia and Alaska into the Bering Sea, and within this broader range they regularly use both coastal and inland marine habitats, including the Salish Sea. Bigg's killer whales therefore occupy a central role as apex predators in coastal and estuarine ecosystems of the northeastern Pacific.

Bigg's killer whales display substantial behavioral and social flexibility that supports their predation strategy. Individuals typically travel in small groups averaging two to six whales, although group size can fluctuate depending on prey availability, social dynamics, or movements between foraging areas (Baird and Dill 1996). Unlike the more stable matrilineal structure of fish-eating resident killer whales, Bigg's whales exhibit fluid associations that shift over time, allowing them to adjust group size and coordination to match hunting conditions (Baird and Dill 1996, Filatova et al. 2026). Smaller groups may enhance stealth when pursuing seals in confined inland passages, whereas larger temporary aggregations may form in areas with concentrated prey. Predation by Bigg's killer whales relies heavily on stealth and coordination. Whereas Southern Resident killer whales often vocalize and use echolocation during fish foraging, Bigg's whales frequently suppress vocal activity when hunting marine mammals, likely to avoid alerting prey (Ford et al. 1998). They may approach haul-out sites quietly, use shoreline features or kelp beds for concealment, and coordinate movements to intercept seals traveling between haul-outs and foraging grounds. Documented tactics include flanking movements, silent surface approaches, and rapid bursts of speed to prevent escape, demonstrating a high degree of behavioral plasticity that enables adaptation across varying environmental contexts.

Bigg's killer whales are present in the Salish Sea throughout the year, and their seasonal occurrence has increased over recent decades as the population has recovered across the northeastern Pacific (Houghton et al. 2015, Murray et al. 2025). Houghton et al. (2015) documented a substantial increase in sightings beginning in the late 1980s and continuing into the early twenty-first century. Peak occurrence within inland waters now tends to occur in late summer, particularly from August through September, and again in early spring (Shields et al. 2018). These seasonal peaks overlap with periods when harbor seal pups and recently weaned juveniles are abundant and potentially more vulnerable to predation. The magnitude of predation by Bigg's killer whales on harbor seals is considerable. Harbor seals represent a major component of the diet of mammal-eating killer whales in coastal British Columbia and adjacent waters (Ford et al. 1998), and energetic modeling suggests that large numbers of pinnipeds, including harbor seals, are consumed annually by the population (Ford et al. 2010). Given that harbor seal populations within inland Washington waters have stabilized at relatively high levels following decades of recovery (Jeffries et al. 2003, Jefferson et al. 2021, Pearson et al. 2025), the increasing and sustained use of the Salish Sea by Bigg's killer whales represents a substantial natural source of seal mortality within this system.

Recent increases in Bigg's killer whale presence in the Salish Sea likely reflect both ecological and prey-driven processes. The recovery and high abundance of harbor seals and other pinnipeds have likely increased the energetic profitability of inland waters for mammal-eating killer whales, whose population growth has been linked to expanding marine mammal prey resources across the northeastern Pacific (Houghton et al. 2015, Shields et al. 2018, Murray et al. 2025). At the same time, environmental variability may influence the spatial distribution and predictability of marine mammal prey within specific basins or nearshore habitats (Sobocinski 2021). Gaydos and Pearson (2011) emphasize that marine mammals, including harbor seals, play central roles in Salish Sea food webs by transferring energy across trophic levels, and as seal abundance increases, inland waters may have become increasingly attractive to apex predators whose movements track prey resources.

The growing presence of Bigg's killer whales has therefore intensified predation risk for harbor seals within inland Salish Sea ecosystems. Because harbor seals function both as predators of fish species, including salmon, and as prey for killer whales, shifts in killer whale occurrence have the potential to influence seal behavior, distribution, and habitat use. Behavioral responses to predation risk may alter where and when seals haul out or forage, with implications for spatial overlap between seals and their prey. Understanding how harbor seals respond to increasing killer whale presence is therefore central to interpreting changes in predator–prey dynamics and broader ecosystem structure within the Salish Sea.

Pacific Salmon

Pacific salmon are foundational components of inland Salish Sea ecosystems, with Chinook salmon (*Oncorhynchus tshawytscha*) holding particular ecological and cultural importance. In this study, Pacific salmon refers to anadromous species of the genus *Oncorhynchus*, including Chinook, coho (*O. kisutch*), chum (*O. keta*), pink (*O. gorbuscha*), and sockeye salmon (*O. nerka*). Although other anadromous *Oncorhynchus*, such as steelhead trout (*O. mykiss*) and coastal cutthroat trout (*O. clarkii clarkii*), also migrate between freshwater and marine environments, they are not included here because, unlike Pacific salmon, they are iteroparous and may spawn multiple times. Here, the term Pacific salmon is used specifically for these semelparous salmon species, whereas salmonids refers more broadly to members of the family Salmonidae, including salmon, trout, and char (*Salvelinus* spp.). Unless otherwise specified, this section focuses primarily on Chinook salmon because of their central role in Salish Sea food webs and their importance to Indigenous cultures, fisheries, and marine predators throughout the region (Gaydos and Pearson 2011, Quinn and Losee 2022). Chinook salmon support marine food webs as prey for numerous predators and remain deeply connected to the cultural practices and fisheries economies of Indigenous nations and coastal communities surrounding the Salish Sea (Gaydos and Pearson 2011, Atlas et al. 2020). Multiple Chinook populations originate from rivers draining into Puget Sound, the Strait of Juan de Fuca, and larger river systems along the outer Washington coast. These populations differ in run timing, juvenile rearing strategies, and marine residency patterns, producing diverse life-history strategies that historically contributed to resilience and strong salmon returns (Quinn and Losee 2022).

Juvenile Chinook enter estuarine and nearshore marine habitats shortly after leaving freshwater systems, and this early marine period is widely recognized as a critical life stage that strongly influences recruitment success (Duffy et al. 2005, Beamish et al. 2010). Conditions within shallow coastal and estuarine zones affect growth, survival, and vulnerability to predation, and many pressures acting on juveniles reflect broader ecosystem processes such as seasonal productivity cycles, prey availability, and predator presence (Duffy et al. 2005, Moore et al. 2008). Juvenile Chinook primarily consume zooplankton and small forage fishes, and survival during this stage depends on rapid growth under favorable environmental conditions (Beamish et al. 2010). As Chinook move into deeper marine waters, they become embedded within complex food webs shaped by both bottom-up and top-down processes. The northeastern Pacific has undergone significant ecological restructuring over the past century due to historical marine mammal depletion and large-scale oceanographic shifts (Springer et al. 2003). These changes altered predator communities and energy pathways, reshaping ecological pressures on salmon populations. Ecosystem modeling studies demonstrate that variation in predation, primary productivity, and fishing mortality can interact to influence salmon abundance and survival across life stages (Whipple et al. 2000). Because Chinook spend several years at sea before returning to spawn, they are influenced by broad-scale environmental and ecological conditions across much of their marine range (Quinn and Losee 2022).

Adult Chinook return to natal rivers by migrating through the Strait of Juan de Fuca and into Puget Sound, creating predictable seasonal aggregations in nearshore and estuarine habitats. These returning adults frequently pass through constricted channels and river mouths where predators such as harbor seals, Steller sea lions, and California sea lions concentrate their foraging activity (Gaydos and Pearson 2011). Diet studies from Puget Sound indicate that harbor seals frequently consume salmon during migration periods when prey availability is high near estuaries and river mouths (Lance et al. 2012). Although salmon consumption by seals is seasonal, the large size of the harbor seal population means that moderate per-capita consumption can translate into substantial total biomass removed from the ecosystem (Chasco et al. 2017, Tucker et al. 2026). Declines in Chinook salmon across many parts of the Salish Sea reflect the cumulative influence of habitat degradation, altered freshwater flow regimes, changing ocean conditions, and predation (Gustafson et al. 1997, Quinn and Losee 2022). These pressures operate across spatial and temporal scales, with habitat loss affecting freshwater stages, reduced marine productivity limiting early ocean survival, and predation shaped by spatial and temporal overlap with marine predators (Moore et al. 2008, Mantua et al. 2010). Harbor seals frequently aggregate at river mouths during migration periods, increasing encounter rates with returning adults (Freeman et al. 2022), while long-term fluctuations in marine mammal populations have altered the predator landscape experienced by salmon across the northeastern Pacific (Springer et al. 2003).

Predator–prey interactions within this system extend beyond direct consumption. Non-consumptive processes, including predator avoidance and behavioral responses to risk, can alter prey distribution, movement, and habitat use, with consequences for survival (Wirsing and Ripple 2010, Wirsing et al. 2021). If harbor seals adjust foraging behavior or spatial distribution in response to Bigg's killer whale presence, these shifts could modify when and where seals encounter salmon. Depending on the direction of seal redistribution, spatial overlap with vulnerable juvenile or returning adult salmon could increase or decrease. Because salmon often migrate through predictable corridors, even modest changes in predator distribution may have disproportionate effects on survival (Wirsing et al. 2021). Overall, Chinook salmon are shaped by interacting with environmental conditions, ecological processes, and predator influences operating across freshwater and marine life stages. As inland Salish Sea ecosystems continue to experience environmental change, understanding how predators such as harbor seals and Bigg's killer whales respond to shifting ecological conditions is critical (Houghton et al. 2015, Shields et al. 2018). Predator behavior influences not only the magnitude of predation on salmon but also the spatial structure of coastal food webs, and continued declines in Chinook salmon underscore the need to integrate predator dynamics, environmental variability, and ecosystem processes to better interpret long-term trends and inform effective management strategies (Quinn and Losee 2022).

Harbor Seal Haul-Out Behavior

Harbor seal haul-out behavior is a central component of their ecology, supporting thermoregulation, reproduction, social interaction, predator vigilance, and efficient access to foraging areas. Haul-out use varies over short temporal scales and is influenced by tide height, weather conditions, and disturbance, as well as broader ecological drivers such as prey distribution and predation pressure (Allen et al. 1984, Cunningham et al. 2009, London et al. 2012). Within inland Salish Sea waters, harbor seals use a wide range of haul-out substrates, including rocky outcrops, mudflats, beaches, tidal channels, kelp beds, floating logs, navigation buoys, and other anthropogenic structures. Haul-out behavior follows predictable seasonal patterns linked to life-history stages. In late spring and early summer, females give birth and select haul-out sites that provide shelter from wave exposure, sufficient elevation to remain accessible across much of the tidal cycle, and proximity to shallow waters suitable for pups learning to swim and forage. Because newborn pups nurse frequently and rest for extended periods, reliable haul-out access is especially important during this period (Cunningham et al. 2009). Following pupping, adults enter the annual molt, typically in late summer and early autumn, during which seals haul out more frequently to facilitate hair replacement, resulting in elevated counts across the population.

Environmental conditions strongly influence when and how seals use haul-out sites. Tidal height is among the most consistent drivers, as seals generally haul out during lower tides when substrate is exposed. Weather variables including wind, precipitation, and air temperature influence the duration and frequency of haul-out events (Allen et al. 1984, London et al. 2012). High winds and heavy rain often reduce haul-out use, whereas calm and mild conditions promote it. Sites that are sheltered from waves receive direct sunlight, and experience limited human disturbance tend to be used more consistently. Spatial variation in haul-out use also reflects site-specific habitat characteristics. Brusa et al. (2025) demonstrated that harbor seal densities within the Salish Sea are associated with water depth, distance to shore, shoreline substrate, exposure, and proximity to river mouths. These physical features influence suitability for resting, thermoregulation, predator avoidance, and tidal accessibility. Sites located near salmon-bearing rivers may experience increased use during migration periods when prey availability is high. In the San Juan Islands, Lance et al. (2012) documented seasonal shifts in diet composition, with increased occurrence of adult salmon during late summer and autumn, highlighting the tight coupling between prey availability and fine-scale seal distribution.

Although harbor seals exhibit moderate fidelity to particular haul-out sites, individuals move among multiple sites within their home ranges across daily, weekly, and seasonal timescales (Hardee 2008, Peterson et al. 2012). Telemetry studies indicate that seals can travel considerable distances and display fine-scale variability in diving and foraging behavior within inland waters (Wilson et al. 2014). This spatial flexibility suggests that haul-out use is responsive to changing ecological conditions, including shifts in prey distribution, disturbance, and predation risk, and underscores the importance of evaluating haul-out patterns within a broader ecological context rather than interpreting site use as static. Predation risk from Bigg's killer whales may also influence haul-out behavior, although long-term quantitative assessments remain limited. Observational records indicate that seals may abandon haul-outs or shift toward shallower or more structurally complex sites when killer whales are present (Houghton et al. 2015). Experimental evidence further demonstrates that harbor seals respond behaviorally to killer whale vocalizations, indicating sensitivity to predation risk even in the absence of direct encounters (Deecke et al. 2005). Because Bigg's killer whales frequently patrol nearshore waters and areas between haul-outs and feeding grounds, seals may alter the timing, duration, or frequency of haul-out events to reduce exposure. These behavioral adjustments reflect trade-offs between resting, energy conservation, and risk avoidance.

Harbor seal haul-out behavior therefore reflects the integration of environmental conditions, life-history requirements, prey distribution, and predation risk. Because haul-out sites function as both resting refuges and spatial anchors within broader movement networks, shifts in haul-out use may signal underlying changes in ecological pressures. In a system where both prey availability and apex predator presence have changed over recent decades, interpreting variation in haul-out patterns requires a framework that accounts not only for direct predation, but also for behavioral responses to risk. Predator–prey interactions are traditionally evaluated through consumptive effects, in which predators influence prey populations through direct mortality, but a growing body of ecological theory emphasizes that predators can also shape prey populations through non-consumptive pathways. The mere presence of a predator may alter prey behavior, movement, habitat selection, and energy allocation, with consequences that cascade through food webs. In marine systems where direct predation events are difficult to observe, behavioral responses to risk may provide some of the clearest signals of predator influence. Within the Salish Sea, the recovery of harbor seals and the increasing presence of Bigg's killer whales create conditions in which both consumptive and non-consumptive processes are likely operating simultaneously. Harbor seals must balance the energetic benefits of accessing prey-rich habitats with the potential costs of increased exposure to predators. If predation risk influences how seals distribute across haul-out sites, these behavioral shifts may alter spatial overlap with salmon and reshape predator–prey interactions at multiple trophic levels.

The following section outlines the theoretical foundation for understanding predator-driven behavioral responses and introduces the concept of non-consumptive effects as a framework for evaluating long-term patterns in harbor seal haul-out usage.

Predator-Prey Theory and Non-Consumptive Effects

Predator–prey interactions in marine ecosystems are shaped not only by direct mortality, but also by behavioral responses that prey exhibit in the presence of predators. Classical predator–prey theory describes predator effects through functional responses, in which predation rates vary with prey density, and numerical responses, in which predator abundance or distribution changes with prey availability (Solomon 1949, Whipple et al. 2000). However, predators can influence prey populations well before a kill occurs, as the perception of predation risk alone may alter prey movement, habitat selection, vigilance, and foraging behavior. These non-consumptive, or trait-mediated, effects can scale up to influence population dynamics, species interactions, and community structure (Wirsing and Ripple 2010, Estes et al. 2011, Wirsing et al. 2021). Non-consumptive effects have been documented across marine taxa, where prey often reduce use of profitable foraging habitats in the presence of predators, sometimes with cascading ecosystem consequences. For example, green sea turtles (*Chelonia mydas*) reduce use of preferred seagrass meadows in areas with tiger sharks (*Galeocerdo cuvier*), leading to measurable changes in seagrass community structure (Heithaus et al. 2007). Many fishes respond to predation risk by altering school structure, shifting to deeper or more structurally complex habitats, or reducing feeding activity, while marine mammals may modify group size, vigilance, movement routes, and habitat use. These behavioral adjustments frequently involve energetic trade-offs that influence individual fitness and, ultimately, ecosystem dynamics.

Within inland Salish Sea ecosystems, harbor seals experience substantial predation risk from Bigg's killer whales. Harbor seals constitute a major component of the Bigg's killer whale diet (Ford et al. 1998, Houghton et al. 2015), and killer whales employ stealth-based hunting strategies that may limit early detection by prey. In response, harbor seals may reduce use of exposed haul-out sites, shift toward shallower or more structurally complex habitats, alter movement routes between haul-outs and foraging areas, or adjust time allocation between resting and feeding. Such responses represent potential non-consumptive effects operating within this predator–prey system. Risk-driven behavioral changes in harbor seals may also influence their interactions with prey species, including Pacific salmon. If seals avoid areas frequently used by killer whales, local predation pressure on salmon may decline. Alternatively, if seals redistribute toward estuaries, river mouths, or protected nearshore habitats where killer whales are less effective hunters, spatial overlap with migrating juvenile or returning adult salmon could increase. Because salmon move through predictable migration corridors, even modest predator redistributions may alter encounter rates in ecologically meaningful ways (Wirsing et al. 2021).

Non-consumptive effects therefore extend beyond the immediate predator–prey pair. Behavioral responses to risk can restructure spatial patterns of habitat use, alter energy transfer pathways, and modify interactions across trophic levels. Estes et al. (2011) demonstrate that changes in apex predator abundance can restructure ecosystems through both direct predation and behaviorally mediated pathways. In the Salish Sea, where harbor seal populations have recovered and Bigg's killer whale occurrence has increased over recent decades, both consumptive and non-consumptive processes are likely operating simultaneously. Despite growing recognition of non-consumptive effects in marine ecosystems, long-term quantitative evaluations of these processes for harbor seals and Bigg's killer whales remain limited. Most studies of harbor seal haul-out behavior have focused on physical and anthropogenic drivers such as tide height, weather, disturbance, and habitat structure (Allen et al. 1984, Cunningham et al. 2009, London et al. 2012), with comparatively less attention to predation risk as a structuring force. Studies of other pinnipeds, however, demonstrate that predation risk can strongly influence space use. Northern elephant seals adjust diving behavior and movement patterns in response to spatial and temporal variation in white shark predation risk (Klimley et al. 2021), and Cape fur seals (*Arctocephalus pusillus*) modify haul-out use and fine-scale movement behavior in response to shark presence (De Vos et al. 2015). These findings suggest that similar processes may operate in harbor seals, but long-term, spatially explicit analyses remain scarce.

The availability of multi-decadal aerial survey datasets for harbor seals (Jeffries et al. 2003, Pearson et al. 2025) and extensive sighting records for Bigg's killer whales (Towers et al. 2012, Houghton et al. 2015) provides a rare opportunity to evaluate these dynamics within inland Salish Sea waters. By examining long-term patterns in haul-out usage alongside increasing killer whale presence, it becomes possible to assess whether predator recovery has corresponded with measurable shifts in harbor seal spatial behavior consistent with non-consumptive effects. Clarifying these processes is critical for understanding how apex predator recovery may influence broader food web dynamics, including spatial patterns of seal–salmon interactions. Evaluating haul-out behavior within a predator–prey framework therefore provides a mechanistic foundation for interpreting long-term ecological change in the Salish Sea.

Human Disturbance and Habitat Modification

Human activities have substantially altered nearshore and estuarine habitats throughout the Salish Sea, reshaping the ecological landscape used by marine mammals, including harbor seals (Simenstad et al. 2011, Sobocinski 2021). Shoreline armoring, coastal development, industrial infrastructure, aquaculture facilities, and increasing vessel traffic have modified physical habitat structure and contributed to cumulative ecosystem change (Moore et al. 2008, Sobocinski 2021). Harbor seals respond behaviorally to human disturbance, with altered haul-out patterns documented in areas experiencing repeated anthropogenic activity (Allen et al. 1984). At the same time, environmental variability in circulation, temperature, and oceanographic processes influences prey distribution and nearshore habitat conditions (Babson et al. 2006, Moore et al. 2008). Together, human-driven and environmental forces shape haul-out site selection, residency time, and movements among sites across spatial and temporal scales (London et al. 2012, Peterson et al. 2012).

Shoreline development has altered many tidal flats, rocky reefs, and beaches that historically functioned as reliable haul-out habitat. The installation of bulkheads, riprap, marinas, docks, and other built structures has changed sediment dynamics, wave exposure, and the accessibility of intertidal surfaces (Sobocinski 2021). These modifications can reduce the availability of natural haul-outs and increase reliance on anthropogenic structures such as log booms, navigation buoys, and floating docks. Although harbor seals can use these modified habitats, such sites often involve higher levels of disturbance and increased overlap with human activity. Vessel traffic represents an additional and widespread source of disturbance within inland waters. Commercial shipping, ferries, recreational boats, kayaks, and whale-watching vessels generate noise, wake, and close approaches that can disrupt haul-out behavior (Allen et al. 1984, London et al. 2012). Seals may flush abruptly when vessels approach too closely, increasing energetic expenditure and reducing time available for rest. Repeated disturbance can reduce site fidelity, promote abandonment of frequently disrupted haul-outs, or shift seals toward more remote locations, with potential consequences for pup survival, molting success, and physiological stress.

Human activity may also influence predator–prey dynamics. Elevated vessel noise can interfere with acoustic cues that harbor seals use to detect approaching predators, potentially altering risk perception. Conversely, frequent vessel traffic may disrupt the stealth-based hunting strategies of Bigg’s killer whales, which rely on limited vocalization and coordinated movements during predation events. The net effect of human activity on predator efficiency and prey vulnerability remains uncertain, but these interactions underscore the importance of considering disturbance when evaluating spatial patterns of haul-out use and predation risk within inland Salish Sea ecosystems. Habitat modification within river systems and estuaries further influences predator–prey interactions. Dams, levees, and altered freshwater flow regimes have changed the timing and spatial distribution of salmon migrations in many watersheds (Sobocinski 2021). Because harbor seals frequently forage at river mouths during salmon runs, shifts in migration timing or staging location can indirectly alter where and when seals access prey. Altered channel morphology or concentrated migration routes may increase encounter rates between seals and salmon in some locations while reducing them in others.

Human activities can also redistribute prey or create localized food concentrations. In some coastal regions outside Washington, harbor seals have aggregated near fisheries operations or areas with predictable prey concentrations (Nelson et al. 2024). Although such patterns are not well documented within inland Washington waters, localized changes in prey distribution or anthropogenic food subsidies could influence seal movements and haul-out selection. Disturbance may further interact with predation risk. If human activity displaces seals from preferred haul-outs and forces use of more exposed sites, vulnerability to killer whale predation could increase. Conversely, seals may occasionally use areas with frequent human presence if predators avoid extremely shallow zones or high vessel-traffic corridors, potentially creating localized refuges within human-modified habitats, a pattern documented in other predator–prey systems (Wirsing and Ripple 2010). Whether similar refuge dynamics occur in the Salish Sea remains uncertain, but the possibility illustrates the complexity of interactions among disturbance, predator behavior, and prey space use.

Understanding how human disturbance interacts with environmental variability and predation risk is essential for interpreting long-term patterns in harbor seal haul-out behavior. Disturbance-driven shifts may obscure or amplify trends associated with prey availability or predator presence, complicating efforts to attribute observed spatial changes to specific mechanisms. As shoreline development and vessel activity continue across inland waters, incorporating anthropogenic influences into analyses of haul-out dynamics remains critical for accurately evaluating predator–prey processes and broader ecosystem change.

Salmon Recovery and Predator Interactions

Efforts to manage marine resources in the Salish Sea are closely tied to long-standing attempts to support recovery of Pacific salmon while accommodating the resurgence of protected marine mammal populations. Chinook salmon have experienced persistent declines across many watersheds despite reductions in harvest and substantial restoration efforts targeting freshwater and estuarine habitat (Sobocinski 2021). These declines carry ecological, cultural, and legal implications. Chinook salmon remain central to the treaty rights and food sovereignty of Indigenous Nations, function as key components of marine and freshwater food webs and serve as the primary prey of Southern Resident killer whales. Consequently, reduced Chinook abundance has become a focal concern for Tribes, managers, and scientists throughout the region.

Marine mammal predation is increasingly recognized as one of several important sources of mortality affecting salmonids in inland Salish Sea waters. Harbor seals, Steller sea lions, and California sea lions consume juvenile and adult salmon, although the magnitude and timing of predation vary by species and location. Bioenergetics modeling for inland Washington waters suggests that harbor seals alone may consume substantial numbers of juvenile Chinook annually (Chasco et al. 2017). The Washington State Academy of Sciences (2022), in a comprehensive review of pinniped predation in Washington portions of the Salish Sea and outer coast, concluded that pinnipeds are abundant predators of salmonids and can contribute meaningfully to mortality in already depressed stocks, particularly where salmon are concentrated in constrained migration corridors. At the same time, the report emphasizes that predation operates alongside habitat degradation, hydro system impacts, and climate-driven shifts in ocean conditions, making it difficult to isolate its relative contribution to long-term population declines. Management responses in Washington and British Columbia reflect this ecological complexity, as concerns about pinniped predation at river mouths and estuarine bottlenecks have prompted discussion of targeted interventions in some areas. Such actions remain controversial and require rigorous scientific evaluation, particularly given that pinniped populations have generally recovered under federal protection while many salmon stocks continue to struggle (Washington State Academy of Sciences 2022). Managers must therefore navigate the challenge of maintaining strong protections for marine mammals while also addressing urgent conservation needs for declining salmon populations.

Bigg’s killer whales have become an increasingly influential component of this system. Their growing and sustained presence in inland Salish Sea waters (Houghton et al. 2015, Shields et al.

2018) exerts direct predation pressure on harbor seals and may influence seal abundance and distribution. If killer whale predation reduces local seal numbers or shifts seals away from key salmon migration routes, predation pressure on salmon could decline. Conversely, if seals respond to elevated predation risk by redistributing toward sheltered nearshore or estuarine habitats, spatial overlap with migrating juvenile or returning adult salmon could increase. The Washington State Academy of Sciences (2022) highlights the importance of considering such ecosystem feedback when evaluating pinniped impacts on salmon recovery. These dynamics underscore the multi-species complexity of predator–prey relationships in inland Salish Sea ecosystems, where salmon declines reflect interacting pressures that include habitat alteration, climate variability, oceanographic change, and predation (Sobocinski 2021).

