



Harbor seal predation on migrating steelhead smolts entering marine waters

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ABSTRACT: After decades of historic exploitation, harbor seal *Phoca vitulina* populations in many marine ecosystems are increasing, and in some cases causing alarm over predation impacts on prey species of conservation concern. To gauge the magnitude of harbor seal predation impact on juvenile Puget Sound steelhead *Oncorhynchus mykiss*, a threatened population under the US Endangered Species Act, we quantified harbor seal predation rates in the Nisqually River estuary and nearshore marine environment of south Puget Sound in Washington State, USA, using 2 independent assessments. First, we developed a prey consumption model for the years 2016–2018 using the proportion of steelhead in seal scat (assessed using DNA metabarcoding, bioinformatics, and hard parts), seal daily energetic requirements, steelhead smolt size and abundance information, and seal abundance estimates. Second, we used acoustic telemetry data from individually tagged steelhead smolts (2014–2019 and 2021) to quantify predation events in the Nisqually River estuary based on spatial and temporal behavioral patterns of both predator and prey. The consumption model estimated that 9.0% (2017) to 32.8% (2018) of steelhead outmigrants (i.e. 'smolts') were eaten by harbor seals, accounting for most of the total mortality incurred in the Nisqually estuary and South Puget Sound (23 km) in 2 out of 3 years. Predation mortality rates through the estuary (5 km), assessed using acoustic telemetry analysis, ranged from 11.0% (2014) to 24.8% (2016). Our results demonstrate that a large proportion of a threatened salmonid population can be lost to harbor seal predation over a small segment of their migration route, even in a relatively natural delta estuary.

KEY WORDS: Predator–prey interactions · Protected species · *Phoca vitulina* · *Oncorhynchus mykiss* · Acoustic telemetry · DNA metabarcoding

1. INTRODUCTION

Variation in abundance and distribution of top predators can cause major shifts in ecosystem structure and function (Power 1990, Estes et al. 1998, McCauley et al. 2012). In recent decades, declines of large marine predator populations in the world's oceans have occurred at a rapid pace (Myers & Worm 2003, Estes et al. 2011). However, in some marine ecosystems, legal protections have led to successful recovery of pre-

viously exploited high trophic level predators like seals (Phocidae) and sea lions (Otariidae) (Magera et al. 2013, Cammen et al. 2019). Though recoveries are great examples of successful conservation policy, sometimes they can yield concerning ecological consequences. For example, recovery of sea eagles (*Haliaeetus* spp.) across the temperate northern hemisphere spurred declines in colonies of several seabird prey species, leading to concern for vulnerable populations already affected by anthropogenic influences (News-

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ome et al. 2010, Hipfner et al. 2012). Because they typically consume large amounts of biomass and range across large geographic areas, top predators can strongly affect prey species they consume directly as well as those at lower trophic levels (Baum & Worm 2009, Estes et al. 2016, Rupil et al. 2022).

Effects of predation on prey of conservation concern are important to understand when defining management strategies, as they meaningfully contribute to population dynamics of prey species (Worm & Meyers 2003, Harvey et al. 2012) and can limit recovery (Estes et al. 1998, Samhuri et al. 2017). Incorporating interspecific relationships into species recovery planning advances conservation outcomes, beyond those of single-species management, toward the maintenance of healthy ecological communities (Soulé et al. 2003). However, management from an ecosystem perspective can be challenging when interacting species within a community are legally protected, and measures intended to support one protected species conflict with the recovery goals of another (Marshall et al. 2016). For example, recovery of northern sea otters *Enhydra lutris kenyoni*—protected by the North Pacific Fur Seal Treaty of 1911, the Marine Mammal Protection Act (MMPA) of 1972, and the Endangered Species Act (ESA) of 1973 in the US—has raised concern in some coastal habitats where increasing sea otter predation may hinder the ability to restore ESA-listed northern abalone *Haliotis kamtschatkana* (Chadès et al. 2012). Managers must quantify the magnitude of the trophic link between predator species and protected prey, place it in the context of the ecological community, and identify factors that alter the strength of the predator–prey relationship to reach a clear understanding of how management goals can be met.

In Puget Sound, an inland sea situated in the Pacific Northwestern US and part of the Salish Sea, steelhead *Oncorhynchus mykiss* have experienced severe declines in abundance over the past 3 decades (Kendall et al. 2017) and are listed as 'threatened' under the ESA (Endangered and Threatened Species 2007). Like the other 5 species of Pacific salmon, steelhead must migrate from freshwater rearing habitat to the Pacific Ocean, then return to their natal stream to spawn and complete their life cycle. For many salmonid populations, migration through the estuarine and nearshore marine environment imposes mortality rates higher than those experienced throughout the remainder of the marine residence period (Parker 1968, Pearcy 1992, Thorstad et al. 2012). Steelhead originating in Salish Sea streams are no exception and typically experience mortality exceeding 60% during their rapid migration

(~2 wk) from the river mouth to the ocean (Melnychuk et al. 2013, Moore et al. 2015, 2021, Healy et al. 2017). This rapid migration, combined with the high mortality rate, strongly suggest that predation is a primary mortality factor. Evidence from telemetry studies shows that predation by harbor seals *Phoca vitulina*, in particular, contributes substantially to mortality of steelhead smolts in Puget Sound (Berejikian et al. 2016, Moore et al. 2021, Moore & Berejikian 2022). A number of avian predators are suspected to prey on migrating Puget Sound steelhead smolts as well, but at least one study examining predation effects on migrating steelhead found that the impact of predation by pinnipeds (seals and sea lions) far outweighs effects of all other predator species (Moore & Berejikian 2022).

Pinniped populations in marine ecosystems on the east and west coasts of the USA increased rapidly after the enactment of the MMPA in 1972 and have remained at levels near carrying capacity in recent decades (Cammen et al. 2019). Recent studies have linked increasing trends in Puget Sound harbor seal abundance to observed declines in marine survival of salmonids originating in the Salish Sea (Nelson et al. 2019, Sobocinski et al. 2020, 2021). Where abundant, populations of harbor seals and other pinnipeds (Phocidae, Otariidae, and Odobenidae) have the potential to impose heavy mortality on imperiled salmonid populations, even if salmonids make up only a small fraction of their diet. Recent bioenergetics models have demonstrated the impact of pinniped predation on Chinook salmon *O. tshawytscha* populations originating in Puget Sound, showing that mortality of juvenile and adult Chinook salmon attributed to predation in recent years exceeds mortality resulting from commercial and recreational fisheries and may considerably limit future returns (Chasco et al. 2017). Predation by harbor seals on highly valued fish stocks was historically mitigated by state-sponsored seal culling programs in Washington State, leading to critically low seal populations in the middle of the 20th century (Newby 1973, Jeffries et al. 2003). The MMPA and protected areas in Washington State have provided a near complete refuge for harbor seals in recent decades. Today, there is considerable debate about whether management of predator populations would yield benefits to highly valued and imperiled prey species, and more information on rates of predation across different habitat types is needed to inform the discussion.

Although previous studies have examined pinniped predation on salmon in Puget Sound (Chasco et al. 2017, Nelson et al. 2019, 2024), these studies focused on aggregate predation across populations, rather

than on a single population. The direct impact to a single population is a necessary component of structuring management actions for recovery. Here, we present 2 independent assessments of the proportion of Nisqually River natural-origin steelhead smolts consumed by harbor seals upon marine entry. First, a prey consumption model was developed for the years 2016–2018 from data on the relationships between (1) the average proportion of harbor seal diet comprised of steelhead, measured using DNA metabarcoding techniques, (2) published harbor seal daily energetic requirements, (3) the number and weight of steelhead migrating through the estuary and South Puget Sound (SPS), and (4) the number of seals residing in SPS. Second, acoustic telemetry data from individually tagged steelhead smolts (2014–2019 and 2021) were used to quantify predation events in the

Nisqually River estuary based on spatial and temporal behavioral patterns of both predator and prey. Together, these 2 complementary methods allowed us to estimate mortality caused by an abundant protected predator on a threatened steelhead population.

