Characterizing juvenile salmon predation risk during early marine residence

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Abstract

Predation mortality can influence the distribution and abundance of fish populations. While predation is often assessed using direct observations of prey consumption, potential predation can be predicted from co-occurring predator and prey densities under varying environmental conditions. Juvenile Pacific salmon *Oncorhynchus* spp. (i.e., smolts) from the Columbia River Basin experience elevated mortality during the transition from estuarine to ocean habitat, but a thorough understanding of the role of predation remains incomplete. We used a Holling type II functional response to estimate smolt predation risk based on observations of piscivorous seabirds (sooty shearwater [*Ardena griseus*] and common murre [*Uria aalge]*) and local densities of alternative prey fish including northern anchovy (*Engraulis mordax*) in Oregon and Washington coastal waters during May and June 2010–2012. We evaluated predation risk relative to the availability of alternative prey and physical factors including turbidity and Columbia River plume area, and compared risk to returns of adult salmon. Seabirds and smolts consistently co-occurred at sampling stations throughout most of the study area (mean = 0.79 ± 0.41, SD), indicating that juvenile salmon are regularly exposed to avian predators during early marine residence. Predation risk for juvenile coho (*Oncorhynchus kisutch*), yearling Chinook salmon (*O. tshawytscha*), and subyearling Chinook salmon was on average 70% lower when alternative prey were present. Predation risk was greater in turbid waters, and decreased as water clarity increased. Juvenile coho and yearling Chinook salmon predation risk was lower when river plume surface areas were greater than 15,000 km², while the opposite was estimated for subyearling Chinook salmon. These results suggest that plume area, turbidity, and forage fish abundance near the mouth of the Columbia River, all of which are influenced by river discharge, are useful indicators of potential juvenile salmon mortality that could inform salmonid management.

Introduction

Assessing predation mortality is an important component of ecological research and resource management, including studies of threatened and endangered species such as Pacific salmon...
(Oncorhynchus spp). Numerous salmonid stocks from the Columbia River Basin on the west coast of North America are experiencing low population abundances and slow recoveries [1]. Mortality of juvenile salmon during the transition from estuarine to ocean habitat has a significant influence on survival to adulthood, and predation is thought to be a primary cause [2–4]. However, a comprehensive evaluation of the spatial distribution of predation risk for different salmon populations during the early marine phase remains incomplete.

An important group of predators near the mouth of the Columbia River are piscivorous seabirds including sooty shearwaters (Ardenna grisea) and common murres (Uria aalge) that occur in high densities in nearshore Washington and Oregon waters during spring and summer [5–7]. The response of seabirds to prey is often characterized by a Holling type II functional response [8–10], which describes predation rate as an asymptotic relationship of increasing prey density, predator attack rate, and prey handling time [11]. Shearwaters and murres in this region forage on aggregations of small coastal pelagic fish (i.e., forage fish) [12, 13], dominated by species including northern anchovy (Engraulis mordax) [14]. Juvenile salmon, referred to as smolts during seaward migration, are similar in length and appearance to forage fish, and become part of the seabird prey community as they migrate from the lower Columbia River estuary to coastal marine habitats. Prey-switching predators, including shearwaters and murres, can vary predation rates when multiple prey species are available and may have significant impacts on less abundant prey [15, 16]. Smolts have been detected in the diets of shearwaters and murres coincident with other prey species [12, 13], suggesting that predation on juvenile salmon during the period of early marine residence may be influenced by the availability of alternative prey [17, 18].

Predation is also influenced by physical and biological processes that affect prey densities and detectability. For example, migration from natal freshwater habitats to the ocean can concentrate smolts in a relatively small area, increasing local densities and potential encounters with co-occurring predators [19, 20]. Turbidity, which increases with river flow [21, 22], can reduce light levels and inhibit the visual foraging range of predatory fish [23–25], which may provide a predation refuge for smolts during downstream migration [26–28]. However, turbid waters near the mouth of the Columbia River attract shearwaters and murres and may increase smolt interactions with avian predators [29]. The survival of Columbia River Basin smolts has also been linked to water temperature and Columbia River plume size [30, 31]. Most smolts occupy nearshore coastal waters during early marine residence [32, 33], and are found in habitats with a narrow range of water temperatures that maximize growth and survival [31]. Variation in Columbia River plume size, as measured by plume volume and surface area [34], has a positive effect on the survival of interior Columbia River Basin subyearling Chinook salmon (O. tshawytscha) [30]. While numerous factors have been linked to smolt survival, relationships between physical processes, prey densities, and predation mortality have not been quantified.