As Bigg's killer whale occurrence continues to increase and predation risk to harbor seals intensifies, understanding indirect behavioral pathways becomes increasingly important. From a management perspective, a central question is whether increasing killer whale presence alters harbor seal behavior in ways that meaningfully change seal–salmon interactions. Long-term aerial survey data on harbor seal haul-out use, combined with systematic records of Bigg's killer whale occurrence, provide a rare opportunity to evaluate whether risk-mediated behavioral responses are reshaping spatial overlap among predators and prey. Clarifying these relationships will inform ecosystem-based management approaches aimed at supporting apex predator recovery while strengthening conservation efforts for declining salmon populations.

Relevance

The Salish Sea is undergoing rapid ecological change driven by shifting ocean conditions, recovery of protected marine mammals, and continued declines in Pacific salmon. Its physical environment, structured by estuarine circulation and strong gradients in salinity and temperature, supports diverse marine communities that include harbor seals, Bigg's killer whales, and salmonids (Sobocinski 2021). Human use of these waters has a long history, from the enduring relationships Indigenous Nations maintain with marine resources to the extensive shoreline development, vessel traffic, and commercial activity that characterize much of the region today (Gaydos and Pearson 2011, Sobocinski 2021). These overlapping ecological and social forces have shaped the condition and distribution of nearshore habitats, with lasting consequences for present-day species interactions.

Harbor seals increased substantially in abundance throughout inland Washington waters following the cessation of culling programs and now occur at high, relatively stable densities across Puget Sound, Hood Canal, and the Strait of Juan de Fuca (Jeffries et al. 2003, Jefferson et al. 2021, Pearson et al. 2025). Their haul-out behavior reflects the combined influence of environmental conditions, prey availability, human disturbance, and predation risk (Allen et al. 1984, Cunningham et al. 2009, London et al. 2012, Brusa et al. 2025). As generalist predators, harbor seals consume a wide range of prey, including salmon during seasonal migration periods and early marine residence (Lance et al. 2012, Chasco et al. 2017), while simultaneously serving as a primary prey item for Bigg's killer whales, whose use of inland Salish Sea waters has increased markedly in recent decades (Ford et al. 2017, Teilmann and Galatius 2018, Scordino et al. 2022). The increasing presence of Bigg's killer whales therefore represents a significant shift in regional predator–prey dynamics. Their reliance on stealth, coordinated hunting, and flexible group composition makes them highly effective predators of pinnipeds (Baird and Dill 1996, Ford et al. 1998, Towers et al. 2012), and their expanding use of inland waters has the potential to influence the behavior and spatial distribution of marine mammals at lower trophic levels. Understanding how harbor seals respond to sustained predation pressure is therefore central to interpreting broader ecological patterns within the Salish Sea.

Predator–prey theory and evidence from marine ecosystems indicate that predators can influence prey not only through direct mortality but also through behavioral responses to perceived risk (Wirsing and Ripple 2010, Estes et al. 2011, Wirsing et al. 2021). For harbor seals, potential responses to Bigg's killer whale presence may include shifts in haul-out site selection, altered use of exposed versus sheltered locations, changes in movement routes, or adjustments in haul-out timing and duration (Houghton et al. 2015). Such risk-mediated behavioral changes could influence patterns of spatial overlap between seals and salmon, particularly in estuarine and nearshore habitats where both species concentrate seasonally (Chasco et al. 2017). These ecological processes unfold within a landscape heavily shaped by human activity, where shoreline modification, industrial development, vessel traffic, and recreational use contribute to disturbance that can affect haul-out reliability and accessibility (Allen et al. 1984, London et al. 2012, Raphael et al. 2015). Human disturbance may interact with predation risk in complex ways, potentially constraining access to preferred haul-outs or altering the relative costs and benefits of using sites with differing levels of predator exposure. Interpreting spatial changes in haul-out behavior therefore requires integrating ecological theory with long-term observational data from a system experiencing simultaneous predator recovery and sustained human use.

The importance of these dynamics is heightened by continued concerns over salmon declines in the Salish Sea. Chinook salmon in particular have decreased despite substantial harvest reductions and extensive habitat restoration efforts (Sobocinski 2021, Welch et al. 2011, Beamish et al. 2010). Marine survival remains a key limiting factor for many populations, with mortality during early marine residence and at migration bottlenecks playing a disproportionate role (Beamish and Mahnken 2001, Beamish et al. 2010, Welch et al. 2011). Because marine mammal predation contributes to this mortality (Chasco et al. 2017, WSAS 2022), shifts in harbor seal distribution or behavior may influence the spatial and temporal intensity of seal–salmon interactions. The Salish Sea is uniquely suited for evaluating these questions due to the availability of multi-decadal datasets. Aerial surveys conducted since the late 1970s provide extensive records of harbor seal abundance and haul-out distribution (Jeffries et al. 2003, Pearson et al. 2025), while long-term sighting and photo-identification data document increasing occurrence of Bigg’s killer whales in inland waters (Towers et al. 2012, Houghton et al. 2015). Together, these datasets provide a rare opportunity to assess whether increasing predator presence has corresponded with long-term spatial shifts in harbor seal haul-out behavior during a period of substantial ecological change.

INTRODUCTION

Top predators play a critical role in structuring ecosystems, and their removal or recovery can trigger cascading effects that influence ecosystem function and stability (Estes et al. 2011). Historically, predator–prey research has emphasized consumptive effects, focusing on direct mortality and population regulation (Ainley et al. 2006, London et al. 2012). Increasingly, however, ecologists recognize that predators also exert non-consumptive effects, whereby prey respond behaviorally to perceived predation risk. These responses can alter habitat use, movement patterns, and foraging behavior, with consequences that scale to population and ecosystem levels (Wirsing and Ripple 2010, Wirsing et al. 2021). These risk-mediated effects are often conceptualized as "fearscapes", in which spatial and temporal patterns of perceived predation risk shape prey behavior and habitat use. Within this framework, animals distribute themselves across landscapes in response to variation in perceived risk rather than direct predation alone. Although non-consumptive predator effects and fearscape dynamics have been extensively documented in terrestrial systems, their role in structuring marine ecosystems remains comparatively less understood, particularly across broad spatial and temporal scales (Heithaus et al. 2008, Gallagher et al. 2017, Wirsing et al. 2021). In marine environments, where direct predation events are difficult to observe and predator movements are highly dynamic, behavioral responses to risk may provide one of the clearest signals of predator influence (Heithaus et al. 2008). However, few studies have evaluated whether fear-driven behavioral responses produce consistent, large-scale changes in habitat use for mobile marine species (Wirsing et al. 2007). This gap is especially pronounced in systems where predator populations and environmental conditions are changing simultaneously, complicating attribution of behavioral responses to any single driver (Heithaus et al. 2008, Estes et al. 2011)

Empirical examples from marine systems demonstrate that predator-driven behavioral responses can restructure ecosystems independent of direct predation. In Bermuda, tiger sharks (*Galeocerdo cuvier*) influence green sea turtles (*Chelonia mydas*) through risk-mediated pathways. When shark presence is high, turtles reduce foraging in exposed seagrass meadows and concentrate in safer habitats, altering grazing patterns independent of direct predation (Heithaus et al. 2007). Where shark abundance has declined, turtles forage more broadly and intensively, contributing to measurable changes in seagrass communities (Murdoch et al. 2007). Comparable risk-mediated responses have been documented in marine systems, but evidence remains limited, particularly at broader spatial scales (Wirsing et al. 2007, Heithaus et al. 2008). Dugongs (*Dugong dugon*) shift grazing behavior and habitat use in response to tiger shark presence, altering seagrass community structure (Wirsing et al. 2007). Northern elephant seals (*Mirounga angustirostris*) adjust diving behavior and movement patterns in response to spatial variation in great white shark (*Carcharodon carcharias*) predation risk (Klimley et al. 2021), and Cape fur seals (*Arctocephalus pusillus*) modify haul-out use and fine-scale movement behavior under predation risk (De Vos et al. 2015). Together, these examples illustrate how predator-driven behavioral shifts can restructure ecosystems, often amplifying the ecological effects of predators beyond what is expected from direct predation alone, and highlight the importance of understanding how risk-mediated processes shape spatial patterns of habitat use in marine systems.

The Salish Sea represents an ideal system to evaluate whether fearscape dynamics generate large-scale changes in habitat use in marine predator–prey systems. This biologically diverse marginal sea of the northeastern Pacific Ocean spans Washington State, USA, and British Columbia, Canada, and encompasses the Strait of Georgia, the Strait of Juan de Fuca, Puget Sound, and a complex network of interconnected waterways. Freshwater inputs from numerous river systems mix with Pacific Ocean waters within major inland basins, giving the region the ecological characteristics of a large estuarine system (Thomson 1994, Sobocinski 2021). Strong biophysical connectivity among freshwater inflows, estuarine circulation, and adjacent coastal processes supports high productivity and diverse biological communities (Thomson 1994, Sobocinski 2021). The Salish Sea and adjacent Washington outer coast support at least 37 species of marine mammals and more than 250 species of fish (Gaydos and Pearson 2011), including Bigg's killer whales (*Orcinus orca rectipinnus*), harbor seals (*Phoca vitulina*), and Pacific salmon (*Oncorhynchus* spp., hereafter salmon). These species are central to ongoing ecological and management discussions, as Bigg's killer whale presence in inland waters has increased in recent decades, harbor seal populations have stabilized following recovery from historical exploitation, and salmon abundances have declined across much of their range (Jeffries et al. 2003, Houghton et al. 2015, Shields et al. 2018, Sobocinski 2021, WSAS 2022, Pearson et al. 2025).

Two ecotypes of killer whales occur in the Salish Sea. Southern Resident killer whales (*O. o. ater*) primarily consume fish, particularly salmon, whereas Bigg's killer whales specialize on marine mammals, including harbor seals, sea lions, and porpoises (Ford et al. 1998). As apex predators, Bigg's killer whales have the potential to influence marine mammal distribution and behavior through both direct predation and risk-mediated pathways. Predator and prey populations are often tightly linked, particularly in marine systems where prey abundance influences predator occurrence through numerical responses (Solomon 1949, Whipple et al. 2000). Although Bigg's killer whales have long been present in the Salish Sea, their use of inland waters has increased substantially since the 1990s (Towers et al. 2012, Houghton et al. 2015, Shields et al. 2018). This increase has been hypothesized to be associated, in part, with the recovery of harbor seal populations following protection under the U.S. Marine Mammal Protection Act in 1972 (Zier and Gaydos 2014, Pearson et al. 2025).

Harbor seals are abundant generalist predators that consume a wide range of prey, including salmonids during key migratory periods (Teilmann and Galatius 2018, Scordino et al. 2022). They rely on nearshore haul-out sites for resting, reproduction, molting, and refuge from disturbance and predation. Haul-out use reflects trade-offs among environmental conditions, prey access, human disturbance, and risk (Allen et al. 1984, Cunningham et al. 2009, London et al. 2012, Brusa et al. 2025). As a primary prey species for Bigg's killer whales, sustained increases in predator presence may influence seal space use even when direct predation events are rarely observed (Houghton et al. 2015). Experimental evidence further demonstrates that harbor seals respond behaviorally to killer whale vocalizations, indicating sensitivity to predation risk even in the absence of direct encounters (Deecke et al. 2002, Deecke et al. 2005). Because harbor seals are important predators of salmon, changes in seal distribution or haul-out behavior driven by predation risk may have indirect consequences for salmon populations. If seals reduce use of areas where killer whale presence is high, predation pressure on salmon in those areas may decrease. However, displacement of seals into alternative habitats, such as estuarine or nearshore environments where migrating salmon concentrate, may increase localized predation pressure. In this way, non-consumptive effects of apex predators may redistribute and increase, rather than reduce, predation pressure on salmon across the landscape.

Variation in haul-out patterns integrates environmental conditions, life-history requirements, and disturbance, and may shift under changing ecological conditions (Allen et al. 1984, London et al. 2012). In marine systems, prey often modify space use under elevated predation risk, and similar responses have been documented in pinnipeds exposed to increased predator presence (Heithaus et al. 2007, Wirsing and Ripple 2010, Wirsing et al. 2021, De Vos et al. 2015). Because harbor seals move among multiple haul-out sites and exhibit flexible spatial use, haul-out patterns reflect how individuals are distributed across sites rather than population size alone (Peterson et al. 2012). Long-term changes in these patterns may therefore provide insight into broader ecological shifts, including responses to predator occurrence and environmental variability. Behavioral responses to predator presence may manifest as changes in haul-out site selection, timing, or duration, potentially altering spatial overlap between harbor seals and their prey. In the Salish Sea, such changes could influence seal–salmon interactions, particularly in estuarine and nearshore habitats where migrating salmon concentrate seasonally (Chasco et al. 2017, Nelson et al. 2019, Freeman et al. 2022, Nelson et al. 2024).

Long-term monitoring programs in the Salish Sea provide a rare opportunity to evaluate these processes across decadal timescales. Multi-decadal aerial surveys document harbor seal haul-out abundance and distribution (Jeffries et al. 2003, Pearson et al. 2025), while long-term sighting records document changes in Bigg’s killer whale occurrence (Towers et al. 2012, Houghton et al.

2015). These datasets make it possible to test whether increasing predator presence generates large-scale fearscape patterns in a marine system, or whether behavioral responses remain localized and variable across space.

To address these objectives, I evaluated whether increasing Bigg's killer whale presence from 1990 to 2022 was associated with changes in harbor seal haul-out usage across Washington State. I first tested whether predator presence was associated with measurable changes in haul-out usage overall. I then evaluated whether these responses reflected consistent spatial redistribution of seals, as predicted under a fearscape framework, or instead produced site-specific and context-dependent changes in haul-out use. Because harbor seals are important predators of Pacific salmon, I also examined whether predator-associated changes in seal behavior altered spatial relationships between haul-out usage and salmon-bearing waterways. To accomplish this, I evaluated how killer whale presence interacted with salmon accessibility and environmental covariates to determine whether seals shifted haul-out usage relative to areas associated with salmon resources. Together, this approach links predator effects on seal behavior to environmental context and potential changes in seal–salmon spatial overlap.

METHODS

To evaluate whether increasing Bigg's killer whale presence generated large-scale fearscape patterns or localized, context-dependent variation in harbor seal haul-out usage, I integrated long-term aerial survey data, predator occurrence records from inland regions where long-term killer whale sighting coverage was available, and spatially explicit measures of prey accessibility and habitat structure across Washington State harbor seal management stocks. This approach was designed to assess whether predator presence produced consistent spatial responses in seal distribution or instead increased variability among haul-out sites. Because harbor seals are important predators of Pacific salmon, this approach also allowed evaluation of how predator-driven behavioral responses may influence spatial overlap with salmon and the distribution of predation pressure on salmon (Lima and Dill 1990, Heithaus et al. 2008, Wirsing et al. 2021).

Analyses were conducted in three stages. First, long-term temporal trends in harbor seal haul-out usage were quantified at both the management stock scale and individual haul-out site scale to establish baseline spatial and temporal patterns from 1990 to 2022. Second, environmental, habitat, prey-related, and predator covariates were evaluated to characterize spatial variation in haul-out usage. Third, these variables were incorporated into hierarchical negative binomial mixed-effects models to determine whether predator presence was associated with broad-scale behavioral responses or localized deviations among haul-out sites.

This multi-stage approach allowed evaluation of both broad-scale temporal trends and fine-scale spatial heterogeneity in haul-out behavior, providing a framework for testing whether predator-driven responses reflect coordinated redistribution or increased spatial variability in habitat use (Schmitz et al. 2010, Wirsing and Ripple 2010).

Study Site

The study encompassed harbor seal haul-out sites across Washington State harbor seal management stocks, including the Northern Inland, Hood Canal, Southern Puget Sound, and Outer Coast stocks (Pearson et al. 2025). These regions span the inland basins of the Salish Sea and adjacent coastal waters along the Washington outer coast. Because consistent Bigg's killer whale sighting coverage was limited to inland waters of the Salish Sea, analyses evaluating predator effects focused on inland stocks (Northern Inland, Hood Canal, and Southern Puget Sound), with additional exclusion of western Northern Inland haul-out sites located near the spatial boundary of the OrcaMaster reporting region to reduce potential edge effects associated with incomplete killer whale sighting coverage. The Salish Sea is a large, semi-enclosed estuarine system characterized by complex bathymetry, strong tidal exchange, and gradients in salinity, temperature, and circulation that influence habitat structure and prey distribution (Sobocinski 2021). Inland basins include Puget Sound, Hood Canal, and the Strait of Juan de Fuca, which are connected to the Pacific Ocean and receive substantial freshwater input from river systems throughout Washington State. Following exclusion of Outer Coast sites and western Northern Inland edge-effect sites, the final predator-analysis dataset included 159 haul-out sites and 2,818 site-year observations from 1990–2022.

Harbor seal haul-out sites within these regions include intertidal rocks, small islands, sandbars, mudflats, and anthropogenic structures such as log booms and navigation buoys (Jeffries et al. 2000). These sites are used for resting, thermoregulation, pupping, and molting, and are distributed across a range of environmental conditions, from protected inland waters to exposed outer coastal environments. Spatial variation among management stocks reflects differences in oceanographic conditions, habitat availability, and prey resources, including the distribution of salmon during seasonal migration periods (Babson et al. 2006, Khangaonkar et al. 2019).

Because the OrcaMaster sighting database is spatially bounded within inland waters of the Salish Sea, haul-out sites located near the western reporting boundary may experience systematic underestimation of killer whale exposure if predators occurring outside the reporting region are less likely to be detected. To evaluate potential edge effects, haul-out sites within the Northern Inland stock located west of −123.5° longitude and within 50 km of the OrcaMaster reporting boundary were identified as potential edge-effect sites. Sensitivity analyses were conducted by excluding these sites from predator analyses and refitting all models to evaluate whether observed predator effects were robust to potential spatial under detection of killer whale occurrence.

First Stage: Determining Harbor Seal Haul-Out Usage Across Washington State Waters

To characterize baseline spatial and temporal patterns in haul-out usage prior to evaluating predator effects, harbor seal haul-out counts were quantified using long-term aerial survey data collected by the Washington Department of Fish and Wildlife between 1990 and 2022 (Jefferson et al. 2021). Surveys were conducted across 251 known harbor seal haul-out sites distributed among four Washington State management stocks: Northern Inland, Hood Canal, Southern Puget Sound, and Outer Coast (Figure 1). These regions encompass a wide range of environmental conditions and spatial configurations, providing a natural gradient for evaluating whether predator-driven responses are consistent across landscapes or vary depending on local ecological context. The surveys represent one of the longest continuous monitoring programs for harbor seals in the northeastern Pacific and provide standardized counts of seals occupying known haul-out sites across Washington State waters. They form the basis for evaluating spatial and temporal patterns in seal distribution.

Because consistent Bigg’s killer whale sighting coverage was limited to inland waters of the Salish Sea, predator analyses were restricted to inland stocks (Northern Inland, Hood Canal, and Southern Puget Sound). In addition, western Northern Inland haul-out sites located near the spatial boundary of the OrcaMaster reporting region were excluded from predator analyses following sensitivity analyses evaluating potential edge effects associated with incomplete killer whale sighting coverage near the western Strait of Juan de Fuca. Following exclusion of Outer Coast and edge-effect sites, the final predator-analysis dataset included 159 haul-out sites and 2,818 site-year observations from 1990–2022.

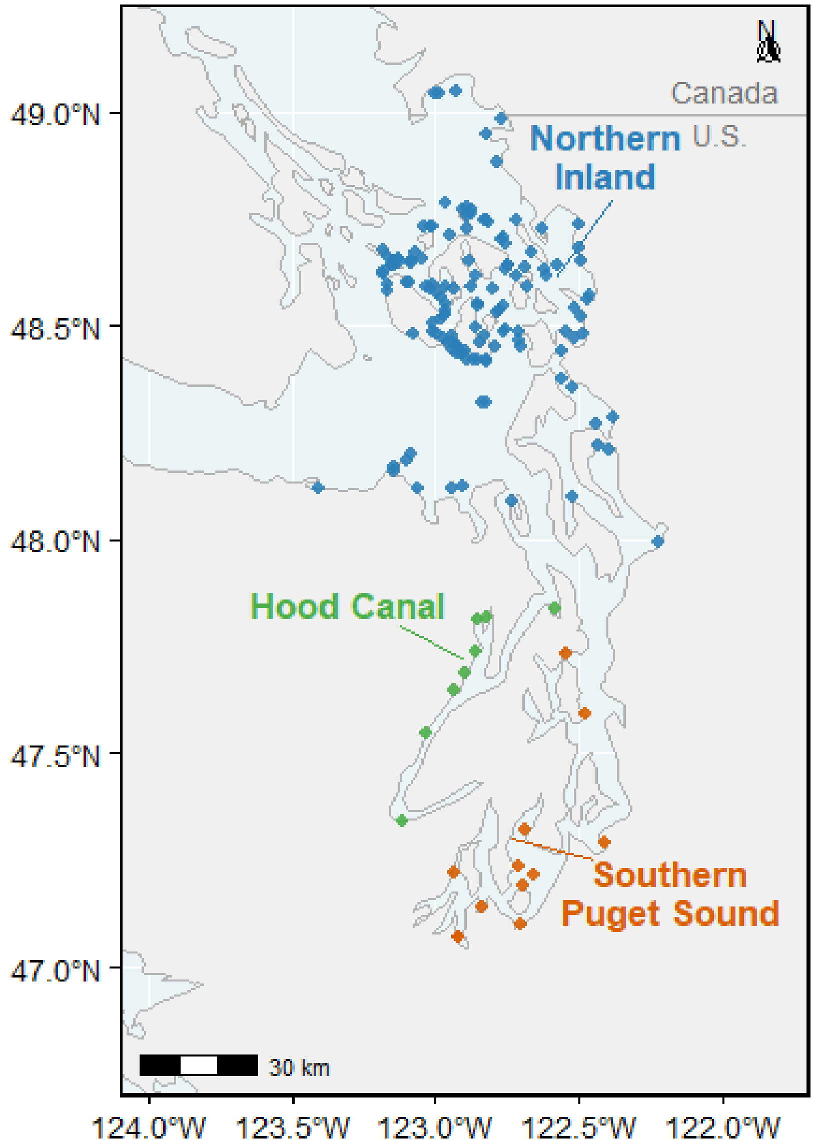

Figure 1. Distribution of harbor seal (*Phoca vitulina*) haul-out sites included in predator analyses across inland Washington State management stocks from 1990–2022. Points represent haul-out locations retained following exclusion of Outer Coast and western Northern Inland edge-effect sites.

Surveys were conducted annually during the peak pupping season from July 17 through September 2, following standardized protocols described in Pearson et al. (2025). Flights were conducted from mid-morning through mid-afternoon to maximize visibility and minimize biases associated with fog, glare, and low light conditions, and were scheduled ≤ two hours before or after low tide when haul-out attendance is typically highest. During each survey flight, observers recorded the date, time, and geographic location of each haul-out site, and high-resolution aerial photographs were used to enumerate pups, non-pups, and total individuals present. Counts were subsequently verified from photographic records to improve accuracy and reduce observer bias. To account for repeated surveys within short time intervals, counts were aggregated within a seven-day window to characterize short-term haul-out usage at each site. When multiple surveys occurred within this interval, counts were averaged to produce a weekly mean for each site, and these weekly means were then used to calculate an annual mean haul-out count for each site. This two-step aggregation procedure reduced sensitivity to short-term variability associated with tidal state, weather conditions, and survey timing while preserving interannual patterns in haul-out usage (Jeffries et al. 2000, Pearson et al. 2025). The resulting response variable represents average haul-out usage per site per year and does not reflect total population size. These aggregated annual site-level estimates provided a consistent measure of haul-out usage across space and time, forming the basis for evaluating whether predator presence was associated with uniform or spatially variable behavioral responses.

Second Stage: Identifying Factors Associated with Haul-Out Usage

Bigg's Killer Whale Presence

Bigg's killer whale occurrence was used as a proxy for spatial variation in predation risk within a fearscape framework and was quantified using sighting records from the Whale Museum's OrcaMaster database (Center for Whale Research; https://www.orcamaster.org). This database compiles long-term sightings contributed by researchers, commercial vessel operators, and trained naturalists throughout the Salish Sea and adjacent coastal waters, providing broad spatial and temporal coverage of mammal-eating killer whale occurrence. Because observer experience varies among contributors, analyses were restricted to sightings reported by skilled observers, defined as individuals with demonstrated experience in marine mammal observation and photo-identification. This filtering step reduces potential bias associated with misidentification and inconsistent reporting effort and is consistent with previous studies using opportunistic killer whale sighting datasets (Towers et al. 2012, Houghton et al. 2015, Shields et al. 2018). Each sighting record included observation date, geographic coordinates, and identification of individuals or social groups when available.

Killer whale presence data were derived from opportunistic sighting records and were not uniformly distributed across the study area. Because detection effort was concentrated within inland waters of the Salish Sea, predator analyses were restricted to inland haul-out sites within regions of relatively consistent long-term sighting coverage. Haul-out sites along the outer coast were excluded from predator analyses because killer whale sighting data were unavailable or extremely limited in these regions, limiting reliable characterization of predator occurrence. In addition, western Northern Inland haul-out sites located near the spatial boundary of the OrcaMaster reporting region were identified as potential edge-effect sites because killer whale occurrence may be systematically under detected near the western Strait of Juan de Fuca where observer coverage declines near the boundary of the sighting dataset. To evaluate the influence of this potential spatial bias, sensitivity analyses were conducted by excluding western edge sites and refitting predator models. Because predator effects remained qualitatively similar following exclusion of these sites, the final predator-analysis dataset excluded these haul-outs to reduce potential underestimation of predator exposure near the reporting boundary.

To reduce pseudo-replication arising from repeated observations of the same social group across consecutive days, sightings were aggregated into biologically meaningful occurrences following established protocols (Houghton et al. 2015, Shields et al. 2018). Specifically, an occurrence was defined as a confirmed encounter of a Bigg's killer whale social group when no sightings of that same group were recorded within the six days preceding or following the encounter. For spatial analyses, all sightings associated with a given occurrence were retained. Spatial exposure was quantified using the minimum in-water distance between each harbor seal haul-out site and any killer whale sighting associated with an occurrence. This approach allowed occurrence events to be treated as biologically independent while retaining the closest spatial encounter between predators and haul-out sites, thereby avoiding potential biases associated with representing multi-day occurrences using a single sighting location or averaged event centroid. This aggregation reflects the movement ecology of transient killer whales while preventing inflation of encounter frequency due to repeated detections of the same individuals.