2. MATERIALS AND METHODS

2.1. Study area

The Nisqually River originates in the Cascade mountain glaciers of Washington State, USA, and flows 125 km to the estuary (Fig. 1), which is situated within the Nisqually National Wildlife Refuge. The lower river consists primarily of intact salmon habitat with healthy riparian vegetation, meeting the marine

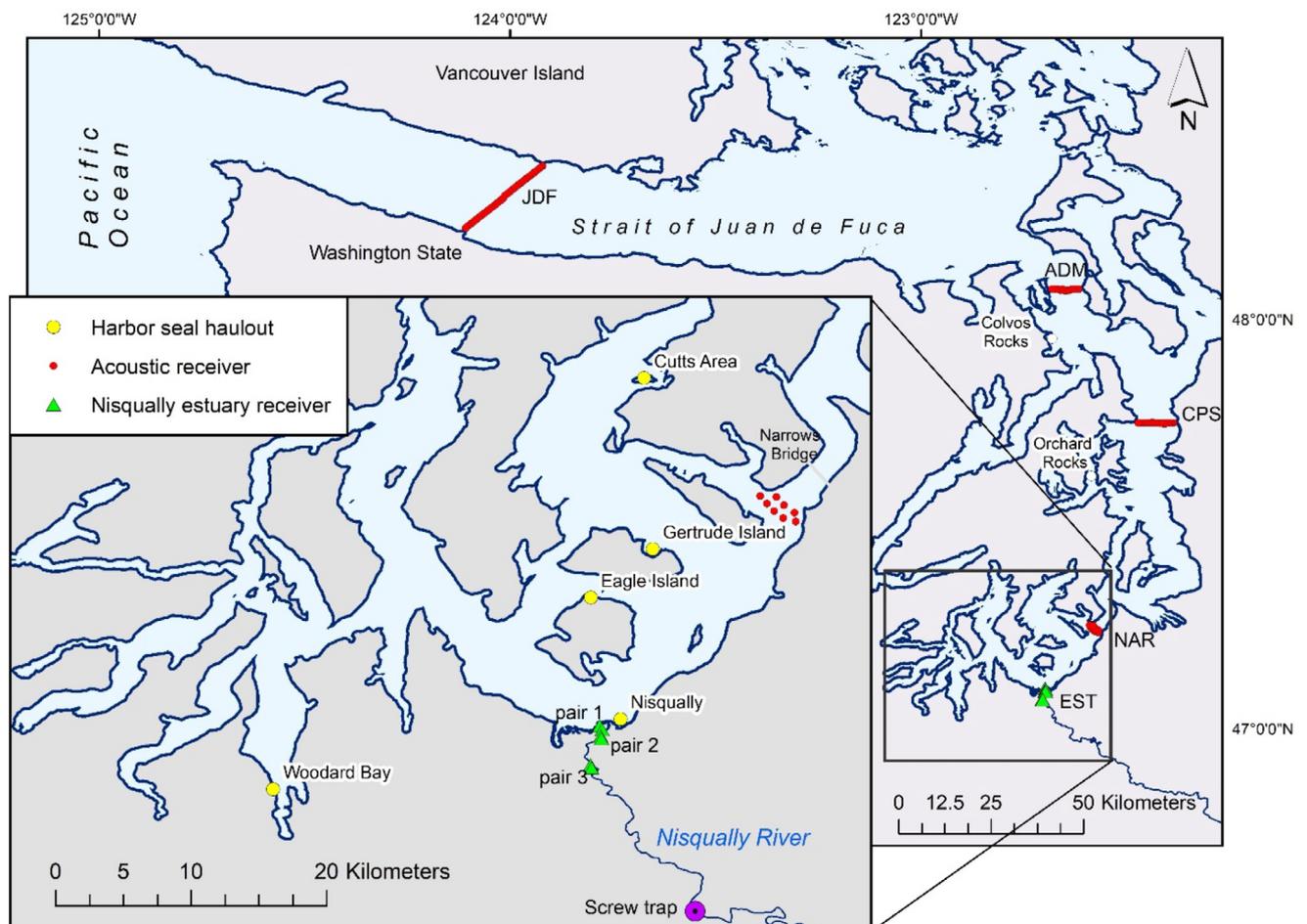


Fig. 1. Puget Sound, with inset showing where the Nisqually River enters South Puget Sound (SPS). Red dots depict locations of moored VR3 or VR4 Vemco acoustic receivers (NAR: Tacoma Narrows, CPS: Central Puget Sound, ADM: Admiralty Inlet, JDF: Strait of Juan de Fuca array), yellow dots indicate locations of major harbor seal haulouts in SPS, green triangles represent locations of Innovasea VR2W acoustic receivers placed annually in the Nisqually estuary (pair 1: downstream = river kilometer [rkm] 0.2 and upstream = rkm 0.6; pair 2: downstream = rkm 1.1 and upstream = rkm 1.3; pair 3: downstream = rkm 3.9 and upstream = rkm 4.1) to monitor tagged steelhead smolts caught and released at the rotary screw trap at rkm 19 (purple circle)

waters of Puget Sound within a largely undeveloped delta. No hatchery-origin steelhead have been released into the watershed since 1994, but approximately 4 million Chinook salmon and 300 000–500 000 coho salmon *Oncorhynchus kisutch* smolts are typically released annually during months of wild steelhead outmigration (Nisqually Steelhead Recovery Team 2014). Despite high-quality rearing and spawning habitat and absence of hatchery influence, the Nisqually steelhead population has severely declined in abundance over the last 3 decades (Nisqually Steelhead Recovery Team 2014).

2.2. Model of steelhead consumption by harbor seals in SPS

Calculating steelhead consumption by SPS harbor seals required estimates of 5 values. We derived 3 of the values directly from data: (1) proportion of harbor seal diet comprised of steelhead, (2) abundance of steelhead smolts entering SPS (calculated using survival of Nisqually steelhead smolts to the river mouth), and (3) average weight of steelhead smolts. The other 2 parameters were derived from peer-reviewed publications: (4) harbor seal population estimate (Jefferson et al. 2021) and (5) daily energetic requirement of an average-sized harbor seal (Howard et al. 2013).

2.3. Steelhead proportion in SPS harbor seal diet

We used published data from Thomas et al. (2022) to estimate the steelhead proportion in the SPS harbor seal diet, selecting samples from 5 major harbor seal haulouts in SPS: (1) Cutts Island, (2) Eagle Island, (3) Gertrude Island, (4) Nisqually estuary, and (5) Woodward Bay (Fig. 1). In total, 829 samples were collected during the steelhead smolt outmigration months of April, May, and June in 2016, 2017, and 2018 (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m743p139_supp.pdf). Samples were processed and preserved using a standardized protocol as described by Thomas et al. (2022).

The proportion of each scat sample comprised of steelhead biomass was quantified using DNA metabarcoding, a technique capable of identifying prey species using massively parallel sequencing of short (e.g. 200 base pairs) diagnostic genetic markers amplified from scat samples, described in detail by Thomas et al. (2022). Steelhead sequences were identified by comparison to previously documented DNA barcodes in GenBank (Benson et al. 2013), and the

percent of steelhead DNA sequences, termed relative read abundance (RRA, %), was calculated as:

$$RRA_i = \frac{1}{S} \sum_{k=1}^S \frac{n_{i,k}}{\sum_{i=1}^T n_{i,k}} \times 100 \quad (1)$$

where S is the number of samples, T is the number of food items (taxa), and $n_{i,k}$ is the number of sequences of food item i in sample k . To obtain an average monthly proportion of steelhead in harbor seal scat samples (p), each sample RRA was converted to a proportion and averaged according to the month the sample was collected. We then used a non-parametric bootstrap procedure to estimate uncertainty in the mean monthly proportions by resampling the data and calculating the proportions 1000 times.

To determine steelhead life history stage, prey 'hard parts' (i.e. bones, otoliths) were strained from the scat sample matrix through a series of nested sieves and identified to the lowest possible taxon by taxonomic experts (Thomas et al. 2022). In samples containing steelhead ($n = 20$), otolith and vertebral measurements were then used to classify hard parts as 'juvenile' or 'adult' (e.g. Nelson et al. 2021).

2.4. Smolt abundance

Steelhead smolts were collected at a rotary screw trap at river kilometer (rkm) 19 in the Nisqually River (Fig. 1) from mid-January through mid-August to sample the entire smolt outmigration. A stratified mark–recapture study design was used to estimate the abundance of steelhead smolts outmigrating annually, detailed by Losee et al. (2021). Briefly, captured steelhead were marked and released back into the river 1.6 km upstream of the trap, and the proportion of the release group recaptured in subsequent days was recorded. Marking schemes were varied weekly, and a G -test (Sokal & Rohlf 1981) was used to test for homogeneous capture rates between adjacent weeks. Blocks of time with statistically similar capture rates were combined into strata. Abundance and uncertainty for each stratum was estimated using the Baily modification of the Lincoln-Petersen estimator (Seber 1982). Stratum estimates were summed to produce monthly abundance estimates for peak outmigration months (April, May, June; Table 1).

2.5. Steelhead smolt survival estimates

Steelhead smolts were captured at a screw trap in the Nisqually River (Fig. 1) during the smolt out-

Table 1. Parameters for the harbor seal consumption model including seal abundance for low, medium (point estimate), and high abundance scenarios (N_s ; data from Jefferson et al. 2021), Nisqually steelhead mean smolt weight and lower and upper bounds in kilograms, Nisqually River smolt abundance (A), and survival estimates from release to first pair of river receivers (Φ_r) and through South Puget Sound (Φ_{SPS}) from estuary receivers to Narrows array (including Nisqually estuary)

| Year | Seal abundance (N_s) | Mean weight (kg) | Weight lower bound | Weight upper bound | A | Φ_r | Φ_{SPS} |
|------|---|------------------|--------------------|--------------------|--------|----------|--------------|
| 2016 | Low = 1314 Point = 1627 High = 2015 | 0.072 | 0.035 | 0.109 | 117376 | 0.70 | 0.71 |
| 2017 | Low = 1314 Point = 1627 High = 2015 | 0.080 | 0.032 | 0.127 | 94740 | 0.90 | 0.65 |
| 2018 | Low = 1314 Point = 1627 High = 2015 | 0.086 | 0.038 | 0.133 | 133597 | 0.92 | 0.53 |

migration period (April – June) in 2014 – 2019 and in 2021. Captured smolts were anesthetized, measured (fork length), and weighed in the field to obtain measurements of each individual (Table S1 in the Supplement). Smolts were then implanted with an Innovasea (formerly Vemco) V7 (7×15.5 mm, 132 d battery life) or V7T (7×19.5 mm, 78 d battery life) acoustic transmitter (69 kHz, 30 – 90 s random ping interval; Innovasea), following surgical implantation procedures outlined by Moore & Berejikian (2017). Transmitter to smolt weight ratio ranged from 0.01 to 0.03, and never exceeded 5%. Steelhead smolts were selected randomly from the catch regardless of size, so were representative of the migrating population. All smolts were held for 18 – 24 h, released at rkm 19, and typically arrived in the estuary within 4 – 5 d (Moore & Berejikian, 2017).