Smolt predation by avian predators during early marine residence is challenging to assess due to difficulties in obtaining diet samples from seabirds at sea. In the absence of direct observations of predation events, models can be used to predict potential predation, or predation risk [35–37]. We used observations of co-occurrence among seabirds, smolts, forage fish, and the expected Holling type II functional response of shearwaters and murres to develop an index of juvenile salmon predation risk. We assessed how forage fish may mediate predation risk, and evaluated the influence of geographic and physical factors including distance from shore, turbidity, and plume surface area on risk variation and magnitude. Because marine survival of juvenile salmon is often measured by the number of returning adults from a cohort [38, 39], we then compared annual risk estimates to lagged returns of adult coho and Chinook salmon to determine if survival is related to predation risk during early marine residence.
Materials and methods

All animal work was conducted according to relevant national guidelines. Fish were collected under the Endangered Species Act (ESA) Section 10 permit #1410–7A, which is the federal procedure for research directed by NOAA that includes ESA-listed species.

This study used data from NOAA Fisheries Northwest Fisheries Science Center’s Juvenile Salmon and Ocean Ecosystems Survey (JSOES) research program designed to examine the ocean ecology of juvenile salmon off the Washington and Oregon coasts [40]. Predator, prey, and environmental data were collected during daylight hours in May and June 2010–2012 on chartered commercial fishing vessels sampling along transects and at fixed stations from the central Oregon coast (Newport) to the northern coast of Washington State. We used data from 198 stations sampled on 42 transects during six surveys (Fig 1).

Predator and prey sampling

Seabirds were counted along transects that began 35–42 km offshore at dawn with the vessel traveling inshore (due east) for 2 h at ~5 m s⁻¹ using standard strip transect survey methods (Fig 1) [41]. We recorded all seabirds that were flying or sitting on the water surface, but only used data on shearwaters and murres that were observed floating on the water surface, as birds on the water were assumed to be more closely associated with prey sampled at trawl stations. We estimated densities of sitting shearwaters and murres in 0.09 km² (300 m x 300 m) strips along the starboard side of the survey track.

After seabird counts were complete, the vessel reversed course to collect environmental and fish samples from 5 to 8 fixed sampling stations along the same transect, moving from inshore to offshore. Each station was spaced approximately 9 km apart along the transect (Fig 1). At each station, a profiling conductivity-temperature-depth instrument (hereafter, CTD; SBE 19plus; Sea-Bird Electronics Inc., Bellevue, Washington, USA; http://www.seabird.com/) was deployed to within 5 m of the bottom, or to a maximum depth of 200 m, to record temperature, salinity, and water clarity (measured by % beam transmittance). A 108 m long Nordic 264 rope trawl equipped with 3.0 m Lite™ trawl doors (NET Systems Inc., Bainbridge Island, Washington, USA; http://www.net-sys.com/) was fished at the surface for 30 min at a rate of 1.5 m s⁻¹ to collect pelagic organisms in the upper 15–20 m of the water column. The net opening was ~30 x 20 m (width x depth) when fishing. All juvenile salmon caught in the trawl were identified and measured to the nearest millimeter (fork length, FL). All non-salmonid organisms were also identified and enumerated, and up to 50 individuals of each species were measured, including fish (FL or standard length, SL) and squid (dorsal mantle length, DML). In instances where more than 50 individuals of a non-salmonid species were caught (e.g., large haul of anchovy), abundance was estimated by weighing a subsample of the catch, counting the subsample, and extrapolating total count based on weight. Trawl catches were standardized to fish km⁻² by dividing the number of fish caught by area fished. Area fished was calculated as the distance between the start and end of the trawl using GPS coordinates (mean: 3.3 ± 0.7 km, SD), multiplied by the width of the trawl (0.03 km).

To delineate potential prey of seabirds from the rest of the trawl contents, fish catches from each trawl were categorized using known species and species groups consumed by shearwaters [42, 43] and murres [13, 44]. All potential non-salmonid seabird prey items were categorized and grouped as alternative prey, including northern anchovy, Pacific sardine, Pacific herring (*Clupea pallasii*) and California market squid (*Doryteuthis opalescens*) (for full species list see [29]). To ensure that appropriately sized fish were included as prey and to allow for variation in prey shapes (e.g., body length versus body depth), we excluded organisms greater than 250 mm FL or DML, corresponding to the mean FL plus 2 times the standard deviation reported...
Fig 1. Study area along the Oregon and Washington, USA, coastline. Each transect is named for a geographic feature in proximity to the inshore end of the line as follows: FS, Father and Son; LP, La Push; QR, Queets River; GH, Grays Harbor; WB, Willapa Bay; CR, Columbia River; CM, Cape Meares; NH, Newport Hydrographic.