Spatial relationships between harbor seal haul-out sites and killer whale occurrences were quantified using in-water distances derived from a raster-based cost-distance framework. A binary land–water raster was constructed from coastal datasets (NOAA Office of Response and Restoration 2023), in which land cells were excluded and water cells were assigned equal movement cost. A transition surface allowing movement among adjacent water cells was generated using the *gdistance* package in R (van Etten 2017), and geographic correction was applied to account for true distances between raster cells. Spatial analyses and raster processing were conducted using the *sf* and *terra* packages in R (Pebesma 2018, Hijmans 2024). This approach constrains movement pathways to water-only routes and avoids unrealistic overland shortcuts that would otherwise bias spatial relationships in a complex coastal system (Adriaensen et al. 2003, Etherington 2016). Using this framework, the minimum in-water distance between each haul-out site and all killer whale sightings associated with independent occurrences within a given year was calculated, representing the shortest feasible marine pathway between predators and haul-out sites. For each site-year combination, the minimum distance to any sighting associated with an occurrence was retained for subsequent analyses.

Exploratory analyses indicated that most killer whale occurrences occurred within several tens of kilometers of haul-out sites. Based on this distribution, a 50-km threshold was used to define predator proximity, consistent with the spatial scale of Bigg's killer whale movements and foraging behavior in the northeastern Pacific (Ford et al. 1998, Ford et al. 2010, Shields et al. 2018). From these distances, two complementary predator exposure metrics were derived for each site–year combination: predator presence, defined as whether at least one killer whale occurrence was detected ≤ 50-km of a haul-out site during a given year, and predator activity, quantified as the number of occurrences within this radius. Together, these metrics captured both the presence of predation risk and variation in predator activity, allowing evaluation of whether behavioral responses are triggered by threshold exposure to predators or vary with the intensity of risk across space.

Pacific Salmon Runs

Pacific salmon availability was included to evaluate whether predator-driven behavioral responses alter seal distribution relative to prey resources and were characterized using escapement data from the Washington Department of Fish and Wildlife Salmonid Population Indicator database. This dataset provides annual estimates of adult salmon returning to spawn in monitored river systems and was used as a coarse index of regional prey availability for harbor seals. For each haul-out site, salmon-bearing waterways were identified using in-water distances, ensuring that accessibility was defined by realistic marine pathways rather than straight-line overland distances. This distinction is particularly important in the Salish Sea, where complex coastline geometry, islands, and peninsulas can substantially alter travel distances between locations (Peterson et al. 2012).

A continuous measure of prey accessibility was calculated as the minimum in-water distance from each haul-out site to the nearest salmon-bearing waterway. Distances were derived using the same raster-based cost-distance framework described above, ensuring consistency across spatial predictors. Shorter distances therefore represent greater potential accessibility to salmon systems and increased opportunities for interaction between harbor seals and migrating salmon. This approach captures a gradient of prey accessibility across the study region while avoiding reliance on arbitrary spatial thresholds and reducing sensitivity to uncertainty in escapement estimates and interannual variation in monitoring intensity among river systems.

Salmon accessibility was included to evaluate whether predator presence altered seal use of areas near salmon-bearing waterways and whether predator-driven redistribution may influence the spatial overlap between harbor seals and salmon across inland waters of Washington State. However, this metric reflects spatial accessibility to salmon systems rather than direct measures of salmon biomass or run size and therefore does not capture fine-scale variation in prey abundance among rivers.

Confounding Variables

Additional environmental variables were included to account for spatial heterogeneity in habitat structure that may influence how predation risk is expressed across the landscape. Covariates included water depth, shoreline type, distance to mainland, and distance to the nearest river mouth. These variables were selected to capture environmental gradients known to influence haul-out suitability, spatial accessibility, and prey distribution in nearshore marine systems (Petersen et al. 2002, Moore et al. 2008).

All distance-based variables were calculated using in-water distances derived from a raster-based cost-distance framework that restricted movement to water cells, ensuring that spatial predictors reflected ecologically realistic movement pathways and were directly comparable across variables. Distance to the mainland shoreline was calculated as the minimum in-water distance from each haul-out site to the nearest point along the mainland coastline, converted to kilometers, and standardized prior to inclusion in models. Distance to mainland shoreline represents the in-water distance to the continental mainland coastline rather than the nearest shoreline; as a result, haul-out sites located on offshore islands may have large values despite being adjacent to local shorelines. This variable was included to distinguish nearshore and offshore sites, which differ in haul-out behavior, accessibility, and potential exposure to disturbance and predation (London et al. 2012, Cunningham et al. 2009). To evaluate both continuous and threshold-based spatial effects, distance to the mainland was incorporated as both a continuous variable and a categorical variable, with sites classified as nearshore (≤ 1.5 km from the mainland) or offshore (> 1.5 km).

Distance to river mouth was calculated as the minimum in-water distance from each haul-out site to the nearest river mouth, defined as endpoints of river polylines intersecting the coastline. Distances were derived using the same raster-based cost-distance framework, converted to kilometers, and standardized prior to inclusion in models. This variable was included as a proxy for proximity to freshwater inputs and associated foraging opportunities, as estuarine and nearshore systems are important feeding areas for harbor seals and their prey (Duffy et al. 2005, Simenstad et al. 2011).

Water depth at each haul-out site was derived from a bathymetric raster (ETOPO 2022, NOAA National Centers for Environmental Information) at approximately 15 arc-second resolution (~500 m). Depth values were extracted at each site, converted to positive values (m), and assigned from the nearest adjacent water cell where sites intersected land pixels to ensure valid marine depth estimates. Depth was treated as a site-level covariate and standardized prior to inclusion in statistical models by mean-centering and scaling by its standard deviation, as bathymetry influences access to haul-out sites and adjacent foraging habitat by structuring nearshore slope, tidal exposure, and water column characteristics that affect prey distribution and accessibility.

Shoreline type was assigned using a modified classification derived from the Environmental Sensitivity Index framework (Petersen et al. 2002, Raphael et al. 2015, NOAA 2023), which incorporates shoreline slope, wave exposure, substrate composition, biological productivity, vegetation type, and the presence of human-built structures such as seawalls or shoreline armoring. When multiple shoreline types occurred within a haul-out site footprint, the dominant category was assigned. This variable was included to represent variation in haul-out substrate and exposure, which influence site suitability and use (Petersen et al. 2002, Raphael et al. 2015). Environmental covariates and predator exposure metrics were incorporated as fixed effects within a hierarchical negative binomial mixed-effects framework. Initial models included predator presence alone, followed by the addition of shoreline type, distance from shore, and distance to mainland. Distance to river mouth and salmon accessibility were subsequently incorporated to evaluate whether prey-related variables explained additional variation in haul-out counts or altered observed predator and habitat relationships. All continuous covariates were mean-centered and scaled by their standard deviation prior to inclusion in statistical models to facilitate model convergence and comparison of effect sizes.

Third Stage: Evaluating Spatial and Temporal Dynamics in Haul-Out Usage

To evaluate associations between Bigg's killer whale presence and harbor seal haul-out usage, and to assess whether predator presence generated consistent spatial responses or localized, context-dependent variation in haul-out behavior, standardized haul-out count data were integrated with predator occurrence records across Washington State harbor seal management stocks from 1990 to 2022. Analyses were conducted using the annual mean haul-out counts calculated for each site as described above, allowing consistent comparison of spatial and interannual variation in haul-out usage. The complete Washington Department of Fish and Wildlife aerial survey dataset included 251 haul-out sites across four Washington State harbor seal management stocks and 10,636 site-year observations spanning 1990–2022. However, predator analyses were restricted to inland stocks (Northern Inland, Hood Canal, and Southern Puget Sound), where long-term killer whale sighting coverage was available. To reduce potential spatial edge effects associated with incomplete killer whale sighting coverage near the western Strait of Juan de Fuca, western Northern Inland haul-out sites located within 50 km of the OrcaMaster reporting boundary were excluded from predator analyses following sensitivity analyses evaluating potential underestimation of predator exposure near the edge of the reporting region. Following exclusion of Outer Coast and edge-effect sites, the final predator-analysis dataset included 159 haul-out sites and 2,818 site-year observations spanning 1990–2022.Statistical analyses were conducted using generalized linear mixed-effects models fit with the *glmmTMB* package (Brooks et al. 2017). Because haul-out counts were highly overdispersed relative to a Poisson distribution, negative binomial models with a log-link function were used throughout all count-based analyses. Site-level random intercepts were included to account for repeated observations through time and persistent spatial heterogeneity among haul-out locations. Stock-level random effects were not retained in final inland-only models because analyses were restricted to three inland stocks with highly uneven sample sizes, and site-level random intercepts captured the primary spatial structure in haul-out usage.

Distributional Assessment

Prior to model fitting, the suitability of Poisson generalized linear models for these count data was evaluated. Poisson models are commonly used for non-negative integer responses because they assume equality of the mean and variance and provide a canonical framework for modeling count processes (McCullagh and Nelder 1989). However, preliminary inspection of the inland haul-out dataset indicated strong violations of this assumption. Mean annual haul-out counts varied substantially among sites and years, and variance greatly exceeded the mean, indicating substantial overdispersion in the response variable. A Pearson residual dispersion test further confirmed substantial overdispersion under a Poisson framework (Table S1). These results indicated that the Poisson variance assumption was inappropriate for the haul-out dataset and that additional sources of variability, including persistent spatial heterogeneity among haul-out sites, needed to be accounted for.

Accordingly, all analyses of haul-out counts were conducted using negative binomial modeling frameworks. The negative binomial distribution incorporates an additional dispersion parameter that allows variance to exceed the mean, providing a flexible and widely used approach for modeling overdispersed ecological count data (Bolker *et al.* 2009, Zuur *et al.* 2009, Hilbe 2011, Harrison 2014). This framework is particularly well suited for long-term wildlife monitoring datasets characterized by substantial spatial heterogeneity and aggregation in counts across sites.

Model fit and distributional assumptions were further evaluated to assess the suitability of the negative binomial framework. Relative to Poisson models, negative binomial models substantially reduced overdispersion and improved overall model fit. Residual diagnostics were assessed using simulation-based methods implemented in the *DHARMa* package (Hartig 2022), including tests for dispersion (*testDispersion*), uniformity of residuals (Kolmogorov–Smirnov test; *testUniformity*), and zero inflation (*testZeroInflation*). Dispersion diagnostics indicated substantial improvement relative to Poisson models, with no evidence of severe residual overdispersion in the final negative binomial models. However, some deviations from ideal model assumptions remained, including evidence of residual non-uniformity and elevated zero inflation, likely reflecting persistent spatial heterogeneity and the large number of low-count site-year observations characteristic of long-term ecological monitoring datasets. Despite these limitations, the negative binomial framework provided a substantially improved and biologically appropriate representation of haul-out count variability relative to Poisson alternatives while accommodating repeated observations and persistent differences among haul-out sites.

Stock-Level Temporal Trends

Temporal trends in harbor seal haul-out usage were first evaluated at the management stock scale using negative binomial generalized linear models with a log-link function. Separate models were fitted for each Washington State harbor seal management stock to estimate long-term trends in mean annual haul-out counts over the 1990–2022 time series, allowing trends to vary independently among stocks and avoiding assumptions of shared temporal dynamics across regions. Year was included as a continuous predictor to quantify directional change in haul-out counts through time.

Model coefficients were exponentiated and converted to annual percent change to facilitate ecological interpretation, calculated as:

$$(\exp(\beta_1) - 1) \times 100$$

which represents the proportional change in expected haul-out counts associated with a one-year increase.

Stock-specific trend estimates, standard errors, confidence intervals, and annual percent changes are presented in Table 1. These models provide a broad-scale characterization of temporal dynamics in haul-out usage and establish a regional baseline against which finer-scale site-level patterns, spatial variability, and predator-associated effects were evaluated.

Hierarchical Modeling of Site-Level Variation

To account for repeated observations across space and time and to evaluate spatial variability in haul-out responses, site-level haul-out counts were analyzed using negative binomial mixed-effects models. Annual observations were nested within haul-out sites, resulting in non-independence among observations due to repeated measurements at the same locations through time. Mixed-effects models are well suited for ecological datasets with repeated measurements because they allow estimation of both population-level effects and site-specific deviations while accounting for hierarchical dependence among observations (Bolker et al. 2009, Zuur et al. 2009, Hilbe 2011).

The hierarchical model was specified as:

$$avg\_count_{it} \sim NB(\mu_{it}, \theta)$$

$$log(\mu_{it}) = \beta_0 + \beta_1\, year_t + b_{0i}$$

where avg_count_{it} represents the mean annual haul-out count at site i in year t, μ_{it} is the expected mean haul-out count for that site-year combination, and θ is the negative binomial dispersion parameter.

The fixed effects β_0 and β_1 represent the population-level intercept and overall temporal trend. Site-level heterogeneity was modeled using random intercepts (b_{0i}) allowing baseline haul-out usage to vary among sites while accounting for repeated observations through time. Site-level random intercepts captured persistent spatial heterogeneity in haul-out usage associated with local environmental conditions, habitat structure, and other unmeasured site characteristics.

Stock-level random effects were not retained in final inland-only models because predator analyses were restricted to three inland stocks with highly uneven sample sizes, and site-level random intercepts captured the primary spatial structure in haul-out usage. Similarly, random slopes for year were evaluated but not retained in final models because temporal trajectories among sites were largely parallel, and random slope variance was minimal relative to baseline spatial variability among haul-out sites (Harrison et al. 2018). Fixed effect estimates from the hierarchical model, including annual percent change associated with year, are presented in Table S2. Variance components associated with site-level random effects were summarized to evaluate the contribution of persistent spatial heterogeneity among haul-out sites (Table S3), providing insight into the degree of spatial variability in haul-out usage across inland Washington waters.

Environmental Covariates and Predator Presence

Model development followed a sequential approach in which predator variables were evaluated first, followed by the addition of habitat and prey-related covariates to assess changes in effect estimates, model fit, and spatial structure in haul-out usage.

Shoreline type at each haul-out site was assigned using Environmental Sensitivity Index (ESI) shoreline classifications (NOAA 2023). ESI categories were grouped into broader habitat types representing general substrate and exposure characteristics, including rocky, sand and gravel, marsh, and artificial shoreline. Each site was assigned a shoreline type based on the nearest mapped shoreline segment, and sites classified as “other” were excluded from shoreline analyses. Sites assigned to rare or ambiguous ESI shoreline classes were grouped as “other,” while sites that could not be spatially matched to an ESI shoreline segment were treated as unclassified. Shoreline type was included as a categorical fixed effect (rocky as the reference category) in hierarchical models. Distance-based covariates were derived using water-constrained distances to ensure ecologically realistic movement pathways. Distance to mainland was calculated as the minimum in-water distance from each haul-out site to the nearest point along the mainland shoreline, and sites were classified as nearshore (≤ 1.5 km) or offshore (> 1.5 km). Distance to river mouth was calculated as the minimum in-water distance from each haul-out site to the nearest river mouth, defined as endpoints of river polylines intersecting the coastline. Distances were converted to kilometers, standardized prior to analysis, and included as continuous fixed effects.

Predator exposure was first evaluated using two alternative formulations representing spatial variation in predation risk. The primary model included a binary indicator of killer whale presence ≤ 50 km of each haul-out site:

$$avg\_count \sim year + kw\_within50 + (1 \mid sitecode)$$

where *kw_within50* indicated whether at least one killer whale sighting occurred ≤ 50 km of a site in a given year.

A secondary model evaluated predator activity using the number of sightings ≤ 50 km:

$$avg\_count \sim year + kw\_n50 + (1 \mid sitecode)$$

The sighting-count variable was included to represent variation in predator activity and to evaluate whether behavioral responses varied with the intensity of predator occurrence across space. Models using predator presence within 50 km received stronger model support and more stable parameter estimates than models using sighting frequency and were therefore retained for primary inference.

Environmental covariates were subsequently incorporated to evaluate whether habitat and spatial characteristics influenced haul-out usage and to assess whether predator effects persisted after accounting for environmental variation. Shoreline type, distance category (nearshore vs offshore), and distance to river mouth were included as fixed effects in extended models.

To evaluate whether predator effects varied with prey accessibility, and whether predator presence altered seal use of areas near salmon-bearing waterways, an interaction between killer whale presence and salmon accessibility was included:

$$avg\_count \sim year + kw\_within50 * salmon\_min\_inwater\_km + (1 \mid sitecode)$$

Salmon accessibility was represented as the minimum in-water distance to salmon-bearing waterways. This interaction allowed assessment of whether predator presence modified spatial overlap between harbor seals and salmon resources and whether predator-driven redistribution may influence the spatial distribution of seal overlap with salmon systems across inland waters of Washington State.

The full model integrating predator presence, habitat characteristics, and prey-related covariates was specified as:

$$avg\_count \sim year + kw\_within50 + dist\_river\_sc + shoreline\_type + dist\_category + (1 \mid sitecode)$$

This model used a random intercept for site to account for repeated observations and persistent differences in haul-out usage among locations. Because several environmental covariates were unavailable for a subset of haul-out sites, environmental models were fit on reduced datasets relative to the primary predator-only analyses. The model including predator presence within 50 km was retained as the primary model based on model support, interpretability, and consistency across analyses and was used for subsequent inference evaluating whether predator-driven responses reflected broad spatial patterns or localized variability among haul-out sites.

Model Diagnostics

Model fit was evaluated using simulation-based residual diagnostics implemented in the DHARMa package. Residual plots were examined to assess overall model fit and to identify potential outliers or systematic deviations that could influence interpretation of spatial patterns in haul-out usage. Formal diagnostic tests included assessments of residual uniformity, dispersion, and zero inflation. Minor deviations from expected residual distributions were observed in some models but were not considered to meaningfully affect model inference (Figure S1). Variance inflation among fixed effects was evaluated prior to model fitting to assess potential multicollinearity among predictors and to ensure stable estimation of effects across spatial and environmental gradients (Zuur et al. 2010).

Competing models were fitted using alternative representations of predator exposure, including current-year presence, cumulative exposure, and predator activity metrics, to evaluate whether harbor seal responses reflected immediate or integrated exposure to predation risk. Model support was evaluated using Akaike's Information Criterion (AIC), with lower values indicating improved model fit and relative support among competing models (Burnham and Anderson 2002). Differences in AIC were used to compare relative support among candidate models, and results were qualitatively consistent across model formulations, indicating that inferred patterns were robust to alternative representations of predator exposure.

Annual mean haul-out counts were used to reduce variability associated with survey timing and effort, allowing clearer evaluation of interannual and spatial patterns in haul-out usage. Model performance was further evaluated using marginal and conditional R^2 values for mixed-effects models (Nakagawa and Schielzeth 2013), which quantify the proportion of variance explained by fixed effects alone and by the full model including random effects. Spatial autocorrelation in model residuals was assessed using simulation-based tests implemented in DHARMa, with residuals aggregated at the haul-out site level and evaluated using site coordinates to determine whether spatial structure remained after accounting for modeled covariates. Residual diagnostics indicated no evidence of substantial remaining spatial autocorrelation, suggesting that observed spatial patterns were adequately captured by the hierarchical modeling framework and included environmental covariates.

Short-Term Responses to Predator Presence

To evaluate short-term behavioral responses to predator presence, and to assess whether immediate exposure to predation risk produced consistent or variable responses across sites, an event-based analysis was conducted using survey-level haul-out counts. Killer whale sightings occurring within 50 km (in-water distance) of each haul-out site were identified, and independent events were defined as sightings separated by at least six days to reduce temporal autocorrelation, consistent with the aggregation procedure described above. For each event, haul-out counts were summarized for the seven-day periods before and after the sighting date. Event-level mean haul-out counts were calculated for each period, and only events with survey data available in both time windows were retained. Percent change in haul-out counts was calculated for each event as:

$$\frac{(after - before)}{before} \times 100,$$

to quantify the magnitude and direction of short-term responses to predator presence.

Differences in haul-out counts between periods were evaluated using paired statistical tests and linear mixed-effects models. In mixed-effects models, period (before vs. after) was included as a fixed effect, with random intercepts for site and event to account for repeated observations and variation among events. This structure allowed evaluation of whether short-term responses to predator presence were broadly consistent across locations or varied among sites.

This analysis was designed to assess the magnitude and spatial variability of short-term behavioral responses to predator presence and to evaluate whether immediate responses to predation risk aligned with broader patterns of localized or heterogeneous haul-out behavior observed across the inland Washington study system.

Predator Temporal Dynamics

To evaluate whether harbor seals responded to immediate versus cumulative predation risk, additional predator metrics were constructed to represent alternative temporal formulations of killer whale exposure. In addition to a binary indicator of killer whale presence within 50 km of haul-out sites in a given year, a one-year lagged presence variable was calculated for each site. A cumulative exposure metric was also defined, indicating whether killer whales were present within 50 km during either the current or previous year.

Together, these variables allowed evaluation of whether haul-out usage reflected immediate responses to predator occurrence or cumulative responses to repeated exposure over time. These alternative predator metrics were incorporated into separate model formulations to evaluate whether lagged or cumulative predator exposure improved model fit or altered inferred relationships between predator presence and haul-out usage. Model support among competing temporal formulations was compared using Akaike's Information Criterion (AIC), with lower values indicating improved model support. This approach allowed assessment of whether behavioral responses to predation risk operated primarily at short temporal scales or reflected longer-term responses to repeated predator exposure across years. Comparing alternative temporal formulations also provided insight into whether predator-associated responses were broadly consistent through time or varied among haul-out sites depending on local exposure history.

Spatial Patterns in Haul-Out Usage

Redistribution analyses were conducted across inland Washington stocks to evaluate whether predator presence produced coordinated spatial redistribution consistent with fearscape predictions or instead generated localized, context-dependent variation in haul-out usage. These analyses focused on year-to-year changes in site-level haul-out usage to assess whether predator-associated responses occurred consistently across sites or varied spatially among locations.

Pairwise distances between haul-out sites were calculated using straight-line distances between site coordinates, as these comparisons were intended to represent relative spatial proximity among sites rather than ecologically realistic movement pathways. Year-to-year changes in mean annual haul-out counts were calculated for each site, and pairwise comparisons among haul-out sites within the same year were evaluated. Site pairs were classified as changing in the same direction (both increasing or both decreasing) or in opposite directions (one increasing while the other decreased). Because pairwise comparisons within each year are not independent, these analyses were treated as descriptive indicators of redistribution patterns rather than formal inferential tests, allowing evaluation of whether changes in haul-out usage were spatially coordinated or spatially variable across sites.

To account for shared temporal trends, site-level changes were centered within year by subtracting the mean change across all sites within each stock-year combination. This metric (Δ_{centered}; hereafter "centered change") represents deviations from the stock-year average, with positive values indicating relative increases in haul-out use and negative values indicating relative decreases. Under a fearscape framework, coordinated redistribution would be expected to produce declines at some sites alongside increases at others, resulting in a higher proportion of opposite-direction changes and negative correlations between paired site changes (Pearson correlation) (Lima and Dill 1990, Heithaus et al. 2008, Schmitz et al. 2010). In contrast, concurrent changes in the same direction would indicate broader regional responses rather than localized redistribution, consistent with shared environmental or temporal drivers operating across sites.

To focus on meaningful redistribution, analyses were restricted to sites exhibiting strong changes, defined as those in the upper quartile of absolute centered change values. Within each year, sites exhibiting opposite-direction changes were paired, and the site with the greater increase in haul-out use was classified as the receiver, while the site with the greater decrease was classified as the donor. Environmental and predator-related characteristics of receiver and donor sites were compared to evaluate whether redistribution occurred in consistent directions or whether changes reflected localized, context-dependent variation across sites.

To further evaluate localized redistribution dynamics, strong positive and negative deviations from annual stock-wide trends were classified as relative “receiver” and “donor” responses within individual years. Receiver sites were defined as sites exhibiting relatively large positive centered changes in haul-out usage, whereas donor sites exhibited relatively large negative centered changes. Receiver and donor classifications were then compared with predator exposure to evaluate whether sites gaining seals were more or less likely to experience nearby killer whale presence than sites losing seals. Receiver status (receiver vs donor) was evaluated using a binomial model including killer whale presence as a predictor. Because the number of strong receiver and donor observations was limited, these analyses were treated as exploratory and interpreted cautiously.

RESULTS

Results are presented following the analytical approach described in the Methods. I first summarized broad-scale temporal trends in haul-out usage at the stock level, followed by site-level patterns from hierarchical mixed-effects models. I then evaluated whether predator presence was associated with consistent spatial responses or localized variation in haul-out usage, including variation across temporal scales and regions. Finally, I examined the influence of environmental covariates and prey accessibility, particularly relative accessibility to salmon-bearing waterways, and evaluated patterns of spatial redistribution to assess whether predator-driven responses reflected coordinated displacement or increased spatial variability among haul-out sites.

Stock-Level Temporal Trends in Haul-Out Usage

Stock-level negative binomial models revealed contrasting long-term harbor seal haul-out trends across Washington State management stocks from 1990 to 2022 (Table 1). Among the four stocks evaluated, only the Coastal stock exhibited a statistically significant increase in haul-out usage over time, with an estimated annual increase of 2.58% (SE = 0.0048, $p < 0.001$). Confidence intervals for this estimate were entirely positive, indicating a consistent long-term upward trajectory, with annual increases ranging from 1.62% to 3.56%.

Table 1. Stock-level negative binomial GLM estimates of annual trends in harbor seal (*Phoca vitulina*) haul-out counts (1990–2022) in Washington State. Percent change calculated as $(e^{\beta} - 1) \times 100$.