Transmitter detections from fixed hydrophones deployed in the Nisqually River estuary, throughout Puget Sound, and near the Pacific Ocean point of entry were used to estimate the early marine survival of tagged steelhead smolts. Six Vemco VR2W hydrophones were deployed in the Nisqually river estuary (EST), and 8 (but only 3 in 2018) Vemco VR3 hydrophones spanned the Tacoma Narrows (NAR; Fig. 1). Vemco VR3 and VR4 arrays deployed across Central Puget Sound, Admiralty Inlet, and the Strait of Juan de Fuca (Fig. 1) were used to quantify detection efficiency of EST and NAR. Receiver files were downloaded using Innovasea VUE software (versions 2.12.7 and previous), exported to a Microsoft Access database, and further analyzed in Microsoft Excel or R (R Core Team 2022). False detections were screened by manually deleting single detection records from the database, unless the detection fit within a plausible transmitter trajectory. Survival probabilities through steelhead migration segments bounded by hydro-

phone arrays were estimated using methods described by Moore et al. (2021). Briefly, Cormack-Jolly-Seber (CJS) mark – recapture models (Cormack 1964, Jolly 1965, Seber 1965) implemented in the 'RMark' package (Laake 2013) for R version 3.6.2 (R Core Team 2022) were used to estimate (1) the probability of smolt survival (Φ) from river release to the first pair of estuary receivers (14 km; Φ_r) and (2) survival probability through the estuary and SPS from the first estuary receiver array to the Tacoma Narrows Bridge (23 km; Φ_{SPS} ; Fig. 1). The CJS model included separate parameters for the detection probability of each array. Model goodness-of-fit diagnostics were satisfactory (Fletcher's c -hat < 1.2; Fletcher 2012).

2.6. Smolt weight

Smolt weight data were not available for all smolts caught in the trap, but they were recorded for acoustic tagged smolts. To obtain a representative distribution of smolt weights for use in the consumption model, we calculated the annual length – weight relationships of acoustic tagged steelhead smolts, then used the relationship to infer lengths of trap-captured smolts. Weights were inferred from the standard length – weight model (Neuman et al. 2012):

$$W_i = aL_i^b \quad (2)$$

where W_i is the weight of the i^{th} fish, L_i is the length of the i^{th} fish, and a and b are constant parameters.

To estimate these parameters via linear regression, we linearized the length – weight model by taking the natural log of both sides of the equation. We used this parameterized length – weight model to predict log-transformed weight data ($n_{2016} = 392$, $n_{2017} = 270$, and $n_{2018} = 233$). Predicted weights were exponentiated to

backtransform to the original scale (W_{pred} , correcting for bias following Hayes et al. (1995).

2.7. Harbor seal SPS population estimate

To represent the number of harbor seals foraging in SPS during scat sample collection, we used the 'SPS' stock spring (March – May) abundance estimates reported by Jefferson et al. (2021), which accounted for all seals south and west of the Tacoma Narrows Bridge (Fig. 1). The estimate is based on sightings of in-water marine mammals recorded during extensive aerial surveys from 2013 to 2016 along transect lines perpendicular to Puget Sound depth contours. Abundance of harbor seals was estimated using multiple-covariate line-transect methods, and then a correction factor was applied to account for seals hauled out at the time of the survey (Jefferson et al. 2021). The correction factor was calculated using data from a harbor seal tagging study, described extensively by Moore et al. (2021). Briefly, 12 harbor seals were captured at 5 haulout sites within Puget Sound, including Gertrude Island, Eagle Island, and Nisqually Estuary in SPS, Orchard Rocks in Central Puget Sound, and Colvos Rocks in Admiralty Inlet (Fig. 1), instrumented with a satellite-linked time depth recorder (TDR) and Fastloc GPS tag (model MK10AF, Wildlife Computers), and released during the spring of 2016. Eleven of the 12 instrument packs were recovered after 66 to 156 d of data collection. The MK10AF tag recorded location and depth data, and included a wet/dry sensor, such that the time each animal was available to aerial in-water surveyors (i.e. not hauled out on land or located at depths <1.5 m) could be quantified using general linear mixed models (see Jefferson et al. 2021). Jefferson et al. (2021) applied the mean probability of being 'available' during spring months between the survey hours of 09:00 and 17:00 h as a correction factor to the uncorrected spring abundance estimate; we used this corrected estimate ('mean scenario') and upper ('high scenario') and lower ('low scenario') 95% confidence interval values to represent a range of SPS seal abundances in the consumption model.

2.8. Prey consumption model

To estimate the number of smolts eaten by harbor seals in SPS per month (Q_i), we used (1) monthly averages of the diet proportion (p) comprised of steelhead from harbor seal scat samples, (2) the daily energetic requirement (EG) of an average-size individual harbor

seal (2.1 kg; Howard et al. 2013), (3) the season-specific SPS harbor seal population estimate (N_s), and (4) the year-specific average Nisqually steelhead smolt weight (w) in kilograms in the following equation:

$$Q_i = \frac{EG d_i N_s p_i}{w} \quad (3)$$

where d_i is the number of days and p_i is the diet proportion in month i .

We then calculated the number of smolts eaten by SPS harbor seals per year (Q_y) as the sum of smolts eaten each month (April [month 4] – June [month 6]) of the steelhead outmigration season within year y :

$$Q_y = \sum_{i=4}^6 Q_i \quad (4)$$

To explore the uncertainty of Q_y , we used stochastic simulations that allowed uncertainty in (1) the number of seals in SPS, (2) proportion of steelhead in seal diet, and (3) smolt size. We used 3 scenarios to represent a high (upper 95% confidence interval, CI), medium (point estimate), or low (lower 95% CI) season-specific SPS harbor seal population estimate (N) based on Puget Sound marine mammal aerial survey data (Table 1; Jefferson et al. 2021). For diet proportions and smolt size, we drew random values from a truncated normal distribution parameterized using the mean and standard deviations of these parameter estimates. To avoid extreme monthly mean values in smolt size and diet proportions, we truncated the normal distributions by excluding values in the upper and lower 10% of the distribution tails.

The simulations proceeded by first picking a seal abundance scenario, then drawing random values of diet proportions and smolt size. The number of smolts consumed was then calculated using Eqs. (3) and (4). Finally, we looped over 1000 Monte Carlo trials for each seal scenario to generate a distribution of the number of smolts consumed in a year (Fig. S2 in the Supplement).

We placed Q_y in the context of the entire Nisqually steelhead run using yearly smolt abundance estimates (A_y) and survival estimates of acoustic tagged steelhead migrating through the river (rkm 19 to 4.2; Φ_r) and through SPS (rkm 4.2 to Tacoma Narrows; Φ_{SPS}). We calculated the proportion of total Nisqually steelhead smolts eaten by harbor seals in the estuary and in SPS each year (PQ_y) by dividing Q_y by the number of smolts available after migration through the river:

$$PQ_y = \frac{Q_y}{A_y \Phi_r} \quad (5)$$

Finally, we calculated the proportion of mortality (PM) in the estuary and SPS due to harbor seals by

dividing Q_y by the total number of mortalities incurred in SPS:

$$PM = \frac{Q_y}{A_y \Phi_r (1 - \Phi_{SPS})} \quad (6)$$

Calculated and literature-derived consumption model parameters are summarized in Table 1. To examine the contribution error around smolt weight (w) and monthly averages of the diet proportion (p), we performed a sensitivity analysis. For 1000 model simulations each, we held w and p constant and compared the resulting values to the original consumption model results with a mean seal abundance scenario.

2.9. Key assumptions

We make an important assumption that the Nisqually River produces nearly all of the smolts migrating through SPS. There are at least 7 small streams in the same region as the Nisqually River that historically supported steelhead populations, but current abundance has not been documented, leaving considerable uncertainty around whether remnant populations persist (Myers et al. 2015). No adult steelhead were observed in one SPS tributary monitored for coastal cutthroat trout *O. clarkii clarkii* from 2008 to 2014 (Losee et al. 2016). It is not likely that SPS tributaries contribute significant numbers of smolts that would migrate through the SPS study area. Further, steelhead populations from major river systems to the north of the Nisqually migrate quickly out of Puget Sound and do not travel south (Moore et al. 2015). No hatchery-reared steelhead were released into any stream in SPS during this study period.