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for Pacific sardine (*Sardinops sagax*) consumed by common murres [44]. We did not use a minimum prey length, as murres and shearwaters consume a range of prey sizes including larval and juvenile life stages of marine organisms [45, 46]. All salmon ≤250 mm FL were categorized as juvenile salmon for calculations of total salmon prey density, including coho (*O. kisutch*), Chinook, chum (*O. keta*), sockeye (*O. nerka*), steelhead (*O. mykiss*), and cutthroat trout (*O. clarkii*). To account for life history variation in length at ocean entry of Chinook salmon, FL and month of capture were used to classify juvenile Chinook salmon as either subyearling or yearling fish based on length-at-age from scale analysis and tagging studies [47, 48]. To facilitate the calculation of predation risk of the three most commonly caught juvenile salmon groups (coho, yearling Chinook, and subyearling Chinook salmon) [29], we analyzed these three salmon groups separately (S1–S3 Figs).

Prey densities in the water column below the trawl depth were measured acoustically during trawling using EK60 or ES60 echosounders (Simrad, Kongsberg Maritime AS, Norway; [http://www.simrad.com/](http://www.simrad.com/)) equipped with hull-mounted, split-beam transducers (7˚ beam-widths measured at half power points) operating at 38 kHz. We used volume backscattering strength (*S*_v*; dB re 1 m⁻¹ [hereafter dB]; see [49]) to quantify acoustic densities through the water column. Acoustic data were processed using Echoview v 5.4 ([http://www.echoview.com/](http://www.echoview.com/)), with the *S_v* threshold set to -60 dB (for full details see [29]). Acoustic data between 0–10 m of the surface were excluded to account for transducer depth (4.25 m) and twice the near-field range of the transducers (5.44 m). To develop an index of acoustically-detected prey available to seabirds, all *S_v* measurements were vertically integrated from 10 m below the surface to 70 m depth, the approximate diving range of sooty shearwaters and common murres [50–52]. Acoustic densities were reported as nautical area scattering coefficients (*s_A*; m⁻² nmi⁻²) [49], indexed in space and time.

To convert acoustic densities to comparable fish densities sampled by the trawl (i.e., fish km⁻²), *s_A* values were converted to fish density (*ρ_a*) using [53]:

\[
ρ_a = \left(\frac{s_A}{σ_{bs}}\right) \times 10^6
\]

Where *σ_{bs}* (5.50 x 10⁻⁶ m²) is the estimated backscattering cross section of a 150 mm (FL) northern anchovy at 38 kHz with an estimated target strength (TS) of -52.6 dB. The 150 mm FL was based on the maximum fork length of adult anchovy observed in fishery surveys [14]. TS was calculated using the target-strength to length equation for South African anchovy (*Engraulis capensis*) [54]:

\[
TS = 20 \times \log(FL_{cm}) - 76.10
\]

There was no statistical relationship between alternative prey densities estimated from the surface trawl and density estimates from acoustic backscatter (Spearman’s correlation: *ρ* = -0.012, *p* = 0.857). Therefore, to quantify the total relative alternative prey density (*A*, fish km⁻²) at each station for the vertical foraging range of shearwaters and murres (i.e., ≤ 70 m water depth), non-salmonid prey densities from trawl sampling were summed with densities of acoustically detected alternative prey (S4 Fig). Alternative prey density estimates for May 2010 only include surface trawl catches because acoustic backscatter data were not collected during that survey. Estimates of juvenile salmon density (*S*, fish km⁻²) were not calculated from acoustic samples because smolts typically occur in the upper 10 m of the water column during the day [55, 56], and this near-surface portion of the water column was not sampled acoustically.
Predator-prey co-occurrence and encounter rate

Predator-prey interactions depend on the co-occurrence of predators with prey at a specific time and place, which increases the probability of a predator encountering, attacking, and consuming prey [57, 58]. In this study, co-occurrence is defined as either shearwaters or murres being present at a station where juvenile salmon were caught in the surface trawl. To quantify co-occurrence, each seabird observation was assigned to the nearest trawl station, using one half the distance between stations as the breakpoint. Because shearwaters and murres consume similar prey and exhibit comparable foraging habits [13, 43, 59], both species were combined in a single predator group for analyses (S5 Fig). To determine areas with consistent predator-prey co-occurrence, we classified stations where seabirds and juvenile salmon co-occurred from those where they did not. Mean co-occurrence was then calculated as the number of times seabirds and juvenile salmon were both present at a station divided by the number of times the station was surveyed. Encounter rate was assumed to be proportional to co-occurrence, based on the observed relationship between foraging seabirds and co-occurring fish schools [e.g., 60].