Stock	**Slope(log)**	**SE**	***p***	**95% CI (log)**	**% Change yr⁻¹**	**95% CI**
Coastal	0.0255	0.0048	<0.001	0.0161–0.0350	2.58%	1.62–3.56
Hood Canal	-0.0096	0.0103	0.351	-0.0299–0.0106	-0.96%	−2.94–1.07
Northern Inland	0.0024	0.0028	0.390	-0.0030–0.0078	0.24%	−0.30–0.78
Southern Puget Sound	-0.0053	0.0093	0.566	-0.0235–0.0128	-0.53%	−2.32–1.29

In contrast, no statistically significant long-term temporal trends were detected for the inland stocks included in subsequent predator analyses (Hood Canal, Northern Inland, and Southern Puget Sound). Estimated annual changes in haul-out usage for these stocks were small in magnitude and not statistically distinguishable from zero. Hood Canal exhibited a slight negative trend of −0.96% per year (95% CI: −2.94% to 1.07%), Northern Inland showed a modest positive trend of 0.24% per year (95% CI: −0.30% to 0.78%), and Southern Puget Sound exhibited a small negative trend of −0.53% per year (95% CI: −2.32% to 1.29%). In all three inland stocks, confidence intervals overlapped zero, indicating substantial uncertainty in both the direction and magnitude of stock-level change in haul-out usage through time.

These stock-level models provided a broad-scale summary of temporal patterns across Washington State harbor seal management stocks but did not capture substantial heterogeneity among individual haul-out sites nested within stocks. Because predator occurrence data were unavailable for the outer coastal stock, subsequent predator analyses focused exclusively on inland stocks. Hierarchical mixed-effects models were then used to evaluate site-level temporal variability and predator-associated changes in haul-out usage across inland Salish Sea stocks.

Regional Patterns in Mean Haul-Out Counts

Mean annual harbor seal haul-out counts per site varied substantially through time across Washington State (Figure 2). Average site usage fluctuated among years, with periods of both higher and lower mean counts evident throughout the study period. Although the LOESS smooth highlights broader temporal patterns, considerable interannual variability was observed across the time series. Annual survey coverage also varied substantially among years (Figure 2, lower panel). The number of surveyed haul-out sites generally remained high throughout much of the study period but declined during several years, particularly in portions of the mid-to-late time series. Because annual summaries were calculated using mean site-level haul-out counts, years with reduced survey coverage were occasionally influenced disproportionately by historically high-abundance haul-out sites, resulting in elevated annual means despite more limited spatial sampling. Consequently, these descriptive summaries should be interpreted as broad patterns in average haul-out usage rather than formal estimates of population-level change.

Importantly, annual averages presented in Figure 2 account for repeated surveys conducted within the same year by averaging counts at the site-year level prior to analysis. However, these descriptive summaries do not account for persistent differences in haul-out usage among sites or hierarchical spatial structure across regions. Substantial variability among individual haul-out sites therefore suggests that localized spatial processes contribute importantly to long-term temporal dynamics in haul-out usage.

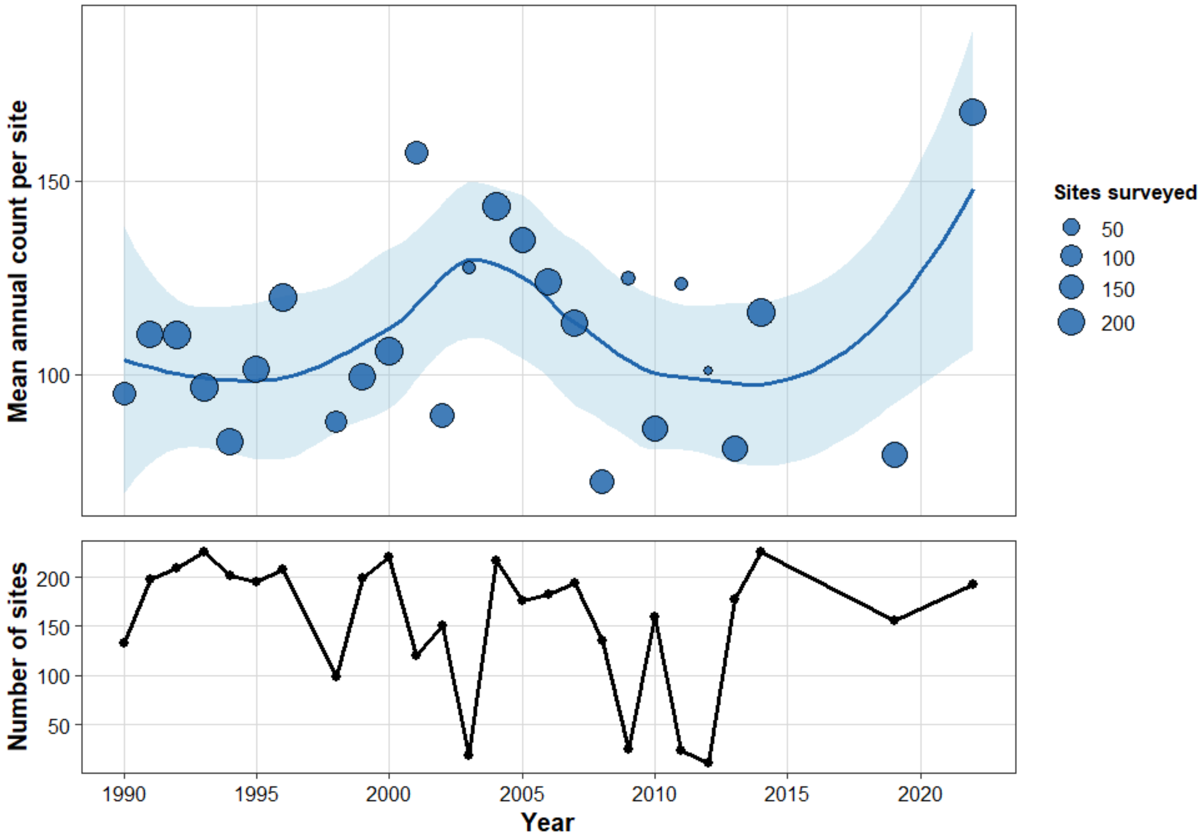

Figure 2. Mean annual harbor seal (*Phoca vitulina*) haul-out counts per site across Washington State from 1990 to 2022 with annual survey coverage. Points in the upper panel show yearly mean site-level haul-out counts, with point size proportional to the number of haul-out sites surveyed each year. The solid line represents a LOESS-smoothed temporal trend with 95% confidence intervals (shaded). The lower panel shows the number of haul-out sites surveyed annually.

Taken together, these descriptive patterns underscore the limitations of relying solely on broad-scale stock summaries to characterize long-term haul-out dynamics. These observations motivated the use of hierarchical mixed-effects models that explicitly incorporated site-level random effects and partial pooling to distinguish broad-scale temporal trends from localized variation among individual haul-out sites.

Site-Level Temporal Trends from Hierarchical Mixed-Effects Models

Hierarchical negative binomial mixed-effects models indicated a modest but consistent increase in harbor seal haul-out counts through time after accounting for repeated observations within haul-out sites. Across inland Washington stocks, haul-out counts increased by approximately 1.53% per year ($\beta = 0.0152 \pm 0.0021$ SE, $p < 0.001$; Table S2). Substantial variation in haul-out usage remained among individual sites. Random intercept variance among haul-out sites was large (variance = 0.993), indicating persistent differences in baseline haul-out usage across locations independent of temporal trends. Observed site-level trajectories and stock-level temporal trends are shown in Figure 3. Individual haul-out sites exhibited broadly similar long-term temporal trajectories despite large differences in absolute abundance, with most sites generally increasing through time although the magnitude of change varied among locations.

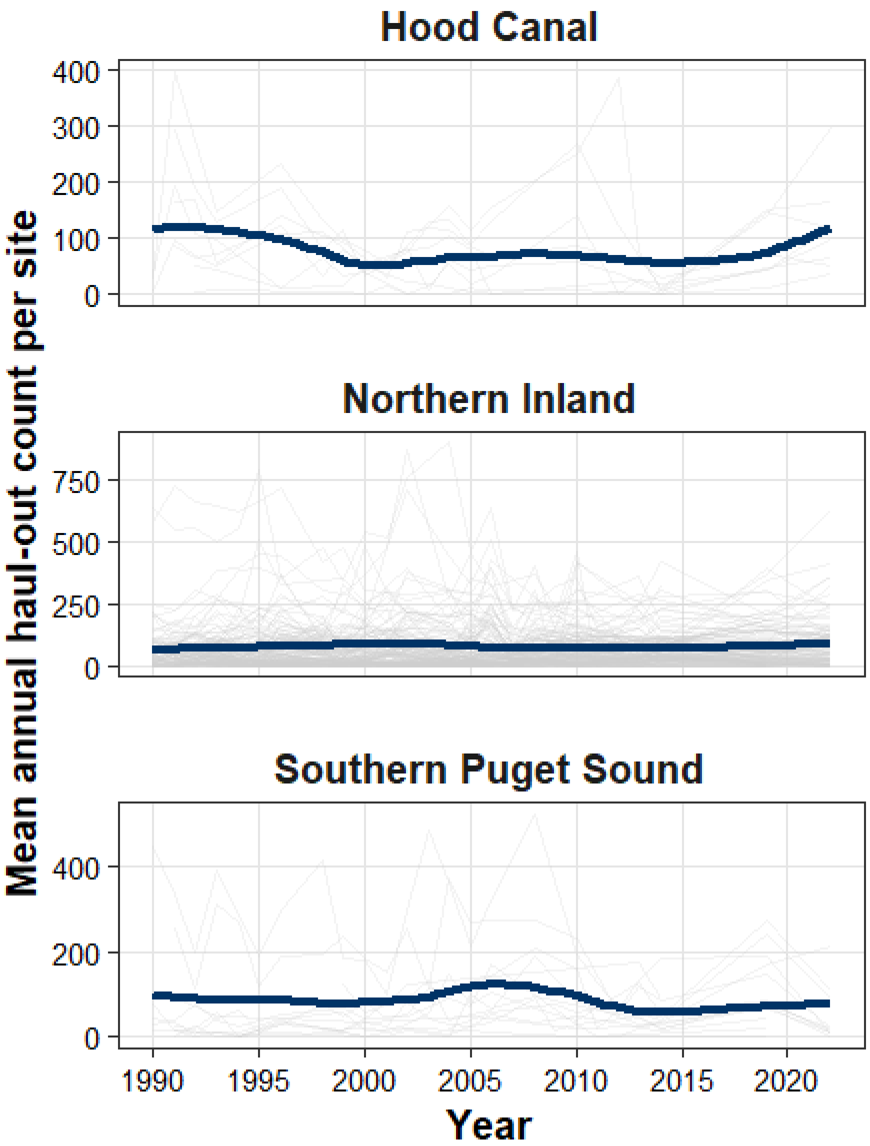

Figure 3. Site-level harbor seal (*Phoca vitulina*) haul-out counts across inland Washington State stocks from 1990–2022. Gray lines represent individual haul-out site trajectories, and blue lines represent LOESS-smoothed stock-level temporal trends. Y-axes are scaled independently among stocks to improve visualization of within-stock temporal variation.

Together, these results indicate that long-term variation in haul-out usage was driven more strongly by persistent spatial differences among sites than by large divergence in temporal trajectories through time, suggesting that predator-associated responses occurred within an already strongly structured spatial system.

Predator Occurrence and Haul-Out Usage

To evaluate whether predator occurrence explained variation in haul-out usage, I examined the spatial distribution and temporal proximity of Bigg’s killer whale sightings relative to harbor seal haul-out sites retained for predator analyses. Killer whale sightings occurred throughout inland waters of the study region from 1990–2022, with substantial spatial overlap between predator observations and inland haul-out locations (Figure 4). Minimum in-water distances between haul-out sites and killer whale sightings were strongly right-skewed, with many observations occurring at relatively short distances from predator sightings (Figure 5). A 50-km threshold was selected *a priori* based on ecologically relevant movement scales of harbor seals and Bigg’s killer whales and to represent predator occurrence within the broader spatial range over which non-consumptive behavioral responses may occur.

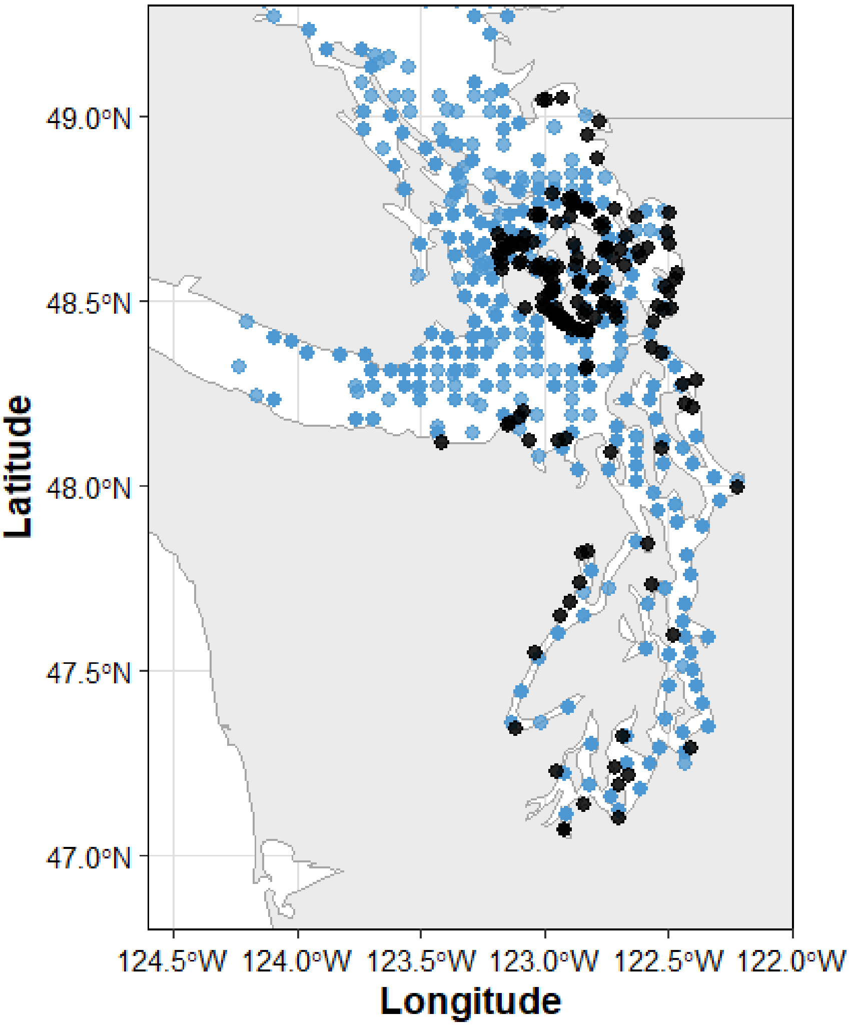

Figure 4. Harbor seal (*Phoca vitulina*) haul-out sites retained for predator analyses and Bigg's killer whale (*Orcinus orca rectipinnus*) sightings across inland Washington waters and adjacent transboundary marine areas, 1990–2022. Harbor seal haul-out sites are shown in black, and Bigg's killer whale sightings are shown in blue. Outer Coast haul-out sites and western Northern Inland edge sites excluded from the final inland predator analysis are not shown. Canadian killer whale sightings are included because all sightings within 50 km of retained haul-out sites were used to define predator exposure.

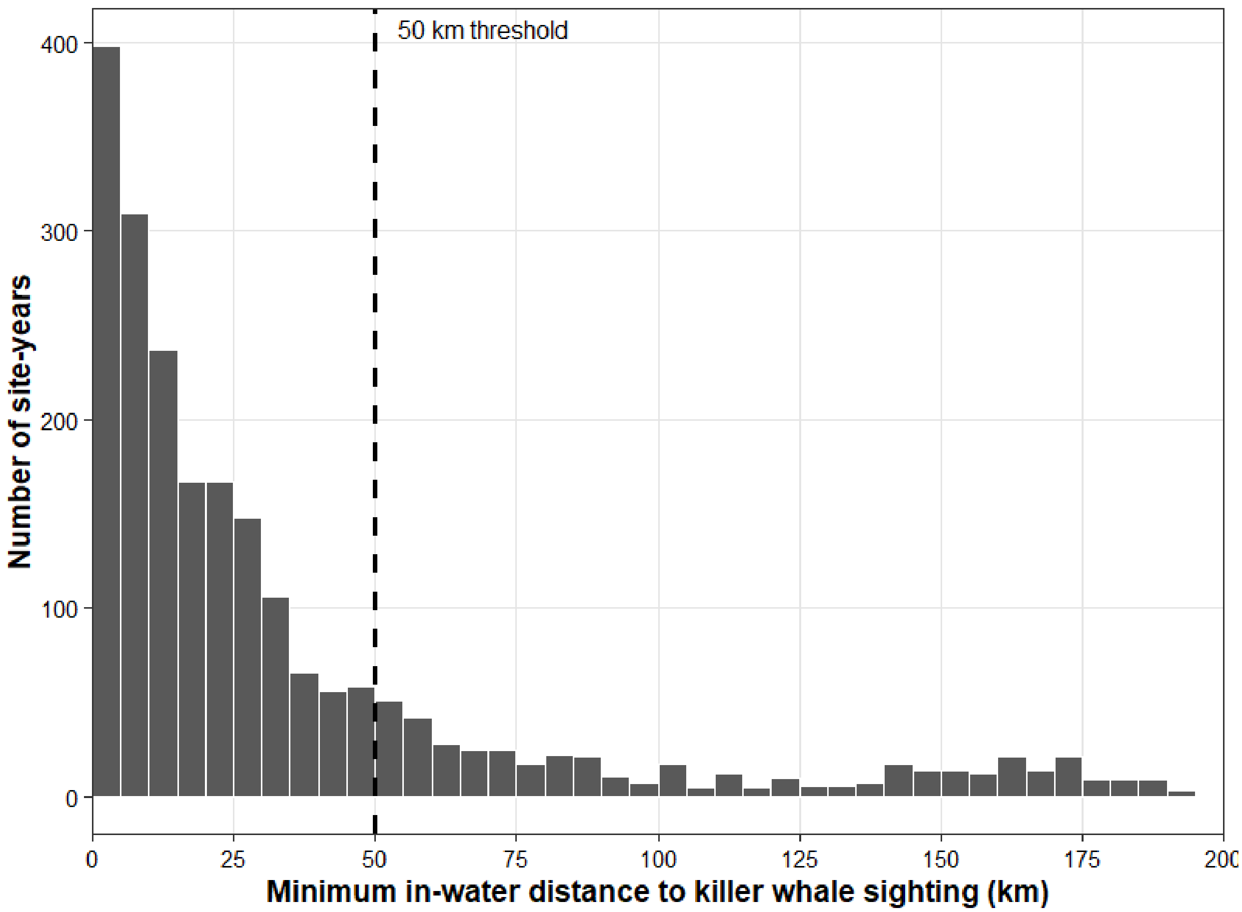

Figure 5. Distribution of minimum in-water distances between inland harbor seal (*Phoca vitulina*) haul-out sites and Bigg's killer whale (*Orcinus orca rectipinnus*) sightings from 1990–2022. Dashed line indicates the 50-km threshold used to define predator presence.

To assess how predator exposure influenced haul-out counts, I compared two representations of predator proximity: a binary presence model (≤50 km) and an activity model based on the number of sightings within this distance. Model comparison using Akaike's Information Criterion supported the binary presence model over the activity model (ΔAIC = 5.66), and this formulation was retained for subsequent analyses.

Hierarchical negative binomial mixed-effects models indicated that haul-out counts were lower in years when killer whales were observed within 50 km of haul-out sites ($\beta = -0.1068 \pm 0.0385$

SE, z = −2.77, p = 0.0055; Table 2), corresponding to an approximate 10.1% reduction in mean haul-out counts. This negative association was consistent across inland Washington stocks despite substantial variation among individual haul-out sites. Haul-out counts also increased through time after accounting for predator presence and site-level variation (β = 0.0152 ± 0.0021 SE, z = 7.26, p < 0.001).

Table 2. Fixed-effect estimates from the hierarchical negative binomial model relating haul-out counts to killer whale (*Orcinus orca rectipinnus*) presence (≤50-km) across inland Washington State management stocks (Outer Coast excluded). Coefficients are on the log scale.

Parameter	**Estimate**	**SE**	***z***	***p***
Intercept	-26.62	4.19	-6.35	<0.001
Year	0.0152	0.0021	7.26	<0.001
Killer whales ≤ 50km	-0.1068	0.0385	-2.77	0.0055

Predicted values indicated that haul-out counts remained consistently lower under predator-present conditions across the study period despite increasing through time in both scenarios (Figure 6). In contrast, the activity-based model showed no relationship between the number of sightings within 50 km and haul-out counts (β = −0.0036 ± 0.0234 SE, p = 0.877) and received weaker model support (ΔAIC = 5.66; Table S4), indicating that predator occurrence, rather than sighting frequency, better explained variation in haul-out usage.

Sensitivity analyses excluding western Northern Inland haul-out sites near the western Strait of Juan de Fuca produced qualitatively similar results to the primary analyses. Estimated effects of killer whale presence on haul-out usage remained negative and of similar magnitude after exclusion of these transition-zone sites, indicating that inferred predator effects were not driven by potential under detection of killer whale sightings near the spatial boundary of the observation dataset.

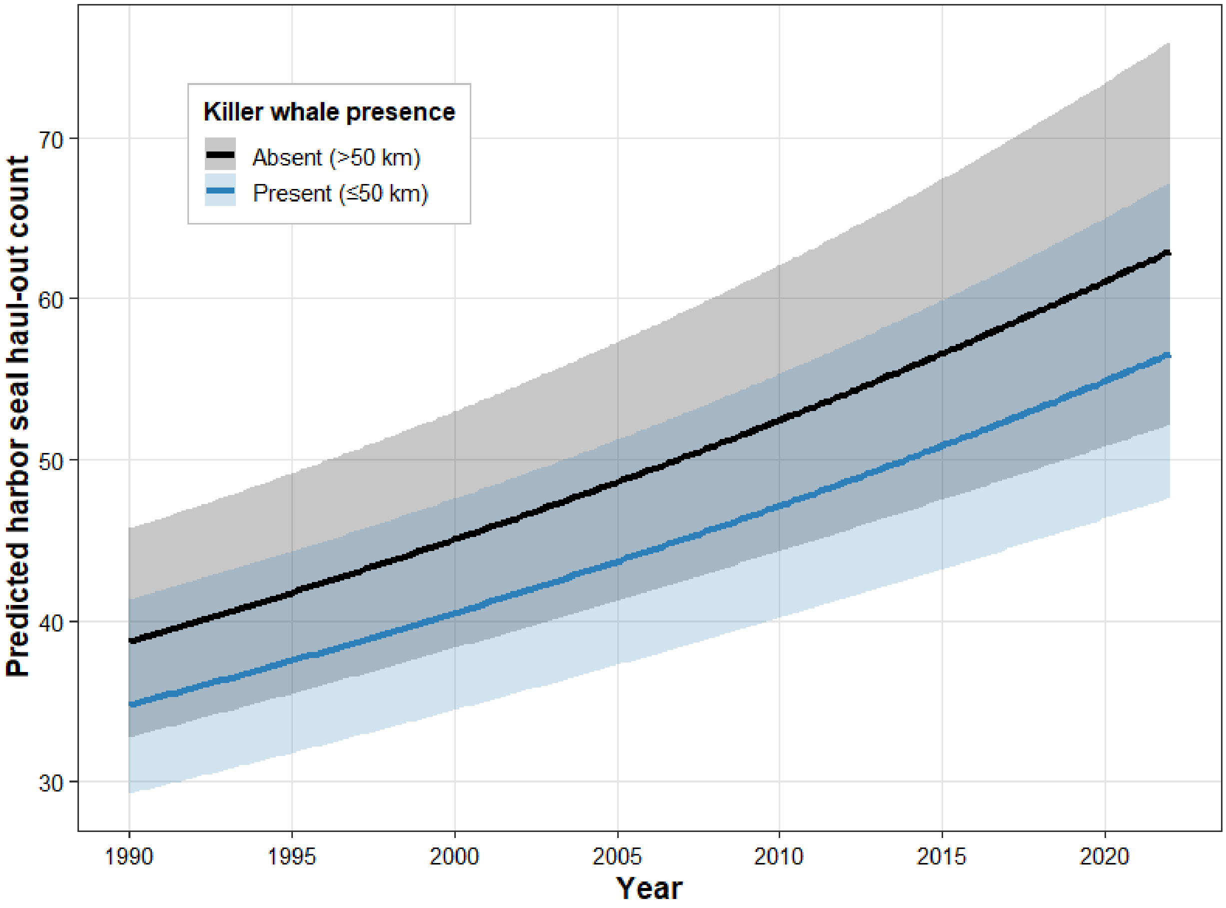

Figure 6. Predicted harbor seal (*Phoca vitulina*) haul-out counts under predator absence (>50 km) and presence (≤50 km) across inland Washington State management stocks from 1990–2022. Lines represent predicted values from the hierarchical negative binomial mixed-effects model, and shaded areas indicate 95% confidence intervals.

Together, these results indicate that the presence of killer whales was associated with reduced haul-out usage across inland Washington stocks, although the magnitude of this response was relatively modest compared to persistent differences among haul-out sites.

Temporal Dynamics of Predator Effects

To evaluate whether predator-associated responses varied across temporal scales, additional models incorporating current-year presence, lagged presence, and cumulative predator exposure were examined. All temporal formulations showed significant negative associations between Bigg's killer whale presence and harbor seal haul-out counts, with estimated reductions ranging from approximately 10.0% to 11.3% across models (Figure 7). Current-year predator presence was associated with a 10.1% reduction in haul-out counts ($\beta = -0.107 \pm 0.039$ SE, $p = 0.0055$), lagged predator presence was associated with a 10.0% reduction ($\beta = -0.106 \pm 0.045$ SE, $p = 0.018$), and cumulative exposure was associated with an 11.3% reduction ($\beta = -0.120 \pm 0.046$ SE, $p = 0.0091$).

Model comparison provided strongest support for the current-year predator presence model, although cumulative exposure received similar support (ΔAIC = 0.91). The lagged model received weaker support (ΔAIC = 2.15), suggesting that previous-year exposure alone did not explain haul-out variation as well as current-year predator occurrence.