The consumption model also assumes that the scat samples used to determine steelhead diet proportion are representative of the entire SPS population. Although all major SPS haulouts are represented (Jeffries et al. 2003), there is annual variation in the distribution of samples from each haulout. Variation in numbers of scat samples collected at different haulout sites each year likely influences the annual consumption model estimates, giving more weight to over-represented haulout locations, so we interpret the results in the context of this potential bias.

2.10. Acoustic telemetry-based assessment of smolt mortality in the Nisqually estuary

Fine-scale behavioral data were collected using acoustic telemetry of the same tagged steelhead

smolts described in Section 2.5. Steelhead smolt mortality in the Nisqually River estuary (i.e. the area between pair 1 and pair 3 receivers; Fig. 1) was quantified using a combination of movement behavior in the estuary and temperature profiles from a subset of acoustic transmitters. Trap-captured steelhead smolts (Table S1), implanted annually (2014–2019 and 2021) with acoustic transmitters (V7 or V7T) and released at rkm 19, were detected on stationary receivers deployed in the Nisqually River estuary (6 VR2W receivers). Three pairs of receivers were deployed in the same estuary locations each year (pair 1: downstream = rkm 0.2 and upstream = rkm 0.6, pair 2: downstream = rkm 1.1 and upstream = rkm 1.3, pair 3: downstream = rkm 3.9 and upstream = rkm 4.1; Fig. 1) to record fine-scale transmitter movement patterns. Because the range of each receiver can extend approximately 400 m, the 'estuary' is then defined here as the first 5 km of the river. Smolts could also be detected on Puget Sound receiver arrays (NAR, CPS, ADM, JDF; Fig. 1). Most transmitters were V7s (described in Section 2.5), but a subset of transmitters ($n = 100$) in 2019 and all 2021 transmitters ($n = 160$) were identical except equipped with a temperature sensor (V7T, Table S1). The V7T transmitters recorded temperatures ranging from 0 to 40°C, so they provided an indication of whether a tagged smolt had been consumed by a warm-blooded predator when it continued transmitting at a typical marine mammalian body temperature (36–38°C; Kuhn & Costa 2006, Melero et al. 2015). The location and time of a predation event could be determined if the tag temperature increased from ambient water temperature (8–11°C) to the internal body temperature of the predator while in range of a receiver.

Spatio-temporal analysis of detection data on 6 annually deployed estuary receivers (Fig. 2A) provided evidence of predation during years when temperature transmitters were not deployed. Steelhead smolts that survived their migration through the estuary were detected sequentially (i.e. in a downstream direction) on receivers deployed in the river channel of the Nisqually estuary (Fig. 2A). Transmitters detected in the estuary that subsequently moved upstream, then downstream, then upstream again at least once (i.e. 2 upstream movements) were assigned a 'back and forth' pattern (hereafter, 'BAF'). An upstream movement was defined as a sequential detection from at least one receiver in a downstream pair to at least one receiver in an upstream pair (though sequential movement from pair 1 upstream to pair 2 downstream did not qualify as upstream movement because river shape and receiver proximity enabled simultaneous detection of a trans-

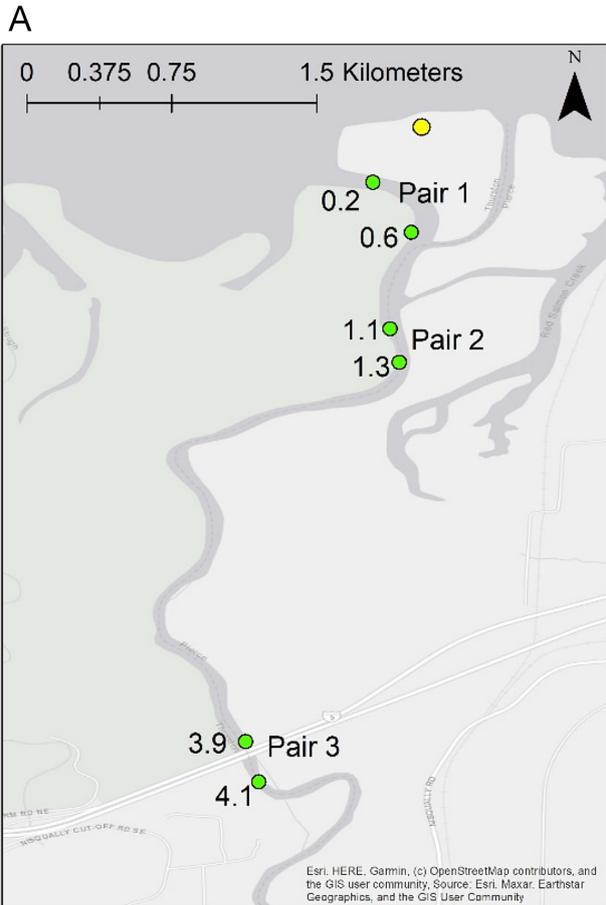
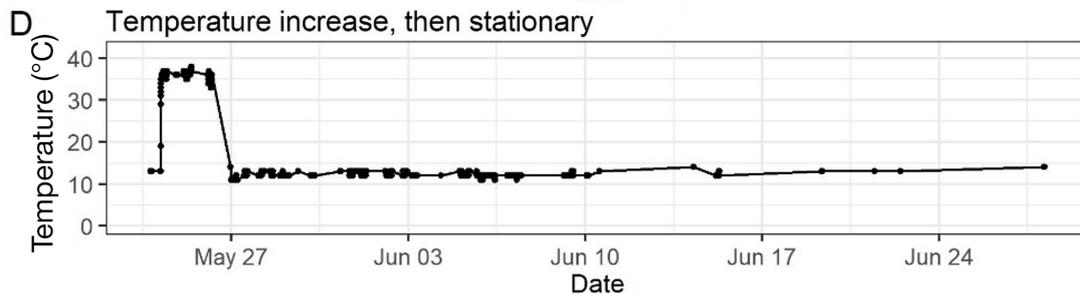
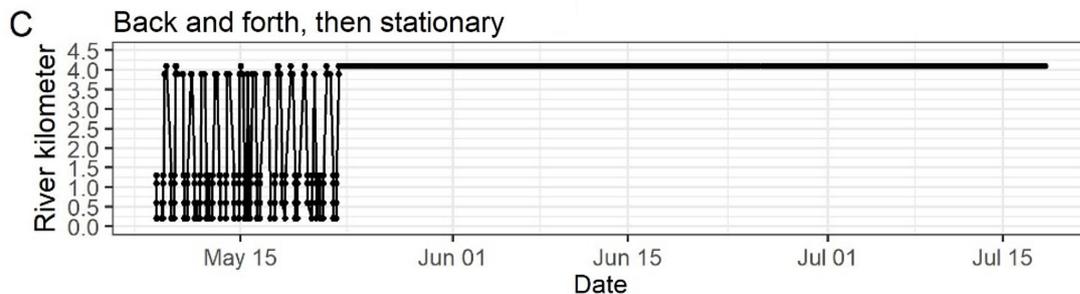
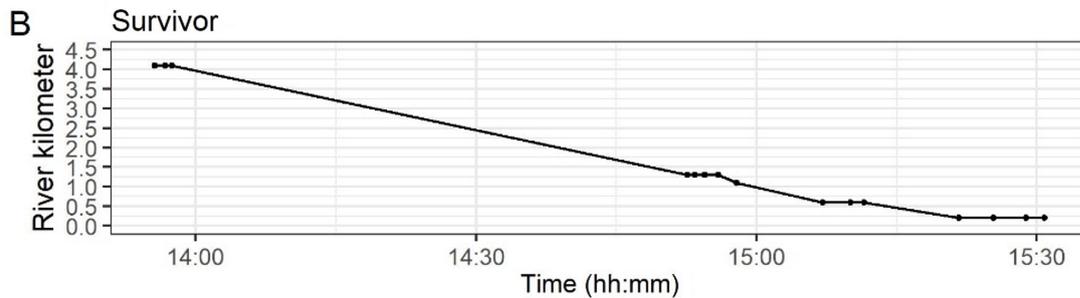


Fig. 2. (A) Nisqually River estuary. Green dots represent the acoustic receivers (with river kilometer [rkm] labels) used for back and forth (BAF) behavioral analysis, and the yellow dot shows the location of the closest harbor seal haulout immediately adjacent to the river mouth. (B) Migration of a typical surviving tagged steelhead from estuary entry at rkm 4.1 to the last estuary receiver at rkm 0.2. (C) BAF behavior of a transmitter that was consumed by a harbor seal that made repeated trips up and down the estuary; the transmitter was then excreted near the acoustic receiver at rkm 4.1, where it remained stationary until the transmitter battery life expired. (D) Typical harbor seal consumption of a temperature sensor tagged steelhead, showing how the transmitter goes from ambient temperature to mammalian body temperature (36–38°C) in the seal stomach, then returns to ambient estuary temperature upon excretion



mitter located in between receivers). Transmitters exhibiting BAF were categorized as putative predation events ('BAF mortalities') given (1) the departure from typical smolt behavior, and that (2) transmitters detected moving upstream more than once were never detected at the Narrows Bridge array or beyond (i.e. CPS, ADM, JDF in Fig. 1), and (3) a subset of BAF transmitters was subsequently categorized as 'stationary', or detected consistently in the same location over a prolonged time period (24 out of 111 times; Fig. 2B), indicating mortality. Transmitters detected at Puget Sound receiver arrays that survived past the estuary ($n = 499$), never displayed a stationary detection pattern. All 28 V7T transmitters showing BAF behavioral patterns simultaneously transmitted elevated temperatures ($>37^{\circ}\text{C}$; e.g. Fig. 2C). The combination of BAF movement over hundreds of meters underwater while at elevated temperatures strongly indicated the transmitter was in a mammalian digestive tract.

Warm transmitter temperatures alone are consistent with avian or mammalian consumption, but simultaneous consistent underwater detections recorded during BAF movement implicate a predominantly aquatic predator. Of the 3 marine mammals regularly observed in SPS (California sea lions *Zalophus californianus*, harbor seals, and harbor porpoise *Phocoena phocoena*), harbor seals are the only species likely to consistently exhibit BAF movement in the estuary; California sea lions are not typically present in inland Washington waters during the period of steelhead outmigration (May through June), and harbor porpoises are not typically found in waters less than 20 m in depth (Raum-Suryan & Harvey 1998). In contrast, harbor seals are regularly observed hauling out at the mouth of the Nisqually River and foraging in the lower river (Jeffries et al. 2003).

In 2019 and 2021, combined behavioral and temperature data from V7T transmitters showed that some predation events defined by increased temperature were not accounted for through BAF behavioral analysis. Predation event categorization using BAF requires that the transmitter spends hours within a predator stomach while the predator is within range of multiple receivers. In contrast, a predation event based on an increase in temperature can be detected in only a few minutes. A total of 13 V7Ts in 2019 and 27 V7Ts in 2021 were detected in the estuary with elevated temperature (Table 2). A

subset of those V7Ts (8 in 2019 and 20 in 2021) exhibited BAF behavior; therefore, a portion of the predation events was not captured by the BAF metric alone. To correct for mortalities not accounted for using BAF patterns alone, we divided the number of temperature-based mortalities by the number of BAF mortalities to arrive at an expansion factor (2019 = 1.6, 2021 = 1.4). The proportion of BAF mortalities in years when temperature data were unavailable (2014–2018) were then multiplied by the average correction factor (1.5) to adjust mortality estimates ('BAF-expanded mortality') during years when temperature data were unavailable.

3. RESULTS

3.1. Diet analysis

Steelhead made up between 0.00 and 1.76% of the monthly biomass consumed by an average harbor seal in SPS during the smolt outmigration months (Table 3). No steelhead DNA was detected in samples collected in April or June of 2016, and the highest proportions of steelhead in harbor seal diet were observed in May and June of 2018 (Table 3). Out of the 829 scat samples analyzed, only 20 (2.4%) contained steelhead DNA. Percentages of scats containing steelhead were highest at the Nisqually and Cutts area haulouts (3.8%), with lower percentages observed at Woodard Bay (1.9%), Eagle Island (1.5%), and Gertrude Island (1.2%). All of the scat samples

Table 2. Telemetry-based predation event results for steelhead smolts tagged in 2014–2019 and 2021. N_{estuary} = number of smolts detected in the Nisqually estuary, with number of temperature-sensing transmitters detected in the estuary in parentheses; BAF: number of predation events determined by 'back and forth' behavioral analysis; temperature increases: number of V7Ts with temperature records $>$ BAF mortality, i.e. proportion of smolts in the estuary categorized as predation events based on BAF analysis; BAF-expanded mortality: BAF mortality expanded to correct for the greater ability to detect predation events using temperature sensor increases rather than using BAF only (correction factor = 1.5; see Section 2.10 for details) in years when temperature data were unavailable

| Year | N_{estuary} (number of V7T) | BAF | Temperature increases | BAF mortality | BAF-expanded mortality |
|------|---|-----|--------------------------|------------------|---------------------------|
| 2014 | 95 (0) | 7 | — | 0.074 | 0.111 |
| 2015 | 88 (0) | 10 | — | 0.114 | 0.170 |
| 2016 | 108 (0) | 18 | — | 0.167 | 0.250 |
| 2017 | 88 (0) | 9 | — | 0.102 | 0.153 |
| 2018 | 193 (0) | 28 | — | 0.145 | 0.218 |
| 2019 | 193 (91) | 19 | 13 | 0.093 | 0.143 ^a |
| 2021 | 144 (144) | 20 | 27 | 0.139 | 0.188 ^a |

^aBased directly on temperature increase of temperature sensor transmitters

Table 3. Average proportion (p) of steelhead in harbor seal diets by month (April, May, June). Data summarized from Thomas et al. (2022)

| Year | Month | Number of samples | p | Lower 95% CI | Upper 95% CI |
|------|-------|-------------------|--------|--------------|--------------|
| 2016 | April | 68 | 0.0000 | 0.0000 | 0.0000 |
| | May | 141 | 0.0101 | 0.0000 | 0.0285 |
| | June | 8 | 0.0000 | 0.0000 | 0.0000 |
| 2017 | April | 73 | 0.0005 | 0.0000 | 0.0016 |
| | May | 129 | 0.0037 | 0.0000 | 0.0112 |
| | June | 87 | 0.0009 | 0.0000 | 0.0028 |
| 2018 | April | 46 | 0.0014 | 0.0000 | 0.0040 |
| | May | 131 | 0.0154 | 0.0022 | 0.0298 |
| | June | 146 | 0.0176 | 0.0031 | 0.0361 |

containing steelhead for which hard parts were present ($n = 10$) contained juvenile bones representative of *Oncorhynchus* species, and one of the samples also contained adult *O. mykiss* bones (Table S2 in the Supplement), indicating that SPS harbor seals were primarily consuming smolts during the spring months.

3.2. Consumption model

The mean seal abundance scenario showed that harbor seals in SPS consumed an estimated 15 772 (95% CI: 3285, 35 149) steelhead smolts in 2016, 7690 smolts in 2017 (2733, 16 909), and 40 245 smolts in 2018 (22 640, 68 563; Fig. 3). As expected, consump-

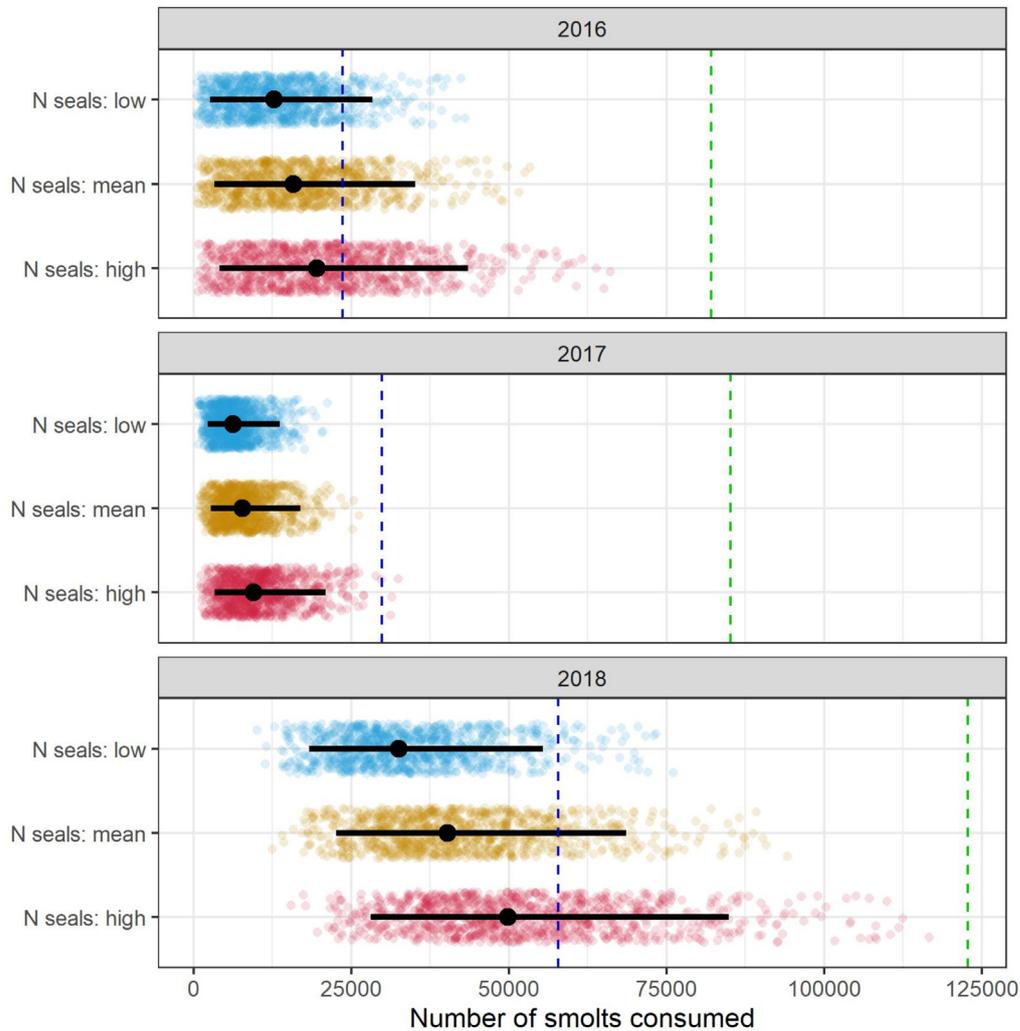


Fig. 3. Prey consumption model results, plotting the mean number of steelhead smolts consumed by harbor seals (black dots) and 95% confidence intervals (black lines) for South Puget Sound harbor seal abundance scenarios estimated by Jefferson et al. (2021) in 2016, 2017, and 2018. Outcomes for each of the 1000 model runs for each scenario (low: blue; mean: yellow; high: pink) are plotted for each year. The green dashed line represents the total number of steelhead smolts estimated to have entered the Nisqually estuary each year (see Eq. 5, Section 2.8), and the blue dashed line represents the number of total mortalities expected based on steelhead smolt survival probability through South Puget Sound (see Eq. 6, Section 2.8)