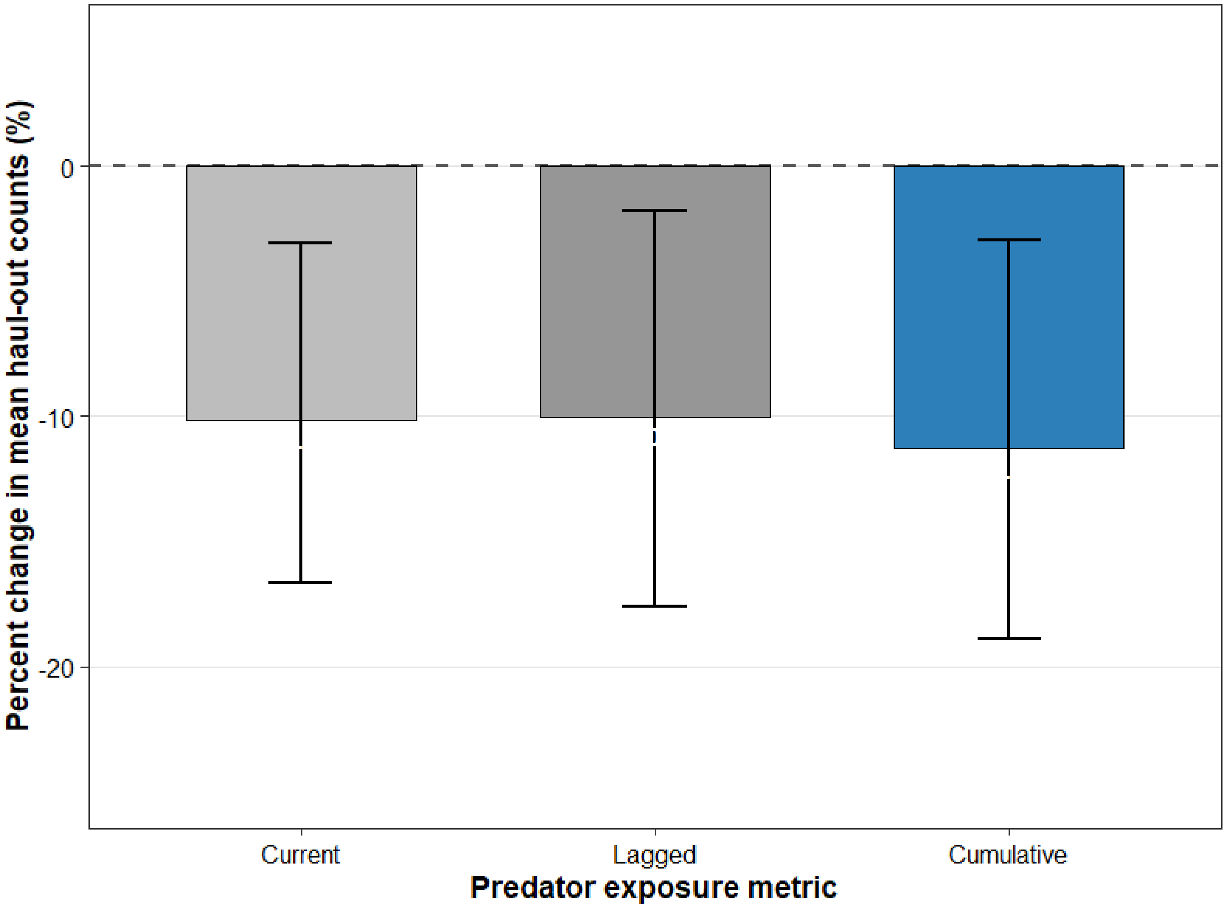

Figure 7. Estimated percent change in mean harbor seal (*Phoca vitulina*) haul-out counts under different temporal formulations of Bigg's killer whale (*Orcinus orca rectipinnus*) exposure. Error bars represent 95% confidence intervals.

Together, these results indicate that predator-associated reductions in haul-out usage were consistent across temporal formulations, but current-year predator presence provided the strongest-supported representation of predator exposure. Cumulative exposure showed a similar effect size and model support, suggesting that predator-associated changes in haul-out usage may persist across short temporal windows, although the clearest signal was associated with predator occurrence during the same year.

Regional Variation in Predator Effects

Exploratory analyses evaluated whether predator effects differed among inland harbor seal management stocks. A mixed-effects model including a stock × predator presence interaction indicated substantial regional variation in effect magnitude (Figure 8). Differences among stocks were evaluated using model-based contrasts of predicted responses on the response scale, with significance determined by whether confidence intervals for percent change excluded zero.

The strongest predator-associated reduction in haul-out counts occurred in Hood Canal, where predicted haul-out counts were approximately 38% lower during years with nearby killer whale presence (95% CI: −57.1% to −11.3%). Northern Inland exhibited a more moderate reduction of approximately 9% (95% CI: −15.8% to −1.4%), consistent with the overall predator effect observed across inland sites. In contrast, Southern Puget Sound showed no statistically significant predator-associated response, with highly uncertain estimates and confidence intervals spanning both positive and negative values.

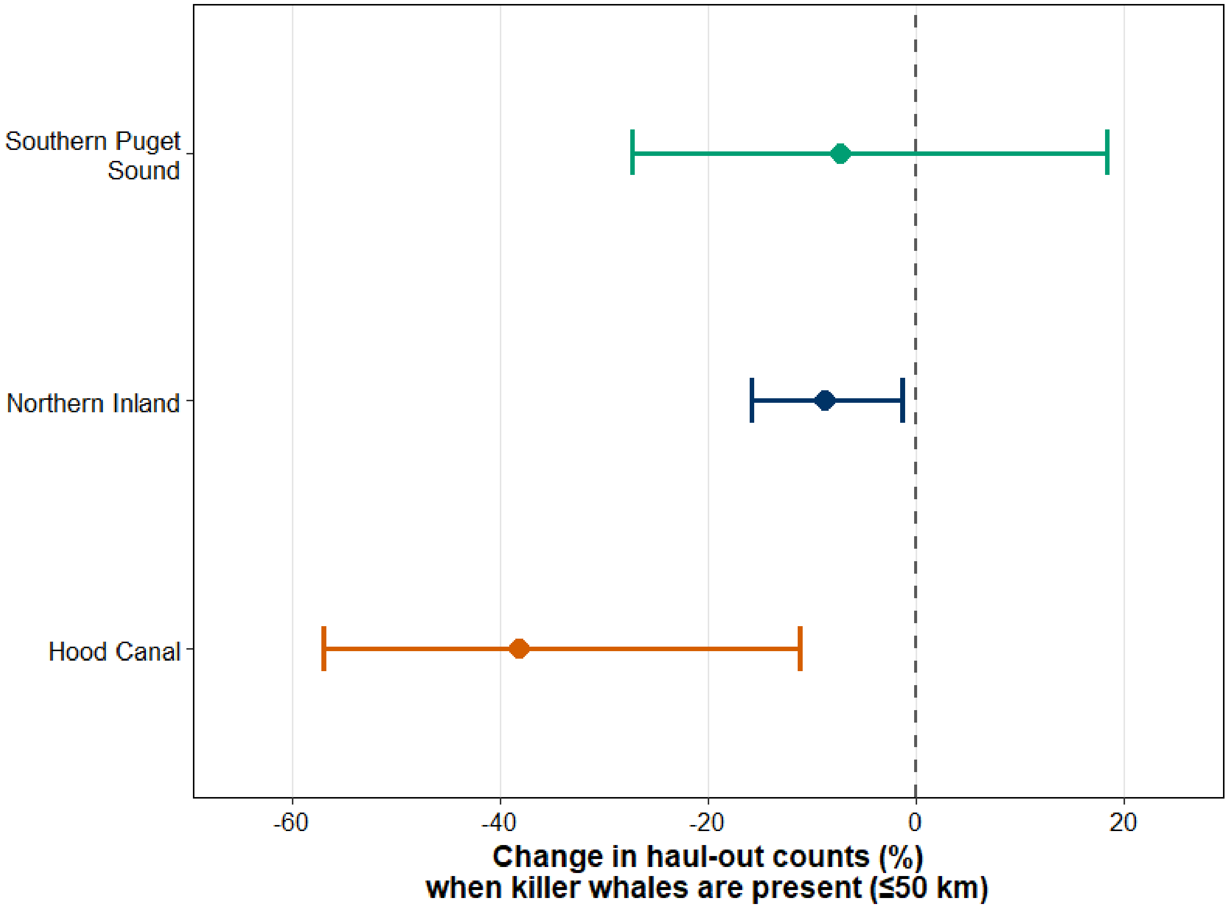

Figure 8. Percent change in predicted harbor seal (*Phoca vitulina*) haul-out counts associated with Bigg's killer whale (*Orcinus orca rectipinnus*) presence (≤50 km) across inland Washington State management stocks from 1990–2022. Points represent estimated percent change and horizontal error bars indicate 95% confidence intervals. Hood Canal exhibited the strongest reduction in haul-out counts, Northern Inland showed a more moderate reduction, and Southern Puget Sound showed no statistically significant predator-associated effect.

Together, these results indicate that predator-associated changes in haul-out usage varied substantially among regions rather than producing uniform responses across inland Washington stocks. This spatial heterogeneity suggests that harbor seal responses to predator occurrence were context-dependent and influenced by local environmental or ecological conditions.

Habitat Context of Predator Effects

To evaluate whether predator-associated responses varied across habitat contexts, models incorporating shoreline type, mainland distance, and site position were examined. Predator effects differed modestly across shoreline types, although interaction patterns were inconsistent among categories. The strongest interaction occurred at sand and gravel shorelines, where predator presence was associated with a larger reduction in haul-out counts relative to rocky shorelines ($\beta = -0.185 \pm 0.079$ SE, $p = 0.020$). Interactions involving artificial and marsh shorelines were not statistically significant, indicating limited evidence for consistent shoreline-specific predator responses overall.

Predator-associated responses were not related to continuous distance from the mainland shoreline, and no interaction between predator presence and mainland distance was detected ($p = 0.306$). Similarly, predator-associated reductions in haul-out usage did not differ between offshore and nearshore sites (interaction $p = 0.999$). Predicted haul-out counts were approximately 10% lower under predator-present conditions at both offshore and nearshore sites, indicating broadly similar predator-associated responses across site positions (Figure S3).

Overall, predator presence was associated with reduced haul-out usage across habitat contexts, but these effects were not consistently structured by shoreline type, mainland proximity, or site position. These findings indicate that broad habitat characteristics alone do not explain consistent spatial variation in predator-associated haul-out responses and further support the interpretation that predator responses were localized and context-dependent rather than uniformly structured across the landscape.

Environmental and Prey Covariates Associated with Haul-Out Usage

Habitat Composition

Shoreline type varied across retained inland haul-out sites, with most sites associated with rocky and sand and gravel shorelines and fewer characterized by artificial or marsh shoreline types. Of the 159 inland haul-out sites retained for environmental and predator analyses, 88 were associated with rocky shoreline, 48 with sand and gravel shoreline, 14 with marsh habitat, and 9 with artificial shoreline.

Among environmental covariates, shoreline types were associated with variation in harbor seal haul-out counts across sites (Table 3). Relative to rocky shoreline sites, artificial shoreline sites exhibited significantly higher haul-out counts ($\beta = 0.937 \pm 0.366$ SE, $p = 0.011$). Sand and gravel shorelines also tended to exhibit higher haul-out counts than rocky shoreline sites, although this relationship was only marginally significant ($\beta = 0.327 \pm 0.175$ SE, $p = 0.062$). Marsh shoreline sites did not differ significantly from rocky shoreline sites. These results suggest that shoreline composition contributes to persistent spatial variation in haul-out usage across inland Washington State.

Table 3. Fixed-effect estimates from the negative binomial mixed-effects model evaluating shoreline type associated with harbor seal (*Phoca vitulina*) haul-out counts across inland Washington State. Rocky shoreline was used as the reference category.

Predictor	**β**	**SE**	***z***	***p***
Year	0.015	0.002	7.00	<0.001
Artificial	0.937	0.366	2.56	0.011
Marsh	0.343	0.273	1.25	0.210
Sand & Gravel	0.327	0.175	1.87	0.062

Water depth was not associated with variation in harbor seal haul-out counts and did not modify the relationship between predator presence and haul-out usage. Depth across retained haul-out sites was generally shallow and strongly right-skewed, with relatively few sites occurring in deeper water (Figure S4), indicating limited evidence that water depth contributed substantially to spatial variation in haul-out usage or predator-associated responses at the spatial scale considered.

Spatial Position

Distance to the mainland shoreline varied substantially across retained inland haul-out sites, with most sites occurring relatively close to the mainland coastline (median = 1.21 km), although some island-associated sites occurred substantially farther offshore (maximum = 10.95 km; Figure 9). Across retained inland haul-out sites, 96 were classified as nearshore and 63 as offshore.

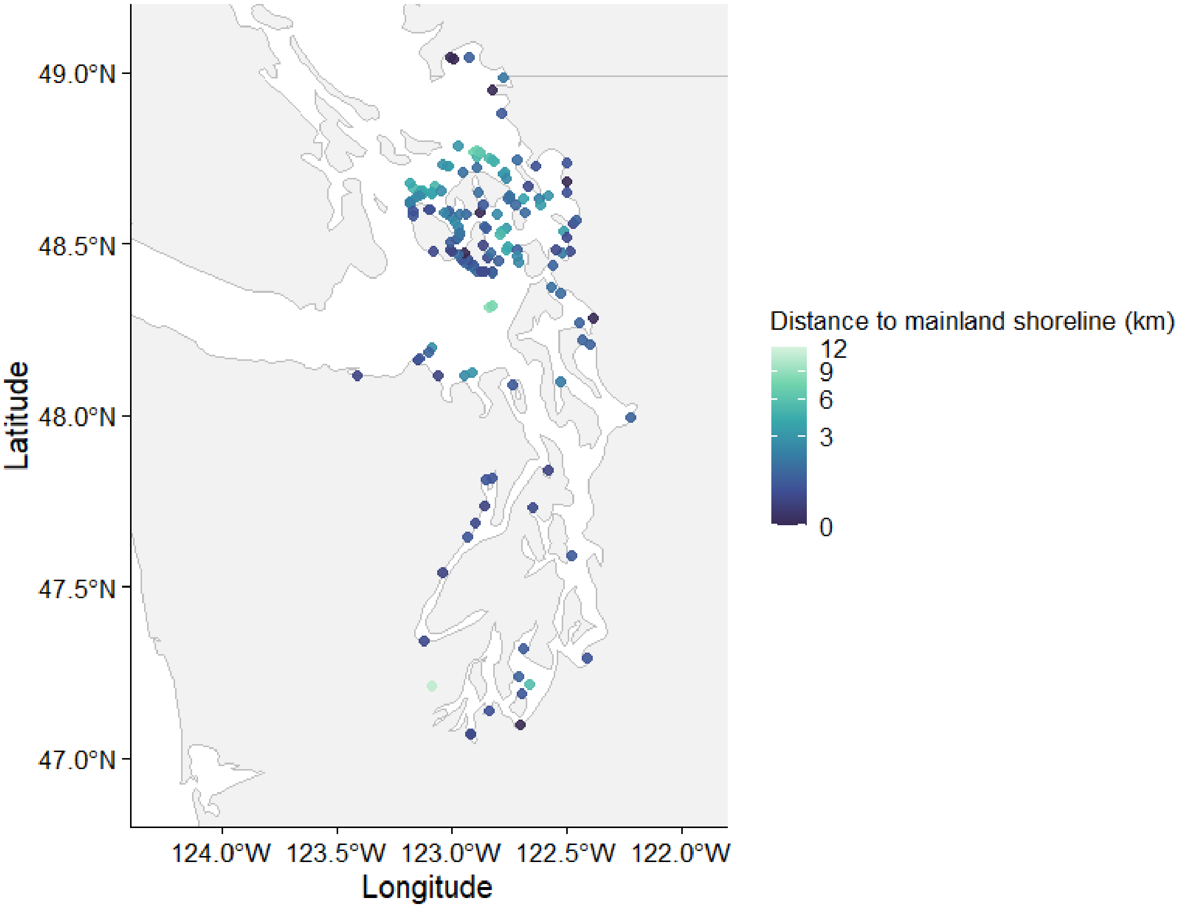

Figure 9. Distance from each harbor seal (*Phoca vitulina*) haul-out site to the mainland shoreline. Distances were calculated as minimum water-constrained paths and may differ from straight-line proximity due to complex coastline geometry. Most haul-out sites occurred within a few kilometers of the mainland shoreline, with larger distances primarily associated with island-associated haul-out sites.

Offshore haul-out sites exhibited substantially higher haul-out counts than nearshore sites ($\beta = 0.779 \pm 0.165$ SE, $p < 0.001$; Figure 10), indicating that broad spatial positioning relative to the mainland explained variation in haul-out usage more effectively than continuous distance measures. In contrast, continuous distance from the mainland shoreline was not significantly associated with haul-out counts ($p = 0.306$), suggesting that categorical site position better captured broad spatial differences in haul-out usage across inland Washington State. Although offshore sites supported higher haul-out counts than nearshore sites, predator-associated reductions in haul-out usage were similar across both site categories (Figure 10).

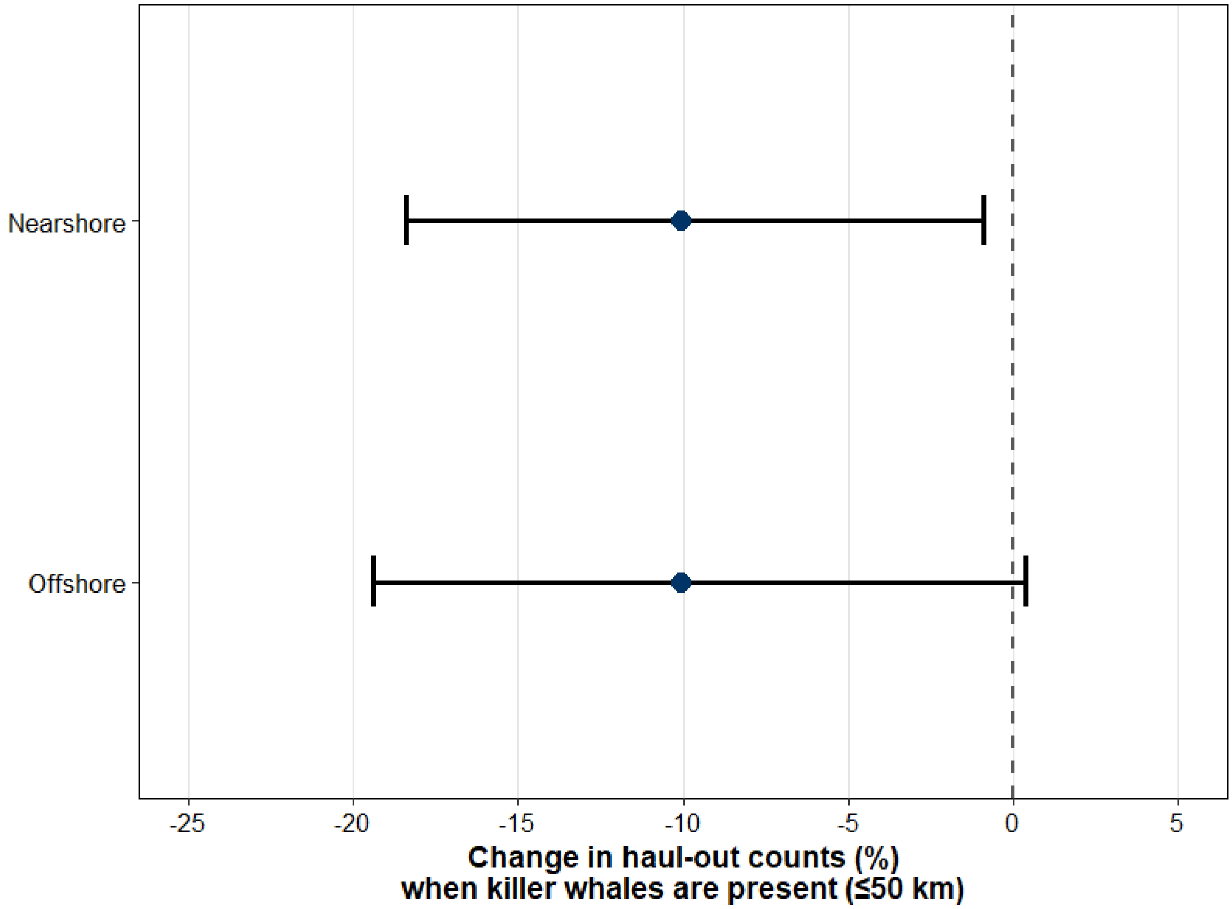

Figure 10. Percent change in predicted harbor seal (*Phoca vitulina*) haul-out counts associated with Bigg's killer whale (*Orcinus orca rectipinnus*) presence (≤50 km) across nearshore and offshore haul-out sites. Points represent estimated percent change and horizontal error bars indicate 95% confidence intervals. Predator-associated reductions in haul-out usage were similar across site positions, with overlapping confidence intervals suggesting little evidence of consistent differences in predator responses between offshore and nearshore haul-out sites.

Distance to the nearest river mouth was not significantly associated with harbor seal haul-out counts ($\beta = -0.106 \pm 0.086$ SE, $p = 0.220$). Although predicted haul-out counts tended to decline with increasing distance from riverine inputs (Figure 11), uncertainty surrounding this relationship was substantial and confidence intervals broadly overlapped across the observed range of sites. These results suggest limited evidence that proximity to riverine inputs consistently structured haul-out usage across inland Washington State.

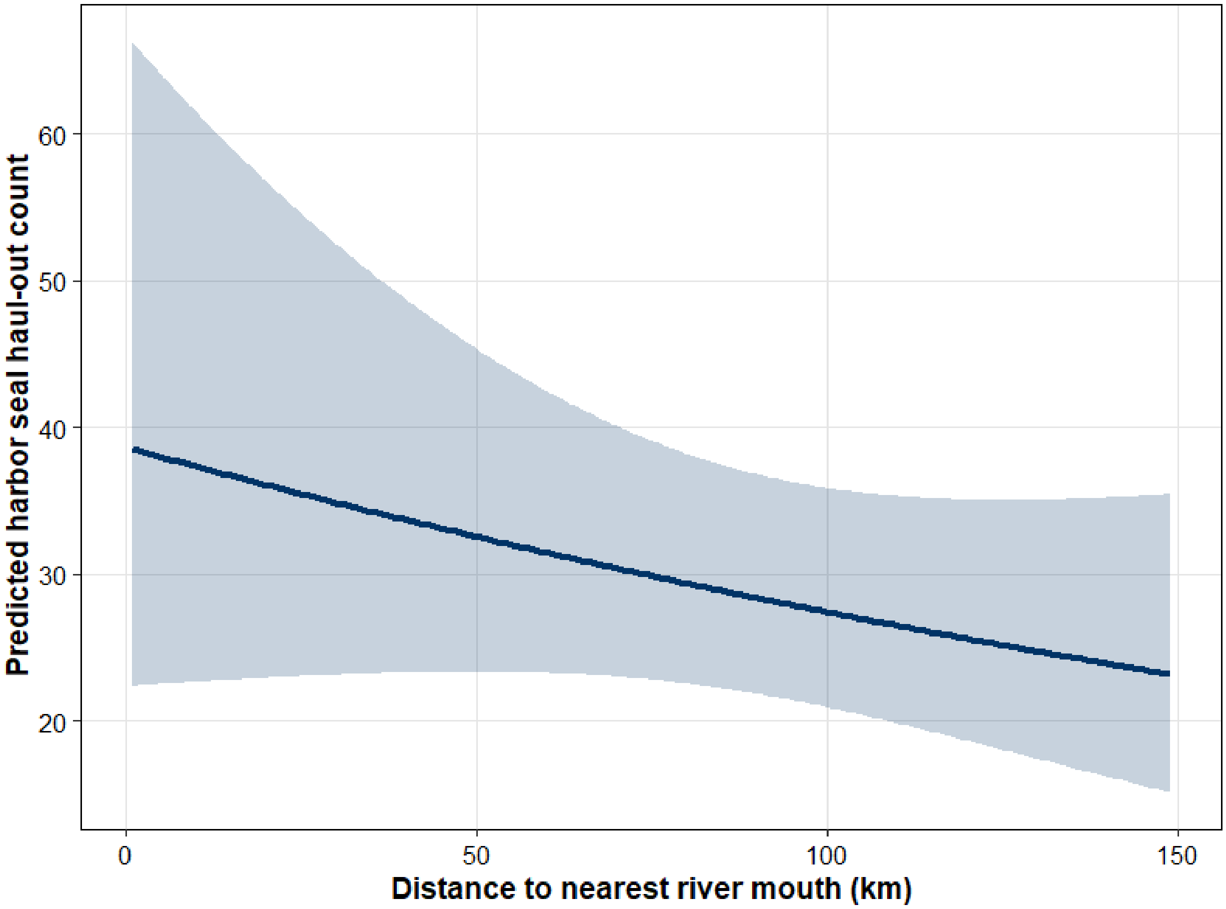

Figure 11. Predicted harbor seal (*Phoca vitulina*) haul-out counts as a function of distance to the nearest river mouth. Predicted counts tended to decline with increasing distance from riverine inputs, although uncertainty surrounding this relationship was high. Shaded regions represent 95% confidence intervals.

Together, these results indicate that broad habitat composition and spatial positioning contribute substantially to persistent spatial variation in harbor seal haul-out usage across inland Washington State. However, predator presence remained negatively associated with haul-out counts after inclusion of environmental and spatial covariates ($\beta = -0.101 \pm 0.039$ SE, p =

0.009), indicating that predator-associated reductions in haul-out usage were not explained solely by habitat structure or prey-accessibility gradients. I next evaluated whether predator occurrence was associated with shifts in haul-out usage relative to salmon-bearing waterways.

Salmon Distance and Predator Interaction

To evaluate whether predator occurrence was associated with shifts in haul-out usage relative to salmon-bearing waterways, I examined the relationship between haul-out counts, in-water distance to salmon-bearing waterways, and predator presence across inland Washington State. Salmon-bearing waterways represent concentrated seasonal prey resources and provide a spatial framework for evaluating whether predator-associated redistribution of harbor seals may influence overlap with Pacific salmon systems.