tion estimates increased with increasing seal abundance scenarios from low to medium to high (Fig. 3). Variation in the seasonal consumption estimate was highest in 2018, when wide confidence intervals bounded the steelhead proportion estimate in May and June (Table 3). Sensitivity analysis of the number of smolts consumed to variation in smolt weight and proportion of steelhead in harbor seal diets shows the contribution of that uncertainty to total error around each estimate (Fig. S3 in the Supplement).

Under mean seal abundance scenarios, harbor seals consumed 19.2% of the 2016 Nisqually steelhead run (95% CI: 2.5, 48.7), 9.0% of the 2017 run (2.3, 22.7), and 32.8% of the 2018 run (16.2, 61.5) in SPS (Fig. 4). Using the low seal abundance estimate, seals consumed

between 7.3% (0.019, 0.183; 2017) and 26.5% (0.131, 0.497; 2018) of the run annually, and consumed between 11.1% (0.029, 0.281; 2017) and 40.6% (0.201, 0.762; 2018) of the run annually under a high seal abundance scenario, although these calculations are based on the number of smolts available in the estuary (Eq. 5; green line in Fig. 3) and do not account for uncertainty in that number.

When compared to SPS mortality estimated by CJS models, harbor seals were estimated to account for 25.7% (2017) to 69.6% (2018) of the total steelhead smolt mortality in SPS under mean seal abundance scenarios, 20.8% (2017) to 56.2% (2018) under low seal abundance scenarios, and 31.9% (2017) to 86.1% (2018) under high seal abundance scenarios in the

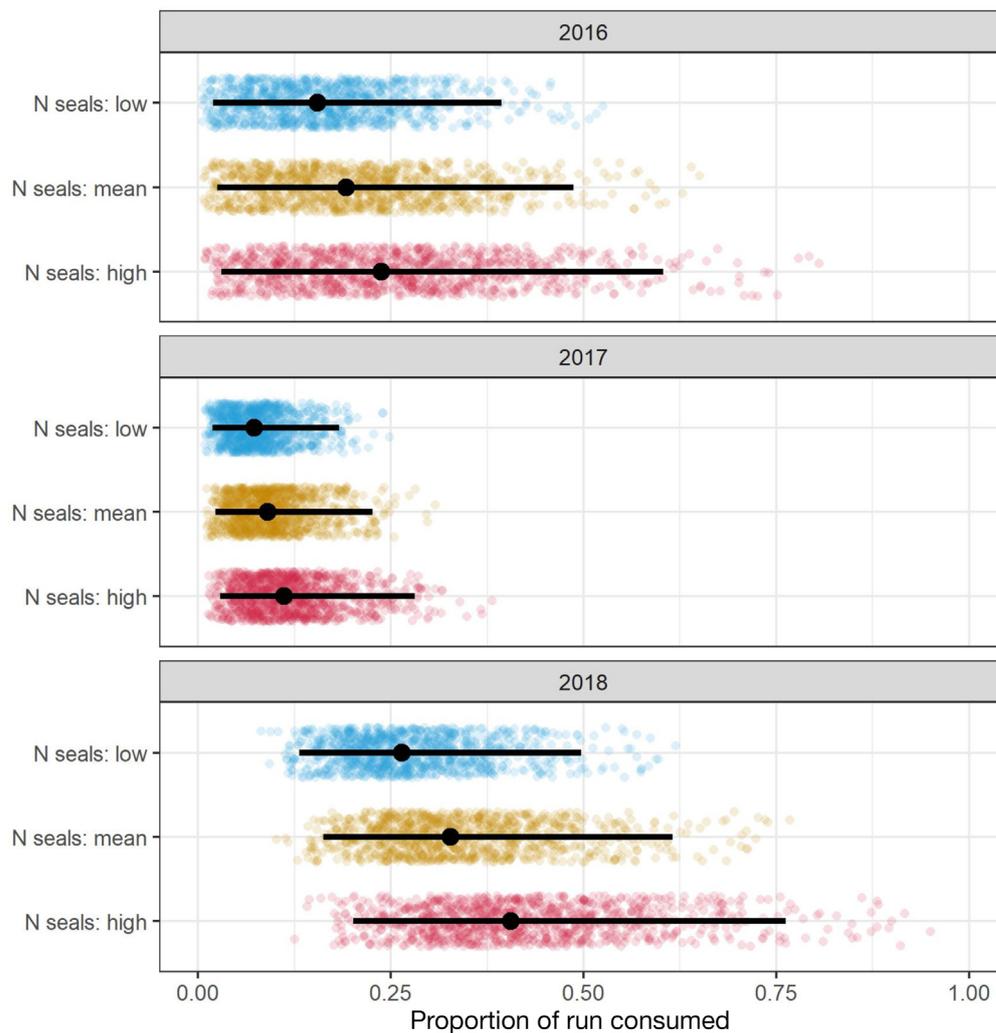


Fig. 4. Prey consumption model results, plotting the mean proportion of the Nisqually steelhead run consumed by harbor seals (black dots) with 95% confidence intervals (black lines), using South Puget Sound stock harbor seal abundance scenarios estimated by Jefferson et al. (2021) in 2016, 2017, and 2018. Outcomes for each of the 1000 model runs for each scenario (low: blue; mean: yellow; high: pink) are plotted for each year

consumption model (Fig. 5). Variation in the percent of SPS mortality attributed to seals was high due to propagation of error from smolt size and diet proportions throughout the calculation (Fig. 5).

3.3. Telemetry-based mortality

BAF-expanded mortality rates ranged from 11.1% of tagged Nisqually steelhead smolts in 2014 to 25.0% in 2016 (Table 2, Fig. 6). Of the 20 predation events located when the temperature increase occurred within detection range of a receiver pair, 5 events were recorded on receiver pair 1 (rkm 0.2–0.6), 7 on pair 2 (rkm 1.1–1.3), and 8 on pair 3 (rkm 3.9–4.1; Table S3 in the Supplement). Harbor seals consumed

tagged smolts throughout the monitored estuary during both ebbing and flooding tidal phases when tidal height exceeded 2.0 m above Mean Low Low Water (Table S3). Smolt length did not appear to affect probability of capture (Fig. S4 in the Supplement).

3.4. Comparison of two mortality assessments

BAF-expanded mortality estimates were generally consistent with the consumption model estimates, falling within the consumption model mortality rate estimate 95% confidence intervals in all 3 years (Fig. 6). More specifically, mean estimates from the BAF analysis exceeded consumption model-based estimates for SPS in 2016 and 2017, but they were

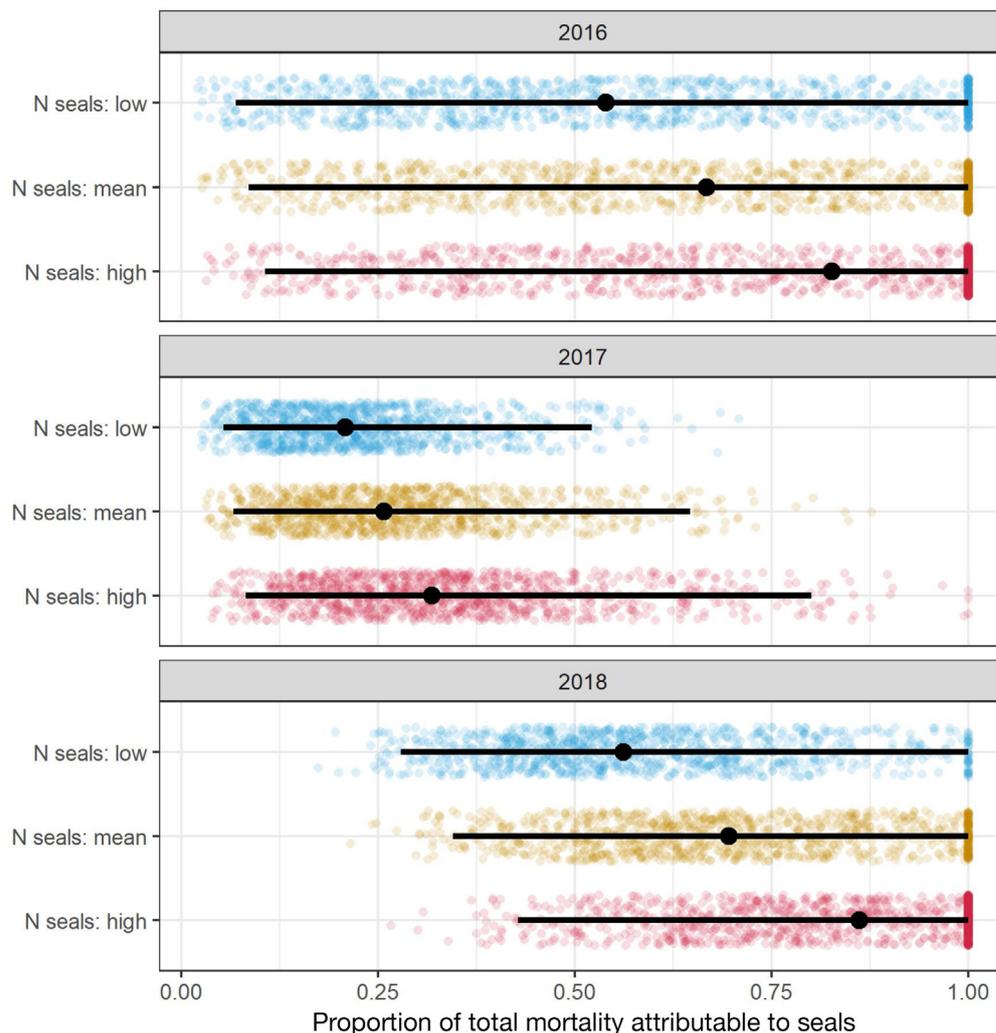


Fig. 5. Prey consumption model results, plotting the mean percent of total South Puget Sound (SPS) steelhead mortality attributed to harbor seals (black dots) with 95% confidence intervals (black lines), using SPS stock harbor seal abundance scenarios estimated by Jefferson et al. (2021) in 2016, 2017, and 2018. Outcomes for each of the 1000 model runs for each scenario (low: blue; mean: yellow; high: pink) are plotted for each year

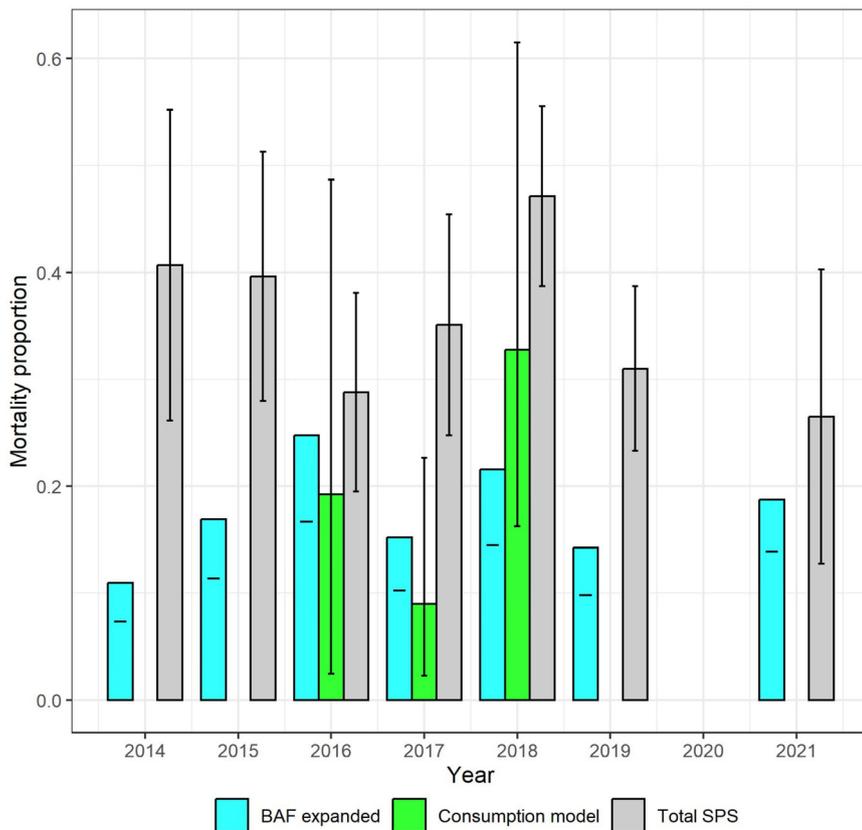


Fig. 6. Comparison of (1) estimates of harbor seal predation rates on steelhead smolts in the Nisqually river estuary calculated using telemetry-based back and forth behavioral analysis ('BAF-expanded'; cyan bars; horizontal black lines = unexpanded BAF mortality estimates), (2) estimates of harbor seal predation rates on steelhead smolts in the Nisqually estuary and South Puget Sound (SPS) calculated using a statistical prey consumption model with the mean SPS seal abundance estimate (green bars \pm 95% confidence intervals; 2016–2018 only), and (3) estimates of total steelhead mortality (gray bars \pm 95% confidence intervals) in the Nisqually estuary and SPS calculated using mark–recapture models populated with acoustic detection data of tagged steelhead smolts

lower in 2018. BAF mortality accounted for variable proportions of the total SPS mortality, with the lowest proportion in 2014 and high proportions observed in 2016 and 2021 (Fig. 6).

4. DISCUSSION

Our results demonstrate that a substantial portion of early marine mortality of Nisqually steelhead is due to predation by harbor seals inhabiting SPS. According to the prey consumption model (mean seal abundance scenario), harbor seals consumed between 9 and 33% of Nisqually River smolts annually migrating through 5 km of estuary habitat plus the first 23 km of their 275 km marine migration from estuary to the Pacific Ocean in 2016–2018. Behavioral data analysis of

tagged smolts indicates that seals consumed 15–25% of the Nisqually steelhead run over the 5 km stretch of estuary during the spring of the same years. Total smolt SPS mortality estimates ranged from 29 to 47%, such that harbor seal predation accounted for a majority of the steelhead smolt mortality occurring in SPS in 2 of the 3 study years for which we had all 3 mortality estimates (2016 and 2018). Predation occurring in the estuary accounted for more than half of the total SPS mortality in 2 of the 7 years (2016 and 2021). Substantial additional mortality due to harbor seals is likely incurred beyond SPS, as harbor seals are known to prey on steelhead in Central and North Puget Sound (Berejikian et al. 2016) and densely populate the remaining migration corridor (Jeffries et al. 2003, Jefferson et al. 2021), but predation rates beyond SPS have not been estimated.

The range of harbor seal predation impacts on the Nisqually steelhead smolt population calculated using a prey consumption model closely corresponds with the predation impacts assessed within the Nisqually estuary using an independent behavior-based telemetry approach. The considerable overlap in the ranges of the predation rates over these 3 years provides strong support that our results represent realistic predation rates. Also, 2016–2018 predation rates appear representative

of the 2014–2021 time period for which we estimated BAF-expanded mortality (range = 11–25%).

Using the consumption model, we were unable to partition predation mortality between the estuary and the remainder of the study area in SPS because scat samples were collected from haulouts throughout SPS and harbor seals are highly mobile. The harbor seal foraging radius can extend beyond 100 km but is typically closer to 20 km from primary haulouts (Peterson et al. 2012). In contrast to the consumption model, BAF-expanded mortality calculations provided a predation estimate for the Nisqually estuary. In 2016 and 2017, BAF-expanded mortality exceeded the prey consumption model estimate for the estuary and SPS, suggesting that a large portion of the predation upon marine entry occurs within the estuary (although the BAF predation rate fell within the 95%

confidence intervals of the consumption model estimate). In 2016, BAF-expanded mortality made up the majority of total SPS mortality and accounted for approximately half of SPS mortality in 2017 and 2018 despite encompassing a much smaller area. Smolts are more concentrated, and perhaps more easily preyed on, in the estuary than after entering Puget Sound, where they are able to disperse across a much larger area. A subset of tagged harbor seals in coastal Oregon exhibited specialized foraging behavior for adult coho salmon returning to the Alsea River, where constricted river channels make capture more efficient (Wright et al. 2007). Harbor seals haul out in large numbers directly adjacent to the Nisqually estuary during the spring months and can therefore easily access migrating smolts. Unexpectedly, steelhead DNA was found in scat samples from the Nisqually estuary at similar rates observed in samples from Cutts Island, which is 28 km from the Nisqually River mouth. Because we know the Nisqually River is the only considerable source of steelhead smolts in SPS, the similar percentages suggest either that SPS harbor seals transit that distance from their haulout to forage in the Nisqually estuary, or that seals hauling out at Cutts Island captured steelhead migrating through more open waters (or both).

In 2018, consumption model predation rate was considerably higher than BAF predation rate, and higher than in previous years. In that year, a large proportion of the scat samples was collected in the Nisqually estuary (Fig. S1), so predators foraging within the estuary were probably better represented than they were in 2016 and 2017. Thus, the consumption model appears to be sensitive to where samples are collected, and we might have seen less variability between years if samples were collected in the same proportion each year of the study. Unfortunately, scat collection is inherently opportunistic, based on tides and seal distribution, so equal representation among study years is difficult to achieve.