In-water distance to salmon-bearing waterways was not significantly associated with harbor seal haul-out counts after accounting for environmental covariates and predator presence ($\beta = 0.071 \pm 0.049$ SE, $p = 0.146$). Similarly, the interaction between predator presence and salmon distance was not statistically significant ($\beta = -0.018 \pm 0.040$ SE, $p = 0.646$), indicating limited evidence that predator occurrence consistently altered haul-out usage relative to salmon-bearing waterways (Figure 12). Predicted relationships between salmon proximity and haul-out usage differed only modestly between predator-present and predator-absent conditions, and confidence intervals broadly overlapped across the observed range of distances.

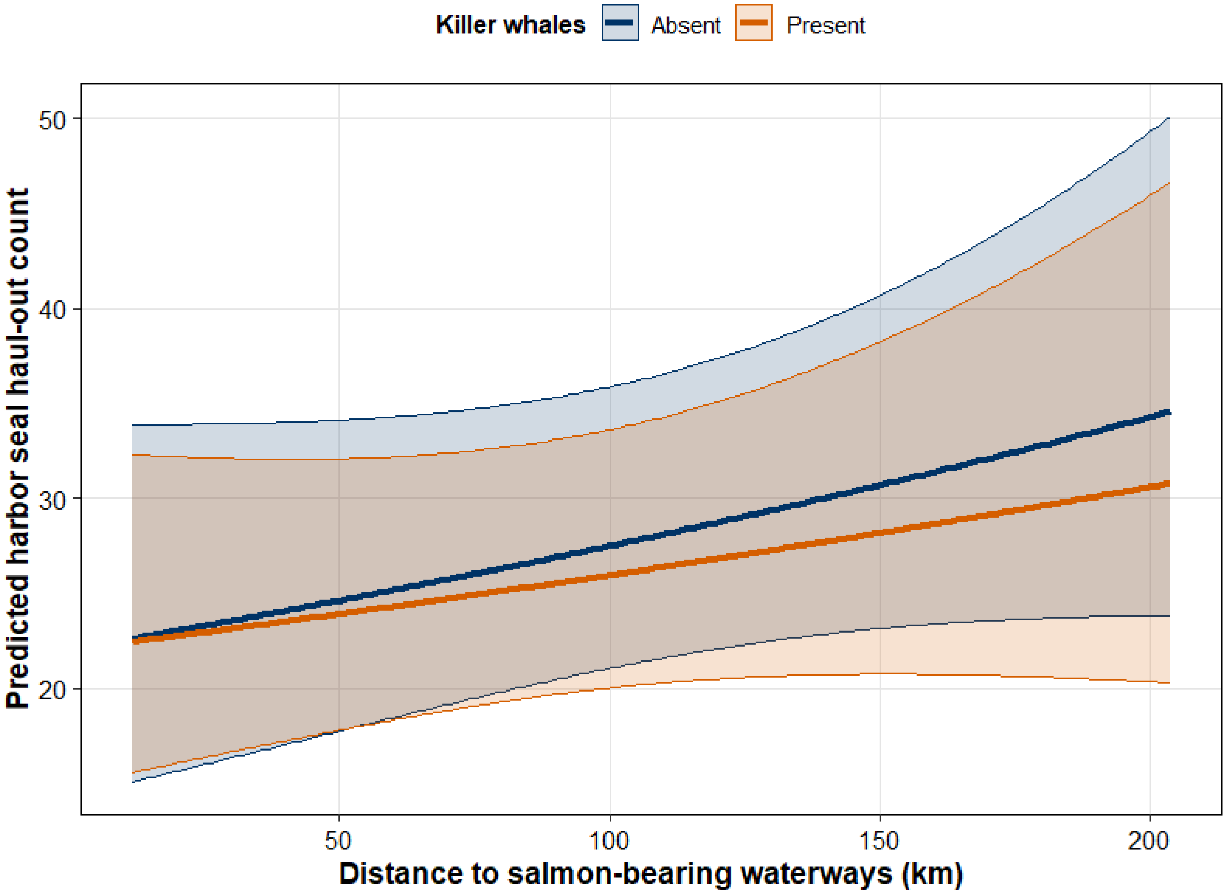

Figure 12. Predicted harbor seal (*Phoca vitulina*) haul-out counts as a function of in-water distance to salmon-bearing waterways under predator-absent (>50 km) and predator-present (≤50 km) conditions. Shaded ribbons represent 95% confidence intervals. Relationships between salmon proximity and haul-out usage were weak and highly uncertain across predator conditions.

Including in-water distance to salmon-bearing waterways did not improve model fit relative to the environmental model without this covariate (ΔAIC = 0.06), and the interaction model received weaker support (ΔAIC = 1.85; Table S7). Further, , a binary measure of salmon presence (≤50 km) was also not associated with haul-out counts ($\beta = 0.121 \pm 0.188$ SE, $p = 0.519$). Together, these results indicate that prey accessibility, as measured by proximity to salmon-bearing waterways, did not strongly structure haul-out usage in this system and did not meaningfully modify responses to predator presence.

Environmental and prey-related covariates were incorporated into hierarchical mixed-effects models to evaluate associations between predator occurrence, habitat characteristics, spatial position, and haul-out usage across inland Washington State. Model progression indicated that inclusion of environmental covariates substantially improved model fit relative to simpler predator-only models (Table 4).

Across all model formulations, predator presence remained negatively associated with harbor seal haul-out counts. In the predator-only model, haul-out counts were lower when Bigg's killer whales were present within 50 km ($\beta = -0.103 \pm 0.039$ SE). This negative association remained consistent after inclusion of river proximity ($\beta = -0.102 \pm 0.039$ SE) and environmental covariates ($\beta = -0.101 \pm 0.039$ SE), indicating that predator-associated reductions in haul-out usage were not explained solely by habitat structure or prey-accessibility gradients.

Distance to river mouth exhibited a weak negative association with haul-out counts across model formulations, with predicted counts tending to be higher at sites located closer to riverine inputs, although this relationship was not statistically significant. In contrast, environmental covariates associated with habitat composition and spatial position explained substantially more variation in haul-out usage. Artificial shoreline sites exhibited higher haul-out counts relative to rocky shoreline sites, while offshore haul-out sites consistently exhibited higher haul-out counts than nearshore locations.

Table 4. Progression of hierarchical negative binomial mixed-effects models evaluating associations between predator presence, prey accessibility, and environmental covariates and harbor seal (*Phoca vitulina*) haul-out counts across inland Washington State waters. Values represent fixed-effect coefficients (β ± SE) on the log scale.

Predictor	**Model 1: Predator**	**Model 2: + River Proximity**	**Model 3: + Environmental Covariates**
Year	0.015 ± 0.002	0.015 ± 0.002	0.015 ± 0.002
Killer Whale Presence	-0.103 ± 0.039	-0.102 ± 0.039	-0.101 ± 0.039
Distance to River (scaled)	—	-0.088 ± 0.081	-0.106 ± 0.086
Artificial Shoreline	—	—	0.937 ± 0.366
Marsh Shoreline	—	—	0.343 ± 0.273
Sand & Gravel Shoreline	—	—	0.327 ± 0.175
Offshore vs. Nearshore	—	—	0.779 ± 0.165

Including salmon accessibility metrics did not substantially improve model fit beyond environmental and spatial covariates alone. The salmon distance model received nearly identical support to the environmental model (ΔAIC = 0.06), while the predator × salmon interaction model received weaker support (ΔAIC = 1.85). Together, these results indicate that habitat composition and spatial position explained more variation in haul-out usage than prey-accessibility metrics, while predator presence remained a modest but consistent negative predictor across model formulations.

Model comparison further supported the importance of environmental covariates in explaining spatial variation in haul-out usage. Environmental models received substantially greater support than predator-only models, whereas inclusion of salmon accessibility metrics provided little additional explanatory power beyond habitat and spatial covariates (Table S5).

Short-Term Responses to Predator Presence

To evaluate short-term behavioral responses to predator occurrence, I compared harbor seal haul-out counts during the 7-day periods before and after independent Bigg's killer whale sighting events. Across 70 independent predator events, responses varied substantially among haul-out sites and events, with some locations exhibiting pronounced declines following killer whale presence while others showed little change or increases in haul-out counts (Figure S4).

Among the 20 site-event comparisons with sufficient survey coverage before and after predator occurrence, median percent change in haul-out counts was negative (−32.1%), although variability among events remained high (interquartile range = 95.1%), indicating that short-term responses ranged from substantial declines to increases following predator occurrence. Mean haul-out counts also tended to decline following killer whale presence (mean change = −26.7 seals), although paired comparisons detected no statistically significant differences between before and after periods (paired t-test: $p = 0.260$; Wilcoxon signed-rank test: $p = 0.351$). Despite the limited statistical support provided by the paired comparisons, mixed-effects models evaluating repeated before/after observations suggested a modest reduction in haul-out counts following predator occurrence ($\beta = -19.34 \pm 8.42$ SE, $t = -2.30$). A post hoc power analysis indicated that the paired comparison had limited statistical power to detect short-term behavioral responses of the magnitude observed (Cohen's $d = 0.26$; power = 0.20). Based on the observed effect size, approximately 118 paired site-event comparisons would be needed to achieve 80% statistical power, compared to the 20 comparisons available in this study. Although statistical support for short-term responses was limited, both median percent change and mean haul-out counts declined following predator occurrence, indicating that observed responses were generally consistent with expectations under increased predation risk.

Mixed-effects models evaluating repeated before/after observations suggested a modest reduction in haul-out counts following predator occurrence ($\beta = -19.34 \pm 8.42$ SE, $t = -2.30$). However, substantial variability remained among sites and predator events, indicating that short-term responses were inconsistent rather than reflecting uniform behavioral reactions to immediate predation risk.

Together, these results indicate that short-term responses to predator occurrence were highly variable and context-dependent across sites and events. Although some haul-out locations exhibited substantial short-term declines following killer whale presence, responses were not spatially consistent across the inland Washington State study region.

Spatial Redistribution in Haul-Out Use

Across Hood Canal, raw changes in harbor seal haul-out counts more frequently occurred in the same direction (60.9%) than in opposite directions (39.1%), indicating that haul-out sites generally increased or decreased concurrently rather than exhibiting coordinated redistribution among sites (Figure 13; Table 5). Raw site-level changes were weakly positively correlated ($r = 0.26$), suggesting that shared temporal variation dominated broad-scale patterns in haul-out usage across the region.

After accounting for shared temporal trends by centering site-level changes within each year, a different pattern emerged. Centered changes more frequently occurred in opposite directions

(54.0%) than in the same direction (46.0%) (Figure 13), and pairwise site changes became weakly negatively correlated (r = −0.10; Figure 14; Table 5). This shift from coordinated to opposing changes indicated that, after removing stock-wide temporal variation, declines at some sites were often accompanied by increases at others, consistent with localized redistribution among haul-out sites.

Table 5. Summary of pairwise directional patterns in year-to-year changes in harbor seal (*Phoca vitulina*) haul-out counts across Hood Canal sites before and after centering within year.

Metric	Raw	Centered
Site pairs changing in the same direction	60.9%	46.0%
Site pairs changing in opposite directions	39.1%	54.0%
Correlation between paired site changes (r)	0.26	-0.10

However, the relatively weak magnitude of the centered relationship indicates that redistribution was spatially limited and did not reflect strong, coordinated displacement across the broader landscape. Instead, opposing site-level changes occurred inconsistently among haul-outs, suggesting localized and context-dependent redistribution rather than predictable movement away from predators or toward specific refuge sites.

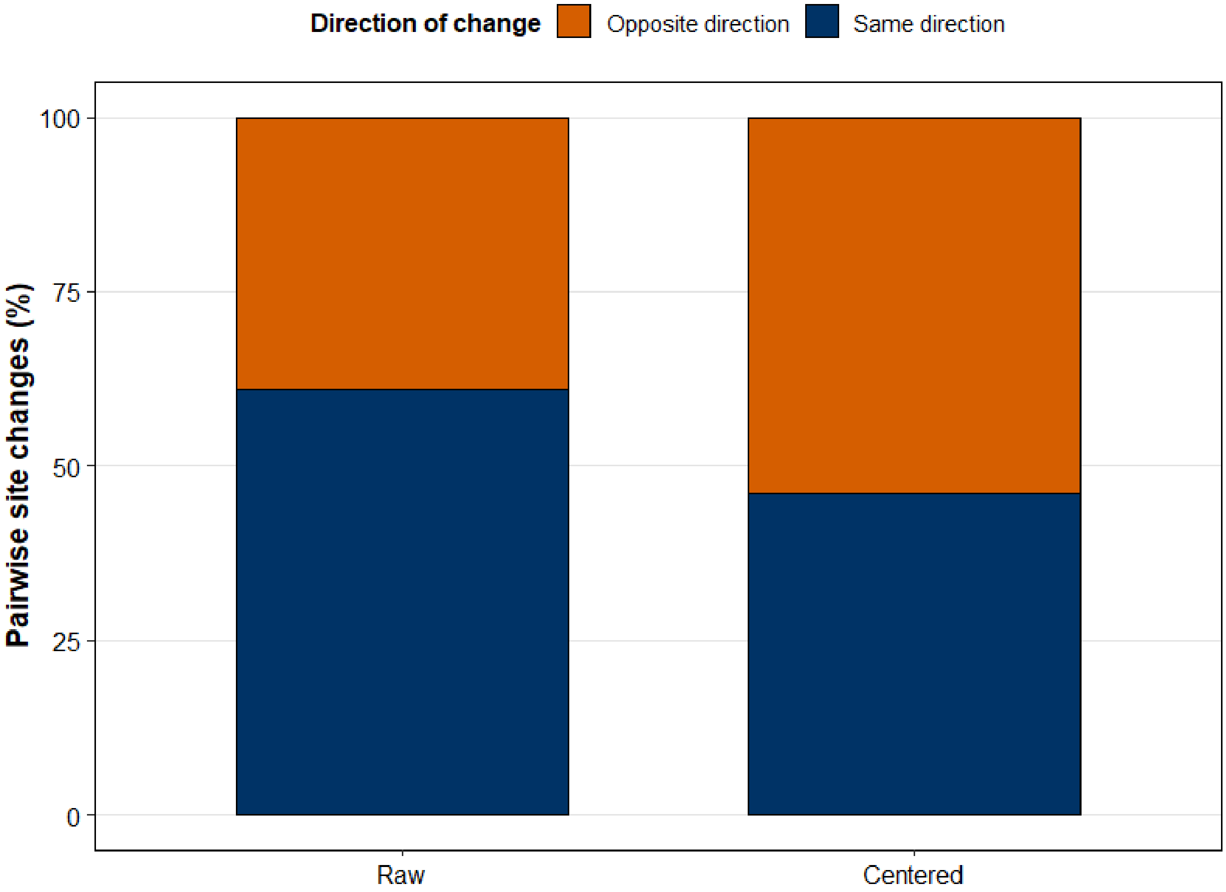

Figure 13. Proportion of pairwise site-level changes in harbor seal (*Phoca vitulina*) haul-out counts across Hood Canal that occurred in the same versus opposite directions. Raw changes more frequently occurred in the same direction, reflecting shared temporal trends across sites. After centering changes within year to account for stock-wide temporal variation, opposite-direction changes became more common, indicating localized redistribution among haul-out sites.

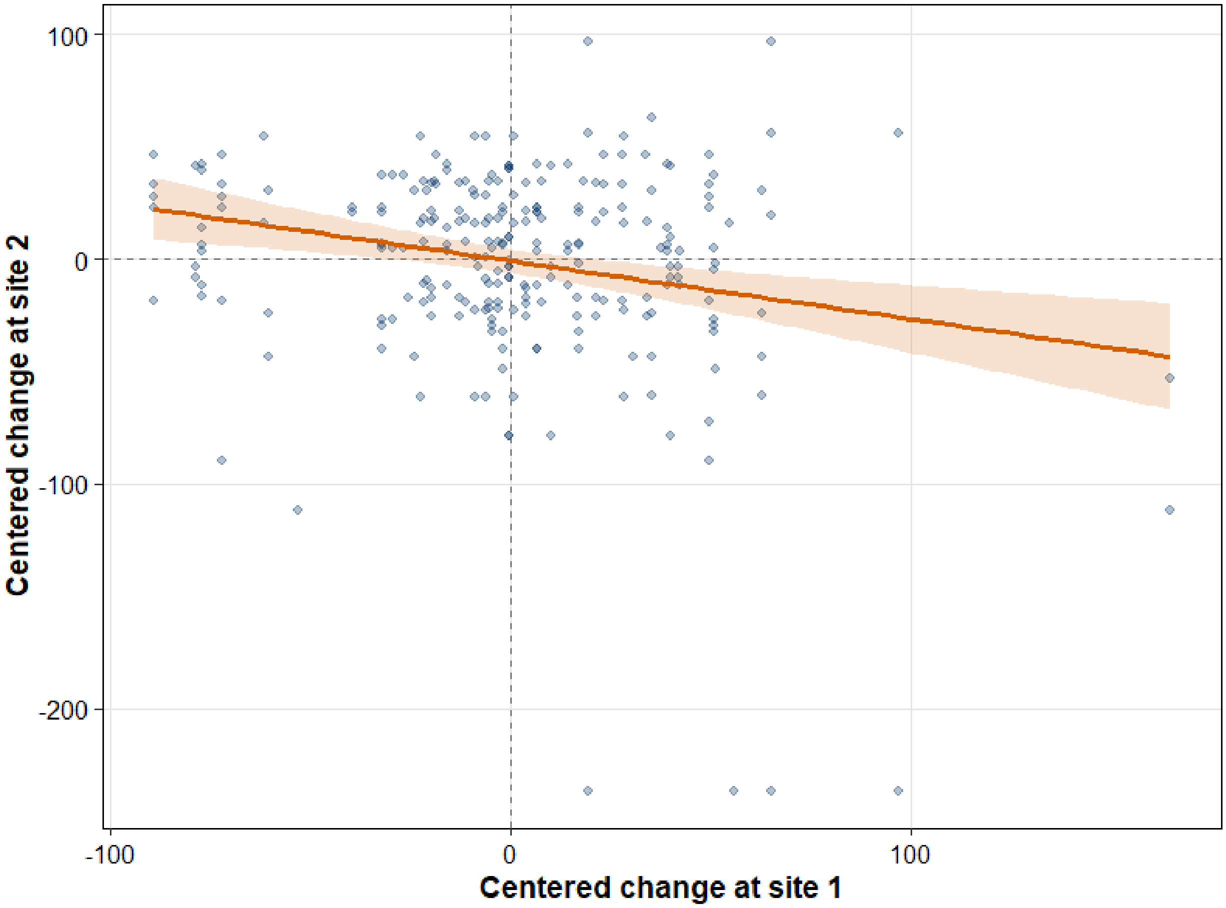

Figure 14. Pairwise comparison of centered year-to-year changes in harbor seal (*Phoca vitulina*) haul-out counts across Hood Canal sites. Each point represents a pair of sites within the same year. The weak negative relationship indicates localized compensatory changes consistent with limited redistribution among haul-out sites.

To further evaluate localized redistribution dynamics, strong positive and negative deviations from annual stock-wide trends were classified as relative "receiver" and "donor" responses within individual years and compared across predator-related covariates. Receiver and donor classifications included 21 site-year observations: 10 receiver observations and 11 donor observations. Killer whale presence within 50 km occurred in 18.2% of donor observations and 0% of receiver observations. Because no receiver observations occurred during predator-present conditions, the binomial model exhibited quasi-separation and produced an unstable coefficient estimate ($\beta = -17.67 \pm 2797.44$ SE, $p = 0.995$). Thus, receiver status could not be reliably associated with predator presence, and sites gaining seals were not predictably distinguished from sites losing seals by nearby predator occurrence.

Together, these findings indicate that while broad-scale haul-out trends were largely synchronous across Hood Canal, underlying site-level deviations revealed weak but detectable localized redistribution among haul-out sites. Redistribution patterns were inconsistent across sites and were not strongly explained by predator occurrence, indicating that haul-out responses were context-dependent rather than reflecting coordinated displacement across the region.

DISCUSSION

Harbor seal haul-out use varied substantially across space and time, with strong site-level differences and modest overall temporal trends. Across inland Washington stocks, the presence of Bigg's killer whales was associated with reduced haul-out counts, although the magnitude and consistency of this effect varied among regions, with the strongest reductions observed in Hood Canal, more moderate effects in Northern Inland waters, and no clear effect in Southern Puget Sound. Rather than producing broad-scale spatial redistribution consistent with generalized fearscape predictions (Heithaus et al. 2008, Wirsing and Ripple 2010), predator presence was associated with localized and context-dependent variation in haul-out usage among sites. Environmental and prey-related covariates influenced haul-out usage but explained relatively little variation compared to persistent spatial structure among sites. This pattern indicates that long-term differences among haul-out locations were stronger drivers of variation than measured environmental conditions.

The context-dependent nature of these responses is consistent with a landscape of fear framework, in which prey alter behavior in response to perceived predation risk rather than responding uniformly across a landscape. Harbor seals likely balance predator avoidance against the benefits provided by individual haul-out locations, including proximity to foraging areas, energetic costs of movement, local habitat characteristics, and social factors. As a result, the same level of predator exposure may produce different responses among sites. Some haul-outs may become less attractive under elevated risk, whereas others may continue to be used because their ecological benefits outweigh the costs associated with predator presence. This trade-off between risk and resource value may help explain why predator occurrence increased spatial variability in haul-out usage without generating strong, coordinated redistribution across the region.

In the absence of killer whales, haul-out counts varied with in-water distance to salmon-bearing waterways, with higher counts generally occurring farther from major salmon-associated areas. When killer whales were present, this relationship shifted, indicating that predator occurrence altered spatial associations between haul-out usage and salmon accessibility. Importantly, predator presence did not consistently shift seals toward or away from salmon-bearing waterways across regions, suggesting that changes in seal–salmon overlap were site-specific rather than directionally structured at broader spatial scales. Site-level change analyses further showed that while broad temporal trends were generally shared across sites, localized deviations in haul-out use varied substantially among locations and were not consistently explained by predator presence, prey accessibility, or habitat characteristics. Together, these findings suggest that killer whale presence contributed to increased spatial variability in harbor seal haul-out behavior rather than coordinated displacement across the landscape. Responses to predation risk were heterogeneous among sites, with some haul-outs increasing in use while others declined under similar levels of predator exposure.

Regional Trends in Haul-Out Usage

Harbor seal haul-out usage across Washington State waters exhibited broad-scale temporal structure during the study period. Because haul-out counts reflect behavioral use of sites rather than total abundance, these patterns represent changes in haul-out usage rather than population size. Stock-level models indicated that temporal patterns differed among management units, with the Coastal stock showing a significant long-term increase in haul-out counts (~2.6% per year), while inland Salish Sea stocks (Hood Canal, Northern Inland, and Southern Puget Sound) exhibited weaker and statistically uncertain trends. Confidence intervals for inland stocks overlapped at zero, indicating that temporal changes in these regions were not distinguishable from no trend. These findings suggest that stock-level summaries capture broad regional differences in haul-out dynamics but may obscure finer-scale variation occurring among individual sites.

When site-level structure was incorporated through hierarchical negative binomial mixed-effects models, a clearer regional pattern emerged. Mean annual haul-out counts increased modestly across sites during the study period (~1.2–1.5% per year, depending on model structure), indicating a shared temporal signal that became apparent after accounting for variation among individual haul-out locations. Most sites followed broadly similar temporal trajectories despite substantial differences in baseline haul-out usage, as indicated by low random slope variance and large random intercept variance. Together, these results suggest that temporal dynamics were generally coherent across the region, while persistent spatial heterogeneity in haul-out use was driven primarily by consistent differences among sites.

This coherence is consistent with regional-scale ecological processes influencing harbor seal behavior across the Salish Sea. Long-term changes in harbor seal populations have previously been linked to post-protection recovery (Jeffries et al. 2003, Jefferson et al. 2021, Pearson et al.

2025), as well as oceanographic and climatic variability (Mantua et al. 2010, Bond et al. 2015, Cavole et al. 2016), although these mechanisms were not directly evaluated here. At the same time, the relatively modest temporal trend combined with strong and persistent site-level differences suggests that local habitat characteristics and site fidelity remain dominant drivers of haul-out usage. Harbor seals are known to repeatedly use specific haul-out locations and respond strongly to local environmental conditions (London et al. 2012, Peterson et al. 2012, Brusa et al. 2025). Together, these findings indicate that regional processes influence how haul-out usage changes through time, while local conditions largely determine where seals haul out within the landscape.

Some degree of spatial heterogeneity in haul-out usage likely reflects sampling variability associated with survey conditions, including tidal state, weather, and observation error. However, temporal trajectories remained broadly parallel across sites, suggesting that interannual variation was consistently captured despite these sources of noise. The persistence of spatial heterogeneity after accounting for shared temporal trends therefore supports the interpretation that differences among haul-out sites reflect underlying ecological variation, including localized responses to habitat characteristics and predation risk. Importantly, these findings indicate that responses to killer whale presence occurred within a system characterized by shared regional temporal dynamics but strong site-level spatial structure. As a result, broad regional summaries alone may underestimate or obscure localized behavioral responses to predation risk, reinforcing the importance of evaluating predator–prey dynamics across multiple spatial scales.

Site-Level Heterogeneity

Although temporal trajectories were broadly similar among sites, substantial variation existed in baseline haul-out usage across the study region. Random intercept variance in the hierarchical model was large, indicating that some haul-out sites consistently supported higher numbers of seals than others. These persistent differences likely reflect spatial variation in habitat characteristics, accessibility, prey availability, and long-term site fidelity, all of which are known to influence harbor seal haul-out behavior in the Salish Sea (London et al. 2012, Peterson et al. 2012, Brusa et al. 2025). Harbor seals frequently exhibit repeated use of specific haul-out locations and strong fidelity to sites across years (Cunningham et al. 2009, Peterson et al. 2012), suggesting that these baseline differences reflect long-standing spatial structuring of haul-out use rather than transient fluctuations. Although fine-scale habitat features and localized prey dynamics were not explicitly measured here, the observed patterns are consistent with persistent ecological and behavioral drivers of site use.