In recent years, predation by harbor seals has become a significant source of mortality for Pacific salmon species in the Salish Sea (Chasco et al. 2017, Nelson et al. 2021, 2024), and the present study adds to the growing body of information quantifying predation impacts on federally protected anadromous salmonid populations. Bioenergetics models similar to the prey-consumption model described in this study estimated percentages lost to harbor seal predation between 39 and 47% of Chinook originating in the Strait of Georgia (Nelson 2020) and between 6 and 49% (depending on prey size data source) of age-0 Chinook salmon from Puget Sound (Nelson et al.

2021). Coho salmon were similarly impacted in the Strait of Georgia, with an estimated 46–59% of annual smolt production lost to seal predation (Nelson 2020, Nelson et al. 2024), but only an estimated 7–8% of Puget Sound coho salmon smolts were consumed by harbor seals in 2016–2018 (Nelson et al. 2021). These estimates of mortality imposed by harbor seals are not directly comparable to our estimates of steelhead consumed because they estimate predation over a broad expanse of marine habitat on multi-population aggregations of outmigrating smolts, whereas our estimates pertain to a specific portion of Puget Sound and to a single population. Our model estimates of predation rates on steelhead also differ from those on Chinook and coho reported by Nelson et al. (2021) because of our ability to apply a year-specific freshwater mortality rate to total smolt production to calculate the number of smolts available to harbor seals in the marine environment. Puget Sound Chinook and coho estimates reported by Nelson et al. (2021) were calculated using total freshwater production estimates and are thus conservative given typically considerable mortality rates incurred during downriver migration (Quinn 2018).

Small monthly diet proportions comprised of steelhead translated into large impacts on the steelhead population because of coupled high energetic demands and high observed abundances of harbor seals in SPS. Steelhead never comprised more than 2% of the harbor seal diet during the Nisqually steelhead outmigrations of 2016–2018, and only 2.4% of SPS scat samples contained steelhead; however, even under low abundance estimate scenarios, harbor seals still consumed between 6000 (2017) and 32 500 (2018) smolts (7–26% of the steelhead run). Similarly, juvenile Chinook salmon comprise only about 2.1% of harbor seal diets in the Salish Sea (Thomas et al. 2017), but bioenergetics models using that percentage and incorporating abundance and dietary requirements calculated harbor seal consumption of Chinook salmon at 8.5 million smolts in 2015 (Chasco et al. 2017). At low diet proportions, steelhead smolts in SPS are not a significant component of the harbor seal diet but are likely taken opportunistically or targeted by only a few specialists. However, steelhead populations in Puget Sound are small, and this study provides a clear example of the possible predation impacts of a large and energetically demanding group of predators on a vulnerable prey population.

Harbor seal predation on other salmon species may affect their likelihood of preying on steelhead smolts, which are far less abundant. As generalist predators, harbor seals consume a broad range of

prey species, influenced heavily by seasonal availability (Lance et al. 2012, Thomas et al. 2022), but may be drawn to larger groups of salmonids, particularly coho salmon. Harbor seals target coho salmon released in large numbers into the Strait of Georgia (Allegue et al. 2020), and Nisqually steelhead experience higher mortality rates during weeks of high hatchery coho salmon smolt abundance in South and Central Puget Sound (Malick et al. 2023). Consistently observed BAF behavior in the estuary suggests seal foraging behavior specific to downstream migrating species throughout the steelhead migration period. Co-migrating coho may be targeted in the river as well. Though smaller than steelhead smolts in size, coho migration timing overlaps nearly completely with that of steelhead in the Nisqually River (Klungle et al. 2018). Pulses of prey may attract predators and increase localized feeding rates (Collis et al. 1995, Middlemas et al. 2006, Evans et al. 2016), but can also promote survival of migrating salmon by overwhelming or swamping predators during migration (Wood 1987, Ward & Hvidsten 2011, Furey et al. 2016). Similarly, a relatively abundant alternative prey species may facilitate higher survival of juvenile salmonids by luring a shared predator away or providing preferred foraging opportunities (Svenning et al. 2005, LaCroix et al. 2009, Moore et al. 2021). Effects of fluctuating spatial and temporal abundance patterns of marine fish species on migrating salmonids, though complex and dynamic, must be studied in conjunction with direct predator–prey interactions to fully explain pinniped predator impacts within the ecosystem.

Salmon and steelhead populations in the Pacific Northwest have suffered effects of habitat loss, harvest pressure, low marine survival, and possibly genetic effects from hatcheries, leaving many populations small and far from reaching recovery goals (Good et al. 2005, Ford 2022). Harbor seals are substantially impacting the survival of steelhead as they migrate through Puget Sound in some years and may be preventing recovery of these small populations. In a similar case off the US California coast, a large population of western gulls *Larus occidentalis* opportunistically consumed large proportions of small, threatened steelhead populations, increasing risk of local extirpation (Osterback et al. 2013). Harbor seals accounted for a majority of steelhead smolt SPS mortality in 2016 and 2018. A smaller proportion of mortality was attributed to harbor seals in 2017 according to both predation assessments, suggesting the prevalence of non-mammalian predators or other sources of mortality. Although variability in con-

sumption model estimates was high due to propagation of multiple sources of error throughout the calculation, there were several model iterations where harbor seals accounted for all of the observed mortality in SPS. This result is supported by the BAF analysis, where in 2016 BAF-expanded mortality (25%) accounted for nearly all of the mortality estimated for SPS ($1 - \Phi_{\text{SPS}}$, Table 3; 29%). The effects of predators that continue to consume prey even when rare or at low densities can disproportionately impact the extinction risk of small prey populations while impacts to large populations may be negligible (MacDonald et al. 1999, Lindley & Mohr 2003, Ward & Hvidsten 2011).

It is unclear whether harbor seal predation in the estuary and southern PS decreases the overall smolt-to-adult survival rate by acting as an additive source of mortality (Anderson & Burnham 1976, Lebreton 2005). Predation mortality may not be additive if it is compensated for through resultant changes in other mortality sources, leaving total smolt-to-adult survival nearly or completely unchanged (i.e. compensatory mortality). Compensation can result from selective predation on a class of individuals within the prey population (Lebreton 2005). For example, predators may select small, sick, or weak individuals from a prey population because they are more easily captured (e.g. Hostetter et al. 2012, Tucker et al. 2016), resulting in higher survival of the predated cohort relative to the survival of the cohort including weak individuals. Compensation may also occur when reduced prey density during one life stage results in increased access to resources (food, habitat, etc.; Jonsson et al. 1998, Zimmerman et al. 2015) that improves survivability. Compensatory mortality processes are unlikely to strongly affect Puget Sound steelhead because only 50 000–130 000 smolts enter the Nisqually estuary over a 2 mo period each year, so a reduction in already low densities is unlikely to provide substantial compensation to the group of remaining survivors, and no size-selective predation was observed (Fig. S4). Thus, it is possible and perhaps likely that predation by harbor seals upon marine entry is substantial enough to represent an additive source of mortality that ultimately reduces population productivity.

Even in intensively studied predator–prey systems, distinguishing between additive and compensatory mortality is notoriously difficult. Recently, 2 studies analyzing the same avian–steelhead predator–prey system in the Columbia River came to opposite conclusions; Payton et al. (2020) found evidence of additive mortality during smolt freshwater outmigration

and during the marine smolt–adult period, while Haeseke et al. (2020) concluded that avian predation mortality incurred in the Columbia estuary was largely compensated for by the time smolts returned as adults. The extent to which mortality is additive or compensatory can depend on species and life stage (Allen et al. 1998). Dominant mortality processes may vary annually or over time stanzas as well (see Pöysä et al. 2004). It is important to understand whether impacts of harbor seal predation on discrete life stages are ultimately affecting steelhead returns, especially when evaluating potential management actions. However, complex and variable ecological relationships confound our ability to characterize mortality processes, and direct manipulative experiments are needed to quantify the effects of predation on population productivity and capacity for recovery.

5. CONCLUSIONS

Predator recoveries pose new challenges for managers of complex ecosystems, who need a clear understanding of predator–prey interactions to make informed decisions. Successful restoration of a predator population in a system may occur before, and to the detriment of, prey species of conservation concern (Marshall et al. 2016, Oken & Essington 2016), though synchronous recovery of both predator and prey are often more effective than sequential, single-species recovery (Samhuri et al. 2017). Despite the difficulty, recovery plans for protected species need to consider impacts of linked predators, competitors, and prey, especially when those species are afforded protections that restrict management actions.

This study provides evidence that harbor seal predation can heavily impact a threatened steelhead population, even in a natural habitat relatively unaffected by human infrastructure. The protected status of harbor seals under the MMPA makes study and management of the issue especially difficult. However, comparison of the prey consumption model results and telemetry-based predation suggests greater impacts in the estuary compared to the broader habitat encountered by smolts upon marine entry. This information then supports design of management actions that focus on excluding harbor seals from areas where salmonid prey are most vulnerable, which is certainly more tractable than actions that would need to be implemented throughout the entire migration corridor. To stem further steelhead decline, timely implementation of adaptive management experiments on predation should be considered.

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