In contrast, random slope variance associated with year was comparatively small, indicating that most sites changed through time at similar rates and broadly tracked the population-level trend. Only a limited number of sites exhibited strongly divergent trajectories, suggesting that site-specific deviations from regional temporal patterns were relatively uncommon. This coherence is consistent with the influence of regional-scale ecological drivers, including oceanographic variability and prey dynamics, which operate across multiple spatial scales in the Salish Sea (Mantua et al. 2010, Bond et al. 2015). At the same time, persistent site-level differences indicate that regional processes do not override local habitat structure. Instead, spatial and temporal processes appear to operate simultaneously, with site-specific characteristics shaping baseline haul-out use while broader regional drivers influence temporal change through time.

Some degree of site-level variability likely reflects sampling differences among locations, including variation in tidal state, weather, and visibility during surveys. However, the consistency of temporal trajectories across sites suggests that interannual variation was captured reliably despite these sources of noise. The persistence of strong spatial heterogeneity after accounting for shared temporal trends therefore supports the interpretation that differences among haul-out sites reflect underlying ecological and behavioral variation rather than sampling variability alone.

This distinction is important for interpreting predator and environmental effects because it demonstrates that observed changes in haul-out usage occurred within a system characterized by strong pre-existing spatial structure. Predator-associated changes in haul-out counts therefore likely reflect localized modifications of site use that increase spatial variability in haul-out behavior, rather than large-scale redistribution of seals across the landscape. Importantly, most haul-out site-years in inland Washington waters experienced some degree of killer whale exposure, suggesting that predator-free refugia may be limited at broader spatial scales and that predation risk may function as a relatively chronic feature of the system rather than a localized or infrequent disturbance. Under these conditions, seals may respond to predation risk primarily through localized behavioral adjustments within existing haul-out networks rather than broad-scale relocation among regions. This context is important for evaluating the ecological significance of predator effects, as it suggests that behavioral responses to predation risk are layered onto persistent site-level differences rather than fundamentally restructuring the overall spatial distribution of harbor seals.

Predator Presence

Across inland Washington State waters, Bigg's killer whale presence within 50 km of haul-out sites was associated with reduced harbor seal haul-out counts (~10–13%), providing strong support for the hypothesis that predator presence influences haul-out behavior. This relationship remained consistent across hierarchical model formulations, indicating that the observed effect was robust to variation in model structure and covariate inclusion. Importantly, predator occurrence explained variation in haul-out usage more effectively than predator activity, as models based on the number of sightings received substantially weaker support. This suggests that the broader spatial presence of predators was sufficient to alter seal behavior, regardless of encounter frequency. Similar threshold-based responses have been documented in other predator–prey systems, where prey respond to the risk of predation rather than the intensity of predator activity (Lima and Dill 1990, Wirsing et al. 2021). In the Salish Sea, harbor seals may therefore respond to the general occurrence of Bigg's killer whales across the landscape rather than tracking fine-scale variation in predator movements.

Temporal analyses further indicated that haul-out counts were lowest under cumulative predator exposure (~16–17% reduction), with weaker effects observed for current-year or lagged predator presence alone. This pattern suggests that seals respond to integrated predation risk across both space and time rather than discrete encounters, potentially reflecting repeated exposure, memory, or learned avoidance of high-risk areas. Such responses are consistent with theoretical and empirical work demonstrating that prey integrates risk across temporal scales when making habitat-use decisions (Heithaus et al. 2008, Klimley et al. 2021). In this system, the persistence of reduced haul-out usage following recent predator exposure suggests that behavioral responses extend beyond immediate encounters and may influence site use over longer time periods. Together, these findings indicate that predator effects are not limited to short-term disturbance but instead reflect sustained behavioral adjustments to perceived predation risk.

These findings are also consistent with the ecology of Bigg's killer whales, which are specialized marine mammal predators with a well-documented reliance on harbor seals and other pinnipeds (Ford et al. 1998, Ford et al. 2010). Increases in Bigg's killer whale occurrence in inland waters over recent decades (Shields et al. 2018, Murray et al. 2025) likely represent a sustained increase in predation risk for harbor seals. Within this context, reductions in haul-out counts may reflect behavioral avoidance of high-risk areas, shifts in haul-out timing, or increased time spent in the water, all of which have been documented in pinniped responses to disturbance and predation risk (Allen et al. 1984, Cunningham et al. 2009, London et al. 2012). These behavioral responses are consistent with non-consumptive predator effects, in which predators influence prey through changes in behavior rather than direct consumption. Importantly, reductions in haul-out counts do not necessarily indicate reductions in seal abundance. Instead, lower counts likely reflect changes in how seals used haul-out sites, including temporary displacement, altered haul-out timing, increased time spent in the water, or shifts among nearby locations. Consequently, predator-associated declines in haul-out counts should be interpreted primarily as behavioral responses to predation risk rather than direct evidence of population-level change.

However, predator effects were not uniform across regions. The strongest reductions occurred in Hood Canal, while Northern Inland exhibited more moderate reductions and Southern Puget Sound showed no statistically detectable effect. This variation is directly supported by interaction models and indicates that predator effects differed systematically among regions and habitat contexts, with the strongest reductions occurring in Hood Canal, weaker responses in Northern Inland, and little evidence of consistent effects in Southern Puget Sound. Similar spatial variability in predator effects has been observed in other systems, where habitat complexity, prey distribution, and predator behavior influence the strength and detectability of risk responses (Wirsing and Ripple 2010, De Vos et al. 2015).

In the Salish Sea, regional differences in circulation, basin structure, and residence time (Babson et al. 2006, Khangaonkar et al. 2019) may influence both predator movement patterns and prey aggregation, potentially shaping where predator effects are strongest. For example, the enclosed nature of Hood Canal may concentrate predator activity or limit escape options for seals (Babson et al. 2006, Khangaonkar et al. 2019), leading to stronger behavioral responses. However, these mechanisms were not directly tested here and should therefore be interpreted as potential explanations rather than definitive drivers. This regional variation reinforces that predator effects operate within a heterogeneous landscape, where local environmental context mediates how predation risk is expressed.

Overall, these results provide strong evidence that predator presence influences harbor seal haul-out behavior through non-consumptive effects, but that the magnitude and expression of these effects vary across space and time. Rather than producing coordinated displacement across the landscape, predator presence appeared to increase spatial variability in haul-out behavior, with localized responses differing among sites and regions. These findings indicate that predator–prey interactions in this system are mediated by both regional processes and local environmental context, highlighting the importance of considering spatial heterogeneity when evaluating the ecological consequences of predator recovery.

Spatial Redistribution in Haul-Out Use

The Hood Canal analysis showed that patterns of haul-out change depended strongly on whether shared temporal trends were considered. In raw counts, sites tended to increase or decrease concurrently, indicating that haul-out use was largely driven by stock-wide processes such as regional population trends or broad environmental conditions. This result is supported by the positive correlation in paired site changes and suggests that haul-out sites generally did not function as direct substitutes for one another, but instead responded similarly to shared regional drivers. Similar synchrony in site use has been observed in other marine mammal systems, where broad-scale environmental variability and population dynamics drive coordinated responses across locations (Mantua et al. 2010, Bond et al. 2015).

After accounting for these shared temporal trends, centered analyses revealed a weaker signal of localized redistribution, with declines at some sites often accompanied by increases at others. However, the magnitude of this redistribution was limited, as indicated by the weak negative correlation between paired site changes, suggesting that shifts in haul-out usage were limited in magnitude and not coordinated across the landscape. Instead, changes varied among sites and were likely influenced by local environmental conditions, site-specific characteristics, and individual behavioral differences, including site fidelity and localized habitat use (London et al. 2012, Peterson et al. 2012). Importantly, these changes lacked consistent direction relative to predator presence, prey accessibility, or habitat features; sites were not systematically more likely to increase near salmon-bearing waterways, closer to mainland habitat, or farther from killer whale activity. This absence of directional patterning suggests that redistribution was not consistently structured by environmental gradients, but instead reflected localized and context-dependent behavioral responses, consistent with patterns observed in other systems where predation risk increases behavioral heterogeneity without producing coordinated displacement (Wirsing and Ripple 2010, De Vos et al. 2015).

These findings suggest that predator presence influenced haul-out usage without producing broad-scale or directional redistribution across sites. Although some evidence of localized redistribution was detected, the analyses were unable to identify consistent destination sites or refuge areas. This suggests that seals were not responding by moving toward a predictable set of alternative haul-outs. Instead, responses may have involved temporary shifts among multiple nearby sites, changes in haul-out attendance, or behavioral adjustments occurring at spatial scales smaller than those captured by the monitored haul-out network. One possible explanation is that predator exposure was widespread across inland Washington waters, limiting the availability of predator-free refugia at broader spatial scales. Under these conditions, predation risk may function as a relatively chronic feature of the system rather than a localized or infrequent disturbance, reducing the likelihood of coordinated relocation among haul-out sites. Instead, seals may respond primarily through localized behavioral adjustments within existing haul-out networks, including changes in haul-out attendance, timing, or fine-scale site use. This interpretation aligns with broader patterns observed throughout the study, where strong site-level spatial structure constrained how behavioral responses were expressed across the landscape (Peterson et al. 2012, Brusa et al. 2025), and is consistent with studies showing that non-consumptive predator effects can alter prey behavior without necessarily producing coordinated movement patterns (Schmitz et al. 2010, Wirsing et al. 2021).

These localized responses may reflect changes in haul-out behavior rather than broad relocation to alternative monitored sites (Allen et al. 1984, Cunningham et al. 2009, London et al. 2012). Individuals may have remained in the water for longer periods, shifted haul-out timing outside survey windows, or temporarily used unmonitored or less accessible haul-out locations. These behavioral adjustments could reduce observed haul-out counts without requiring large-scale spatial displacement and are consistent with studies showing that perceived predation risk can alter pinniped resting behavior, fine-scale habitat use, and time allocation between vigilance and other activities (Peterson et al. 2012, De Vos et al. 2015, Wirsing et al. 2021). Distinguishing among these mechanisms would require higher-resolution movement and behavioral data, such as telemetry, finer temporal survey coverage, or expanded monitoring of haul-out locations. Such approaches could help clarify whether predator-associated changes primarily reflect altered activity patterns, temporary use of alternative haul-out locations, or other behavioral responses not captured through broad-scale aerial monitoring.

Salmon Accessibility

Prey availability is expected to play a central role in shaping harbor seal distribution, particularly given the importance of Pacific salmon in harbor seal diets in the Salish Sea (Lance et al. 2012, Chasco et al. 2017, Schwarz et al. 2018). However, its influence in this study was not straightforward. Although haul-out counts were descriptively higher where salmon-bearing waterways occurred within 50 km, this relationship was not supported after accounting for other covariates, indicating that simple binary measures of salmon proximity did not explain spatial patterns in haul-out usage. This may partially reflect ecological variation among salmon-bearing waterways themselves, as systems classified as supporting salmon ranged from small seasonal streams to large river systems that likely differ substantially in salmon abundance, timing, and foraging value to harbor seals. As a result, static measures of prey accessibility may not adequately capture the dynamic and localized nature of foraging opportunities, particularly in systems where prey distributions vary substantially across space and time (Quinn and Losee 2022).

In contrast, distance-based measures of prey accessibility revealed clearer spatial patterns, with haul-out counts varying as a function of in-water distance to salmon-bearing waterways. Under predator-absent conditions, haul-out counts increased with distance from salmon-bearing waterways, suggesting that haul-out sites were often spatially separated from primary salmon-associated foraging areas. This pattern may reflect a decoupling of haul-out and foraging locations, where seals travel between distinct resting and feeding areas rather than concentrating both activities near prey resources (London et al. 2012, Peterson et al. 2012). Predator presence modified this relationship weakly, indicating that predation risk may influence how seals use space relative to prey accessibility, although the interaction was limited in magnitude and should be interpreted cautiously. Importantly, predator presence did not consistently shift seals toward or away from salmon-bearing waterways across regions, suggesting that changes in seal–salmon spatial overlap were site-specific rather than directionally structured at broader spatial scales. For example, predator-associated reductions in haul-out usage were strongest in Hood Canal, whereas Southern Puget Sound exhibited little evidence of consistent predator effects despite similar broad predator exposure metrics. One possible explanation is that the relative value of individual haul-outs differed among regions and sites. Haul-outs located near productive foraging habitats or important movement corridors may continue to provide substantial energetic benefits despite increased predation risk, whereas lower-value sites may be abandoned more readily. Under a landscape-of-fear framework, individuals are expected to balance predator avoidance against resource acquisition, producing heterogeneous responses among locations rather than uniform behavioral shifts across the region. Likewise, some haul-out sites exhibited reduced usage near salmon-bearing waterways under predator-present conditions, whereas others showed little change or opposite responses. Together, these findings suggest that increasing Bigg's killer whale presence is unlikely to produce consistent regional shifts in how seals use areas associated with salmon-bearing waterways across the Salish Sea.

These findings indicate that continuous spatial measures of salmon accessibility explained variation in haul-out usage more effectively than simple binary proximity measures. In-water distance likely reflected the energetic and spatial costs associated with movement between resting and foraging areas (Cunningham et al. 2009, Peterson et al. 2012), suggesting that the spatial configuration of prey resources influenced haul-out selection more strongly than prey occurrence alone. This interpretation is consistent with previous work showing that harbor seals respond to localized and seasonal prey pulses rather than static prey distributions (Thomas et al. 2011, Allegue et al. 2020). However, because predator-associated effects relative to salmon accessibility were relatively weak and inconsistent among sites, the extent to which predation risk altered spatial relationships between seals and salmon-bearing waterways remains uncertain.

Regional differences in predator-associated responses relative to salmon accessibility may also reflect broader environmental and habitat differences among inland stocks. Hood Canal, where predator-associated reductions in haul-out usage were strongest, is characterized by a relatively narrow and spatially constrained basin structure that may limit movement options and increase the spatial extent of perceived predation risk. In contrast, more open and spatially connected regions such as Southern Puget Sound and the Strait of Juan de Fuca may provide greater flexibility in haul-out selection and movement pathways. Differences in shoreline configuration, haul-out availability, river accessibility, and localized habitat structure may therefore influence how predator exposure interacts with prey accessibility across regions. These findings suggest that relationships between predator presence and salmon-associated habitat use were mediated by regional environmental context rather than driven by a single consistent behavioral response across Washington State inland waters.

These findings indicate that prey accessibility alone did not explain haul-out usage patterns, but instead interacted with predator presence and environmental context to shape spatial variation in site use. However, because this study did not directly evaluate foraging behavior, movement patterns, or prey consumption, implications for seal–salmon interactions remain inferential.

Overall, these results support the broader conclusion that predator–prey interactions in this system were shaped by multiple interacting ecological factors rather than prey accessibility alone (Brown and Kotler 2004, Heithaus et al. 2008).

Habitat Characteristics

Habitat characteristics were strongly associated with variation in harbor seal haul-out usage. Shoreline type was one of the strongest predictors, with sand and gravel and artificial shorelines supporting higher haul-out counts than rocky shorelines. These differences likely reflect variation in accessibility, substrate, and exposure, with more gently sloping or human-modified shorelines potentially providing more suitable haul-out conditions. Similar associations between substrate, accessibility, and haul-out use have been documented in harbor seals, where site selection is strongly influenced by local physical characteristics (Petersen et al. 2002, London et al. 2012). Distance from the mainland also influenced haul-out usage, with offshore sites generally supporting higher counts than nearshore sites, although this effect was more evident between broad habitat categories than along a continuous distance gradient. In contrast, water depth was not strongly associated with haul-out counts, whereas haul-out counts were generally higher at sites located closer to river mouths and riverine inputs. This relationship may reflect variation in prey accessibility or environmental conditions associated with river systems, although riverine habitats likely differed substantially in salmon abundance, seasonal use, and ecological importance to harbor seals. Importantly, this broad-scale association with river proximity did not translate into consistent directional redistribution toward salmon-bearing waterways, as site-level redistribution analyses showed no tendency for sites closer to salmon to systematically gain seals, potentially reflecting substantial ecological variation among river systems as well as localized behavioral responses among sites. Overall, the magnitude of habitat effects remained modest relative to strong site-level differences, indicating that broad habitat structure influences haul-out use while persistent local site characteristics remain dominant drivers of spatial variation.

After accounting for habitat characteristics, predator effects remained evident but were somewhat reduced, suggesting that responses to predation risk were partially mediated by environmental context. However, habitat variables did not consistently explain variation in predator effects. Predator–habitat interaction models indicated that the strength of predator effects did not differ significantly among shoreline types and was not strongly associated with distance from the mainland. A weak interaction between predator presence and nearshore versus offshore position suggested that predator effects may have been somewhat stronger at offshore sites, although this pattern was limited and not consistently supported across habitat gradients. Offshore haul-outs may offer fewer nearby refuge opportunities and require longer movements to reach alternative haul-out locations following predator encounters. In contrast, nearshore sites often occur within more complex shoreline environments and may provide greater flexibility for localized behavioral adjustments. Although this pattern was relatively weak, it suggests that movement constraints and refuge availability may influence how predation risk is expressed across different haul-out contexts. Together, these results indicate that while habitat characteristics influence baseline haul-out usage, they do not provide a simple framework for predicting how seals respond to predation risk. Instead, predator effects appeared to occur across a range of habitat contexts, reinforcing the importance of perceived predation risk over specific physical habitat features, consistent with broader studies showing that prey responses to predators are often governed more strongly by perceived risk than by static habitat structure alone (Brown and Kotler 2004, Heithaus et al. 2008, Wirsing et al. 2021).

In practice, this suggests that habitat characteristics were more important for determining where seals consistently hauled out, whereas predator presence influenced how those sites were used through time. Offshore haul-out sites and sites associated with artificial, or sand-and-gravel shorelines generally supported higher seal counts overall, but predator-associated reductions occurred across multiple habitat contexts rather than being confined to a particular shoreline type or spatial configuration.

Model evaluation indicated that most variation in haul-out usage was associated with persistent site-level and stock-level structure rather than measured environmental covariates, with fixed effects explaining a relatively small proportion of total variation compared to the full hierarchical model. This finding further supports the broader conclusion that long-standing spatial structure and local site characteristics are dominant drivers of harbor seal haul-out distribution. Within this framework, predator presence represented a secondary but consistent influence that modified site use without overriding underlying spatial patterns. Weak residual spatial autocorrelation additionally suggests that some unmeasured spatially structured processes likely influenced haul-out usage, including fine-scale habitat characteristics, localized prey dynamics, or site-specific environmental conditions not fully captured by the covariates included in this study.

The stronger relationship between haul-out counts and cumulative predator exposure, compared to current-year predator presence alone, further supports the interpretation that seals responded to integrated predation risk across time rather than solely to immediate encounters. This pattern is consistent with broader theory surrounding non-consumptive predator effects, where prey integrate repeated or persistent exposure into long-term behavioral decision-making (Heithaus et al. 2008, Klimley et al. 2021). Importantly, predator effects were expressed within an already highly structured spatial system, indicating that behavioral responses to killer whale presence were layered onto existing habitat and site-use patterns rather than fundamentally restructuring seal distribution across the landscape. Together, these findings suggest that habitat structure largely determines where seals haul out, while predator presence influences how those sites are used through time.

Implications for Predator-Prey Dynamics

The recovery of Bigg's killer whales represents a major ecological shift in the Salish Sea. As apex predators, they influence prey not only through direct predation but also through behavioral responses to perceived risk, commonly referred to as non-consumptive effects (Lima and Dill 1990, Heithaus et al. 2008, Wirsing et al. 2021). In this study, killer whale presence was consistently associated with reduced harbor seal haul-out usage across inland Washington waters, although the magnitude of these effects varied among regions and sites. Hood Canal exhibited the strongest predator-associated reductions in haul-out counts, Northern Inland showed weaker but generally negative responses, and Southern Puget Sound showed little evidence of consistent predator effects. Rather than producing coordinated redistribution away from predator-exposed areas, predator presence was associated with localized and heterogeneous changes in site use, with some haul-out sites increasing while others declined under similar predator conditions. Short-term responses to predator presence were also highly variable and not consistently supported, suggesting that seals did not respond uniformly to individual predator encounters but instead adjusted haul-out behavior over longer temporal scales and within localized habitat and prey-accessibility contexts.

These findings suggest that predator recovery in the Salish Sea may influence harbor seal behavior primarily by modifying how seals use existing haul-out sites rather than by causing large-scale redistribution across the landscape. Strong site-level structure remained the dominant driver of haul-out usage throughout the study, indicating that local habitat characteristics, prey accessibility, and long-term site fidelity constrained how predator responses were expressed spatially. Predator effects therefore appeared to operate within an already strongly structured spatial system, where behavioral responses were layered onto persistent differences among haul-out sites rather than restructuring overall seal distribution. This pattern is consistent with studies showing that predation risk in marine systems often produces context-dependent behavioral responses shaped by habitat configuration, movement constraints, and localized environmental conditions (Heithaus et al. 2008, De Vos et al. 2015). More broadly, these results suggest that the recovery of Bigg's killer whales represents more than the return of a top predator. Increasing predator occurrence has the potential to influence prey behavior, habitat use, and species interactions through non-consumptive pathways, even when direct predation events are rarely observed. Consequently, ecosystem responses to predator recovery may emerge through changes in prey behavior and spatial overlap with resources rather than through mortality alone.

These results also have implications for understanding predator–prey overlap involving Pacific salmon. Harbor seals are important predators of salmon throughout the Salish Sea (Chasco et al. 2017, Nelson et al. 2019, Nelson et al. 2024), and predator-associated changes in seal haul-out behavior may therefore influence where seals overlap spatially with salmon-bearing waterways. However, predator presence did not consistently shift seals toward or away from salmon systems across regions, and relationships between predator exposure and salmon accessibility were relatively weak. Instead, responses varied among sites and environmental contexts, suggesting that predator recovery is unlikely to produce simple or uniform reductions in seal–salmon overlap across the region. Rather, any effects on salmon predation pressure are likely to occur at localized spatial scales and vary depending on site-specific habitat characteristics, prey accessibility, and predator exposure history.

Regional differences in predator-associated responses may also reflect differences in basin geometry and movement constraints across inland waters. Hood Canal is a relatively narrow and semi-enclosed system, where haul-out sites near terminal basin regions may experience predator exposure across a large proportion of the available marine landscape and have fewer opportunities for spatial refuge within a 50-km radius. In contrast, haul-out sites near the Strait of Juan de Fuca and other open inland waterways occur within more spatially connected environments, where movement pathways and potential refuge areas are less constrained. Under these conditions, predator risk may function differently across regions, potentially contributing to the stronger and more consistent predator-associated reductions observed in Hood Canal relative to other inland stocks.

Overall, these findings suggest that non-consumptive predator effects in the Salish Sea were not driven by a single landscape-scale mechanism operating uniformly across Washington State waters. Instead, responses depended on regional basin structure, persistent site-level differences, prey accessibility, and the widespread nature of predator exposure across inland waters. Predator-associated reductions in haul-out usage were strongest in Hood Canal, more moderate in Northern Inland waters, and weak or inconsistent in Southern Puget Sound, indicating that responses to predation risk varied substantially among regions. Strong site fidelity and persistent spatial structure also appeared to constrain broad-scale redistribution, causing predator effects to emerge primarily through localized behavioral adjustments within existing haul-out networks rather than coordinated displacement across the landscape. As Bigg's killer whale populations continue to recover, ecosystem responses may therefore emerge through changes in the spatial heterogeneity of prey behavior and predator–prey overlap rather than through predictable landscape-scale displacement of harbor seals. Consequently, managers should expect localized and context-dependent behavioral responses that vary among stocks, habitats, and individual haul-out sites rather than simple or uniform reductions in seal use of salmon-associated areas.

Study Limitations and Future Directions

Despite the broad spatial and temporal coverage of this dataset, several limitations should be considered when interpreting these results. First, predator exposure was inferred from documented Bigg's killer whale sightings rather than direct measures of predator presence at individual haul-out sites. Opportunistic sighting records may underestimate predator occurrence in some areas or years, particularly in regions with lower observation effort (Houghton et al. 2015, Shields et al. 2018). However, sensitivity analyses excluding western Northern Inland haul-out sites near the western Strait of Juan de Fuca produced qualitatively similar results to the primary analyses, indicating that inferred predator effects were not strongly influenced by potential under detection of killer whale sightings near the spatial boundary of the observation dataset. As a result, the proximity metrics used here likely represent conservative estimates of predator exposure, consistent with limitations identified in other studies relying on opportunistic marine predator observations.

Second, the spatial threshold used to define predator presence (≤ 50 km) captured regional predator proximity but did not necessarily reflect direct predator–prey encounters at individual haul-out sites. Bigg's killer whales can travel rapidly across large areas (Ford et al. 2010), and harbor seals may respond to predation risk across spatial or temporal scales that differ from those represented by available sighting data (Heithaus et al. 2008, Wirsing et al. 2021). Consequently, the observed associations between predator presence and haul-out counts should be interpreted as broad-scale behavioral responses to predation risk rather than direct predator–prey interactions.

Finally, haul-out counts represent a behavioral measure of site use rather than a direct estimate of population size. Changes in observed counts may therefore reflect altered haul-out behavior, shifts in site use, or variation in haul-out attendance during surveys rather than changes in total seal abundance. In addition, aerial surveys provided only discrete temporal snapshots of haul-out usage and could not capture fine-scale behavioral responses occurring outside survey windows. Consistent with this limitation, short-term analyses in this study revealed highly variable and non-significant immediate responses to killer whale presence, suggesting that fine-scale behavioral responses may not be consistently detectable at the temporal resolution of available survey data. Such variability is inherent to haul-out monitoring datasets and has been widely documented in pinniped studies, where haul-out attendance varies with environmental conditions, disturbance, and individual behavior (Allen et al. 1984, London et al. 2012 The short-term analysis was also limited by the relatively small number of site-event comparisons available for evaluation. Consequently, the absence of statistically significant short-term effects should be interpreted cautiously and does not necessarily indicate the absence of biologically meaningful short-term responses.

Additional limitations stem from the relatively coarse resolution of several environmental covariates. Metrics such as distance to salmon-bearing waterways and shoreline classifications likely captured broad spatial gradients but may not fully represent localized prey dynamics, habitat quality, or fine-scale movement behavior. Salmon-bearing waterways likely differed substantially in run size, seasonal timing, species composition, and ecological importance to harbor seals, but these differences were not incorporated into the prey accessibility metrics used here. As a result, sites classified similarly in terms of salmon proximity may have differed considerably in actual prey availability. Similarly, the analyses focused on monitored haul-out sites and therefore could not evaluate whether seals temporarily used unmonitored or less accessible locations in response to predator presence. This limitation is particularly important given that predator-associated responses in this study appeared to increase spatial variability in haul-out behavior without producing coordinated redistribution across monitored sites.

Future research could build on these findings by incorporating more detailed information on predator movements, prey availability, and fine-scale seal behavior. Telemetry studies tracking both harbor seals and Bigg's killer whales would provide insight into how seals respond to predator encounters across shorter spatial and temporal scales and could help distinguish between temporary displacement, altered haul-out timing, increased time spent in the water, and broader changes in movement behavior. Similarly, higher-frequency monitoring before and after predator occurrences could help resolve short-term behavioral responses that may not be detectable using annual aerial survey data. Continuous haul-out monitoring, drone-based surveys, or remote camera systems may be particularly useful for identifying immediate responses to predator encounters and determining how quickly seals return to affected haul-out sites. Such approaches have been used successfully to quantify predator–prey interactions and movement responses in marine systems (Heithaus et al. 2008, De Vos et al. 2015) and would directly address the localized and context-dependent predator effects identified here by linking behavioral responses to real-time predator exposure. Importantly, predator-associated effects were detected despite the relatively coarse temporal and spatial resolution of the available haul-out and predator-occurrence datasets. This suggests that finer-scale behavioral and movement studies may reveal more immediate or more clearly resolved responses to predation risk than were detectable through broad-scale aerial monitoring alone.

Additional work examining seasonal prey dynamics, foraging behavior, and environmental variability would also improve understanding of how harbor seals balance predation risk with foraging opportunities across the Salish Sea (Thomas et al. 2011, Allegue et al. 2020). Because harbor seals are important predators of Pacific salmon and other forage fish (Chasco et al. 2017, Nelson et al. 2019, Nelson et al. 2024), clarifying how predator-driven behavioral responses influence seal–salmon overlap may provide broader insight into ecosystem dynamics as marine mammal populations continue to recover.

Conclusion

Predators influence ecosystems not only through direct consumption but also through the behavioral responses they induce in prey. This study evaluated whether increasing Bigg’s killer whales’ presence in the Salish Sea was associated with changes in harbor seal haul-out behavior, with particular emphasis on the non-consumptive effects of predation risk. By integrating long-term haul-out monitoring data with records of predator occurrence and environmental variables, this research examined how ecological context shaped patterns of haul-out usage across Washington State inland waters.

Harbor seal haul-out usage exhibited substantial spatial heterogeneity across sites and through time. Although population-level analyses indicated a modest overall increase in haul-out counts through time, site-level models showed that most haul-out sites followed broadly similar temporal trajectories, with variation driven primarily by persistent differences among sites. Habitat characteristics, including shoreline type, proximity to mainland habitat, and accessibility to salmon-bearing waterways, were associated with variation in haul-out usage, indicating that environmental context played an important role in structuring site use. Predator presence represented an additional ecological driver influencing harbor seal behavior, with Bigg’s killer whale presence consistently associated with reduced haul-out usage across inland waters, supporting the role of non-consumptive predator effects in this system. However, predator effects were highly context dependent and varied among regions, habitats, and haul-out locations.

Although localized redistribution among haul-out sites was evident after accounting for shared temporal trends, these changes did not occur in consistent directions relative to predator presence, prey accessibility, or habitat characteristics. Instead, predator-associated responses primarily reflected increased spatial variability in haul-out behavior, suggesting that non-consumptive predator effects emerged through heterogeneous and site-specific responses. These findings highlight that predator recovery may alter prey behavior in complex and context-dependent ways that are difficult to predict at broad spatial scales. As a result, frameworks that assume uniform prey displacement in response to predators may overlook important localized dynamics that shape ecological interactions and prey overlap with shared resources such as Pacific salmon.

Overall, these findings demonstrate that harbor seal distribution in the Salish Sea is primarily structured by persistent site-level spatial differences, with predator presence acting as a secondary but consistent influence layered onto this existing framework. Importantly, predator effects in this system did not produce the predictable landscape-scale displacement expected under generalized fearscape frameworks. Instead, predator recovery appeared to increase spatial variability and behavioral heterogeneity in how seals used space across regions and through time, consistent with studies showing that non-consumptive predator effects can alter prey behavior without producing coordinated redistribution (Schmitz et al. 2010, Wirsing et al. 2021). This distinction is particularly relevant in the Salish Sea, where changes in harbor seal behavior may influence spatial overlap with prey species such as Pacific salmon in localized and context-dependent ways. These findings suggest that increasing Bigg's killer whale presence is unlikely to produce simple or predictable reductions in harbor seal overlap with salmon systems across the region. Rather than restructuring seal distribution uniformly across inland waters, predator effects operated within an already strongly structured spatial system shaped by regional basin structure, habitat structure, prey accessibility, and long-term site fidelity. Consequently, management approaches that assume uniform behavioral responses across Washington State waters may oversimplify predator–prey dynamics in the Salish Sea. More broadly, this study demonstrates that predator recovery can influence ecosystems through behavioral pathways that increase variability in prey behavior rather than producing uniform shifts in prey distribution. Long-term ecological datasets provide valuable insight into how predator–prey relationships evolve across space and time, and highlight the importance of incorporating behavioral variability and spatial heterogeneity into ecosystem-based management and conservation strategies.

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APPENDIX

Table S1. Poisson GLM diagnostics showing overdispersion in harbor seal (*Phoca vitulina*) haul-out count data in Washington State (1990-2022).

Metric	**Value**
Mean haul-out count	76.63
Variance of haul-out count	9509.68
Pearson dispersion statistic	124.40
Interpretation	**Severe overdispersion; Poisson invalid**

Table S2. Fixed-effect estimates from the hierarchical negative binomial model of harbor seal (*Phoca vitulina*) haul-out counts across Washington State. Percent change is shown for the year effect.

	Estimate	**Std. Error**	**z-statistic**	**p-value**	**Pct-change-per-year**
Intercept	-26.615742	4.192651	-6.348	1.1e-03	2.18e-10
Year	0.015212	0.002097	7.255	8.8e-03	4.03e-13

Table S3. Full fixed-effect estimates from hierarchical negative binomial mixed-effects models used in the model progression analysis evaluating predator, prey, and environmental influences on harbor seal (*Phoca vitulina*) haul-out counts across inland Washington State waters. Model 1 included predator presence only, Model 2 added prey accessibility, and Model 3 incorporated environmental covariates. Values are presented on the log scale.

Model	Term	Estimate	Std. Error	*z*	*p*
Model 1: Predator	**Intercept**	-25.990	4.219	-6.160	<0.001
	Year	0.015	0.002	7.056	<0.001
	Killer Whale Presence	-0.103	0.039	-2.661	0.008
Model 2: + Prey	**Intercept**	-25.949	4.220	-6.149	<0.001
	Year	0.015	0.002	7.045	<0.001
	Killer Whale Presence	-0.102	0.039	-2.628	0.009
	Distance to River (scaled)	-0.088	0.091	-1.079	0.281
Model 3: + Environmental Covariates	**Intercept**	-26.694	4.289	-6.224	<0.001
	Year	0.015	0.002	6.995	<0.001
	Killer Whale Presence	-0.101	0.039	-2.599	0.009
	Distance to River (scaled)	-0.106	0.086	-1.227	0.220
	Artificial Shoreline	0.937	0.366	2.556	0.011
	Marsh Shoreline	0.343	0.273	1.254	0.210
	Sand & Gravel Shoreline	0.327	0.175	1.870	0.062
	Offshore vs. Nearshore	0.779	0.165	4.730	<0.001

Table S4. Comparison of temporal predator exposure metrics used to evaluate associations between Bigg's killer whale (*Orcinus orca rectipinnus*) occurrence and harbor seal (*Phoca vitulina*) haul-out counts across inland Washington State. Lower AIC values indicate better model support; ΔAIC values represent differences relative to the best-supported model.

Model	AIC	logLik	Δ AIC
Current-year Predator Presence	28,269.63	-14,129.82	0.00
Cumulative Predator Exposure	28,270.54	-14,130.27	0.91
Lagged Predator Presence	28,271.79	-14,130.89	2.15

Table S5. Comparison of final negative binomial mixed-effects models evaluating predator occurrence, environmental covariates, and salmon accessibility associated with harbor seal (*Phoca vitulina*) haul-out counts across inland Washington State.

Model	**AIC**	**Δ AIC**	**Key Findings**
Predator-only Model	27,947.33	16.56	Predator presence negatively associated with haul-out counts
Environmental Model	27,930.77	0.00	Offshore position and artificial shorelines positively associated with haul-out counts
Salmon Distance Model	27,930.84	0.06	Salmon proximity did not improve model fit
Salmon Interaction Model	27,932.62	1.85	Predator x salmon interaction not supported

Table S6. Fixed-effect estimates from the inland-only negative binomial mixed-effects model evaluating associations between predator occurrence, environmental covariates, and in-water distance to salmon-bearing waterways on harbor seal (*Phoca vitulina*) haul-out counts. Outer Coast sites were excluded due to limited killer whale sighting coverage. Values are shown on the log scale.

Model	**Term**	**Estimate**	**Std. Error**	***z***	***p***
Model + Distance to Salmon (km)	**Year**	0.015	0.002	6.82	<0.001
	Killer Whale Presence	-0.066	0.046	-1.42	0.155
	Distance to Salmon (km)	0.063	0.045	1.39	0.166
	Distance to River Mouth (km)	-0.121	0.087	-1.38	0.166
	Artificial Shoreline	0.963	0.367	2.62	0.009
	Marsh Shoreline	0.302	0.275	1.10	0.273
	Sand & Gravel Shoreline	0.300	0.176	1.70	0.089
	Offshore vs. Nearshore	0.773	0.165	4.68	<0.001

Table S7. Comparison of negative binomial mixed-effects models evaluating associations between predator occurrence, salmon accessibility, and harbor seal (*Phoca vitulina*) haul-out counts across inland Washington State.

Model	**AIC**	**Δ AIC**
Environmental model	27,930.77	0.00
+ Salmon Distance	27,930.84	0.06
+ Salmon Interaction	27,932.62	1.85

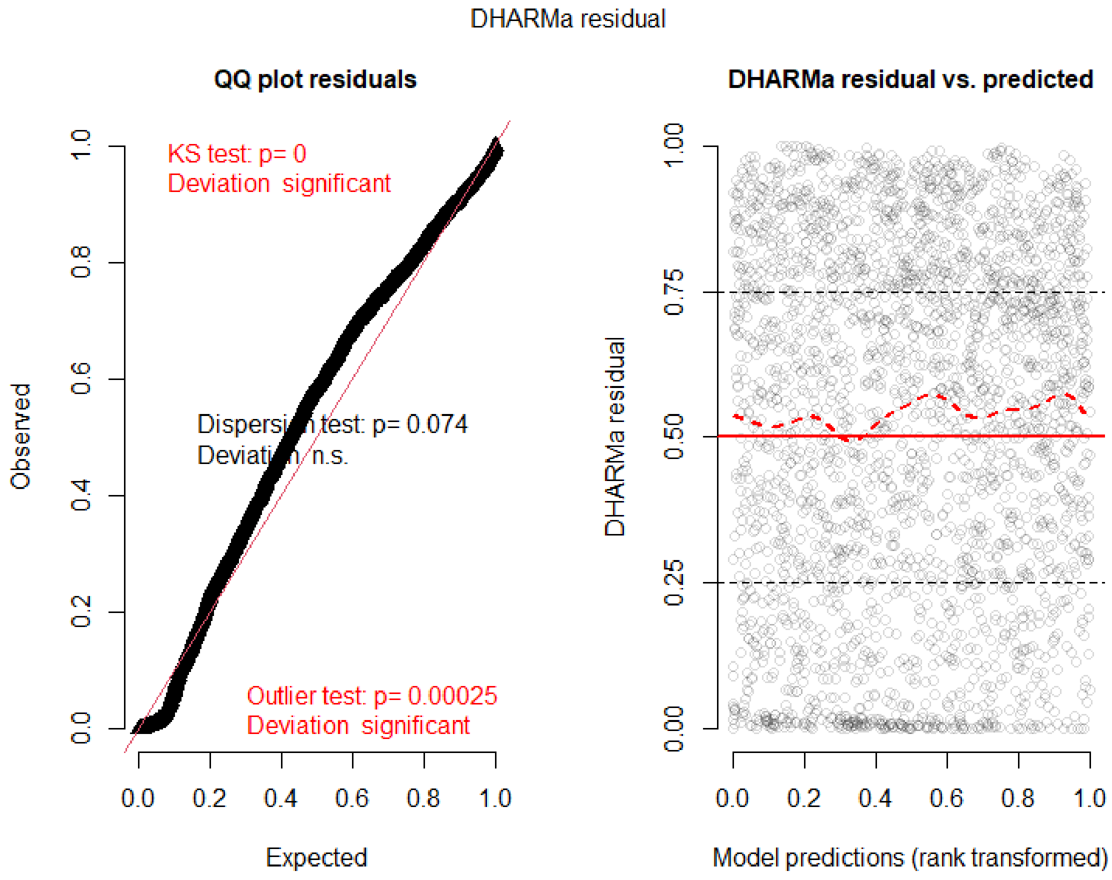

Figure S1. Diagnostic plots of DHARMa residuals for the final inland negative binomial mixed-effects model of harbor seal (*Phoca vitulina*) haul-out counts. The QQ plot (left) indicated significant deviation from the expected uniform distribution (Kolmogorov–Smirnov test, $p < 0.001$), although no evidence of overdispersion was detected (dispersion test, $p = 0.074$). The residuals versus predicted plot (right) showed slight structure across fitted values, and the outlier test was significant ($p < 0.001$), suggesting minor residual deviation likely associated with unmodeled site-level heterogeneity. Overall, diagnostics indicated acceptable model performance for ecological inference despite some deviation from ideal residual behavior.

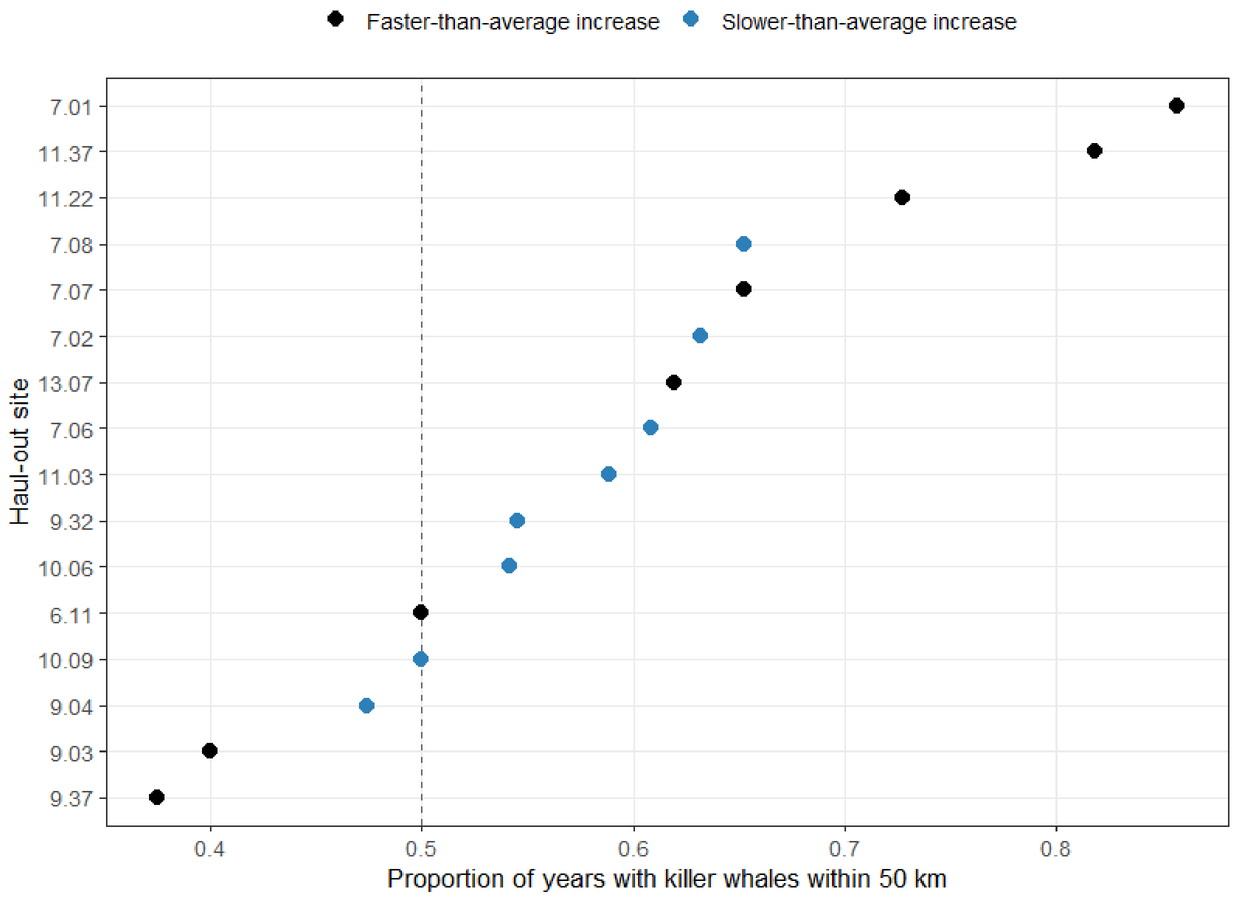

Figure S2. Predator exposure at inland harbor seal (*Phoca vitulina*) haul-out sites exhibiting divergent temporal trajectories relative to the population-level trend after exclusion of potential edge-effect sites. Points show the proportion of years in which Bigg's killer whales (*Orcinus orca rectipinnus*) were observed within 50 km of each haul-out site. Divergent site-level trajectories occurred across a broad range of predator exposure values, indicating that localized temporal variation in haul-out usage was not consistently structured by predator exposure alone.

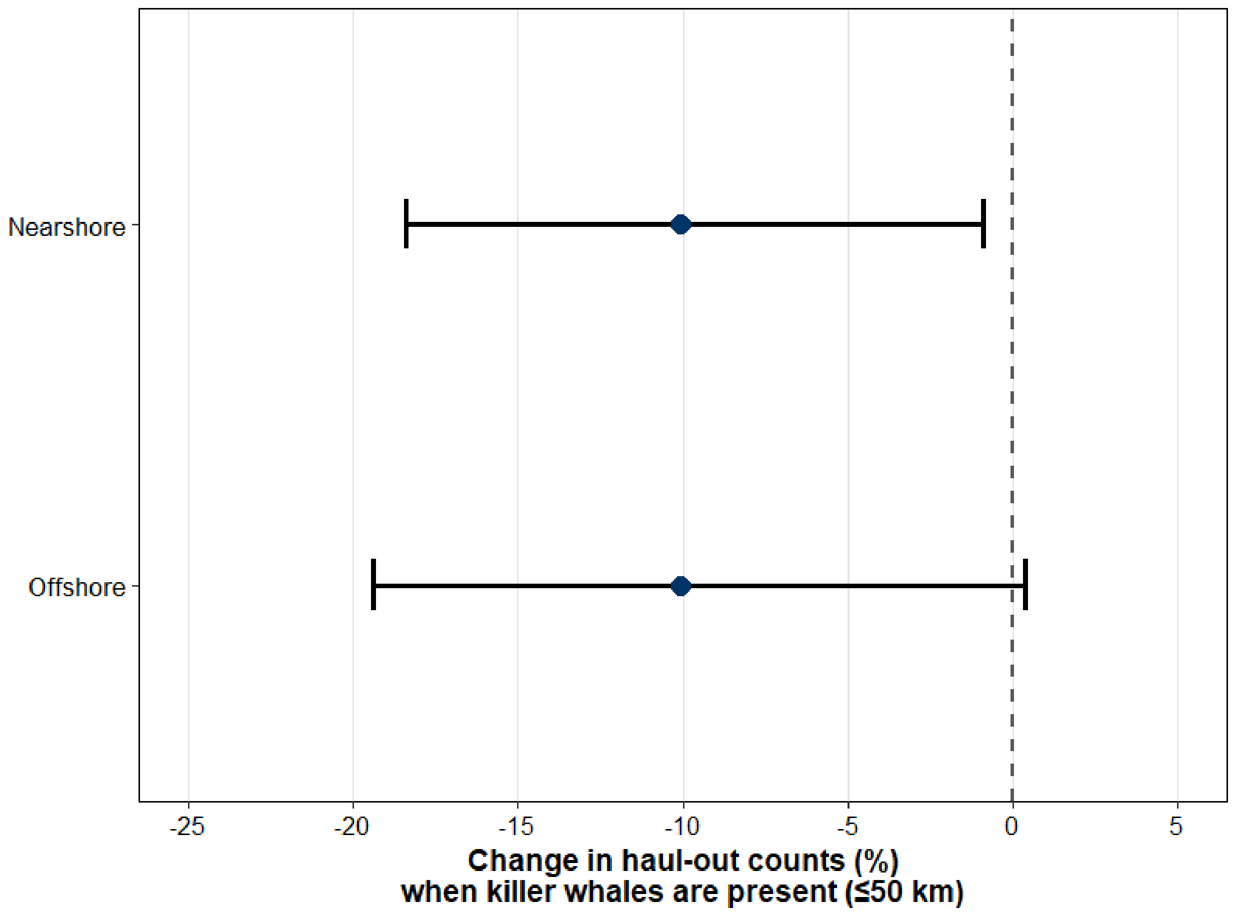

Figure S3. Percent change in predicted harbor seal (*Phoca vitulina*) haul-out counts associated with Bigg's killer whale (*Orcinus orca rectipinnus*) presence (≤50 km) across nearshore and offshore haul-out sites. Points represent estimated percent change and horizontal error bars indicate 95% confidence intervals. Predator-associated reductions in haul-out usage were similar across site positions, with no significant interaction between predator presence and site position.

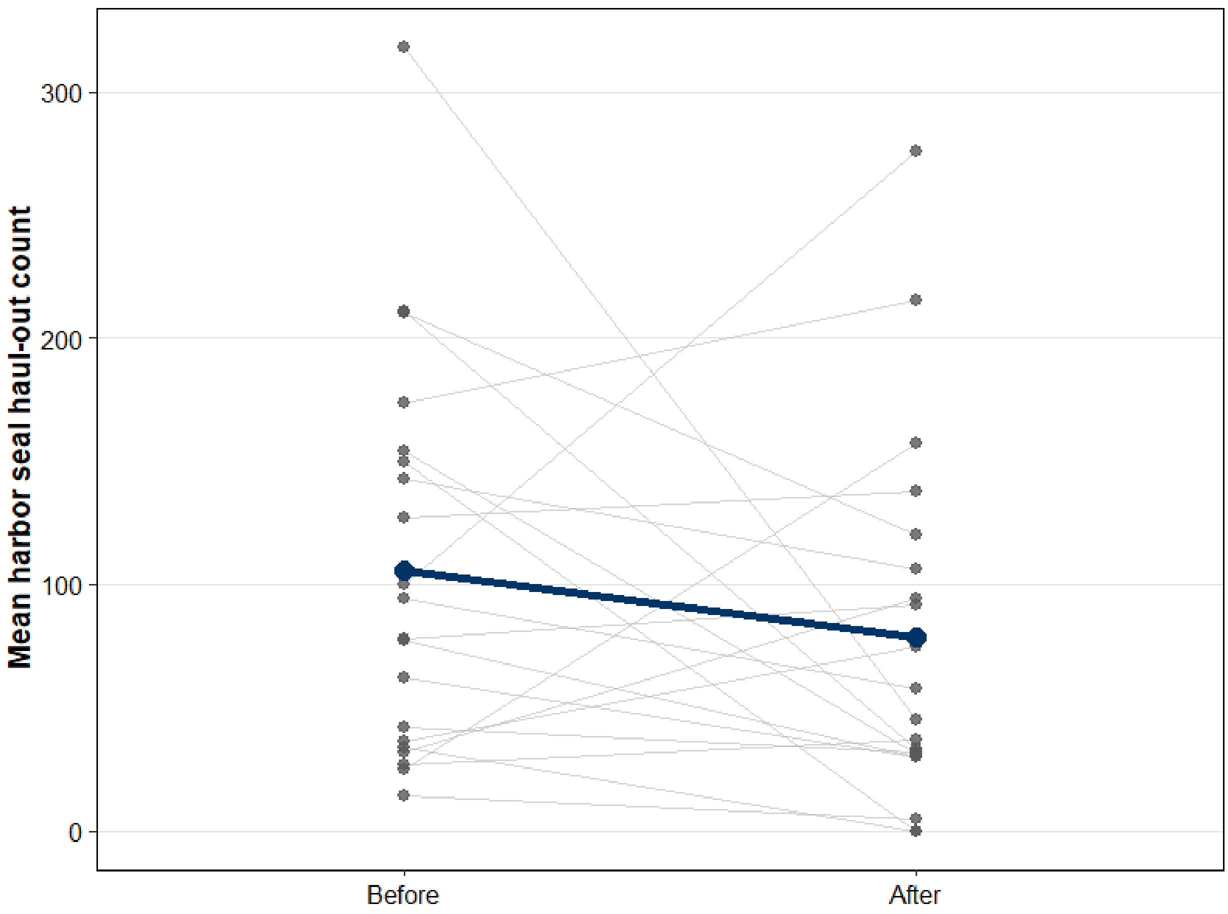

Figure S4. Mean harbor seal (*Phoca vitulina*) haul-out counts within 7 days before and after independent Bigg's killer whale (*Orcinus orca rectipinnus*) sighting events within 50 km. Points represent paired site-event means, with gray lines connecting before and after observations. The blue line shows the overall mean response.