Estimating predation risk

We used the Holling type II functional response [11] to relate potential predation upon juvenile salmon (C) to the density of co-occurring prey:

\[ C = \frac{aN}{1 + ahN} \]  

where \( N \) is prey density, \( a \) is the combined predator attack and consumption rate (i.e., rate of successful predation), and \( h \) is prey handling time.

Because juvenile salmon are often consumed coincident with other prey items [16], we assumed equal consumption probabilities for juvenile salmon and alternative prey and hypothesized that potential juvenile salmon predation varies with overall prey density available to predators. To estimate prey density available to predators at each station, we summed all juvenile salmon densities (\( S \), fish km\(^{-2}\)) and alternative prey densities (\( A \), fish km\(^{-2}\)), and used these values to parameterize \( N \) (fish km\(^{-2}\)). To calculate the proportion of juvenile coho, yearling Chinook, or subyearling Chinook salmon at each station, we divided the density of fish from each of the three salmon groups (\( s_i \)) by the total prey density (\( N \)). This allowed us to estimate potential predation of juvenile coho, yearling Chinook, or subyearling Chinook salmon (\( J_i \), smolts consumed time\(^{-1}\)) as separate components of total potential prey consumption:

\[ J_i = \left( \frac{aN}{1 + ahN} \right) \times \frac{s_i}{N} \]  

Seabird attack and consumption rate (\( a \), fish time\(^{-1}\)) was set to 0.6, based on in situ observations of seabirds successfully attacking and consuming fish [8, 9]. Handling time (\( h \), time) was assumed to be low, based on in situ observations of seabirds consuming fish within seconds of capture [8, 9], and was conservatively set to 0.1.

Predation pressure (\( P \)) was used as a scalar based on seabird density (birds km\(^{-2}\)), calculated as the total number of shearwaters and murres observed at each station divided by the area surveyed. Predation risk (\( R_i \)) experienced by individual juvenile coho, yearling Chinook, and subyearling Chinook salmon was expected to increase with greater predation pressure and decrease with greater total densities of smolts (\( S \)). Thus, to estimate predation risk (\( R_i \)), potential smolt predation (\( J_i \)) was multiplied by predation pressure (\( P \)) and divided by total juvenile
salmon density \((S)\) at each station:

\[ R_i = \frac{J_i \times P}{S} \]  

(5)

Predation risk was calculated separately for juvenile coho, yearling Chinook, and subyearling Chinook salmon at each sampling station for each of the six surveys, resulting in unique, spatially-indexed risk estimates.

**Variation in risk**

We compared spatially-indexed predation risk estimates across stations and surveys among the three salmonid groups using a Kruskal-Wallis test [61]. Persistent high-risk areas (i.e., risk hotspots) for juvenile coho, yearling Chinook, and subyearling Chinook salmon were identified by calculating mean predation risk at each station across all surveys. Spatiotemporal variation in risk was visualized using kernel density estimation in ArcMap 10.3 (ESRI, Redlands, CA).

To estimate the change in risk when alternative prey were absent, we re-calculated potential smolt consumption \((J_i)\) using only estimates of juvenile salmon density, and then re-calculated predation risk \((R_i)\) based on these estimates. Differences in risk estimates with and without alternative prey were compared using a Mann-Whitney rank sum test [61].

The influence of environmental factors on predation risk was evaluated using generalized additive mixed models (GAMMs) with a negative binomial error structure and log link function with the ‘mgcv’ package [62] in R version 3.3.2 [63]. Sampling station was included as a random effect to account for spatial autocorrelation. GAMMs with predation risk as the response variable were parameterized separately for juvenile coho, yearling Chinook, and subyearling Chinook salmon. Covariates in each GAMM included *in situ* measures of turbidity measured by water clarity (% beam transmittance) at 3 m depth sampled during each survey; latitude; distance from shore (km); and contemporaneous daily plume surface area (km\(^2\)) estimated by a hydrodynamic model of Columbia River plume circulation, using salinity values of 28 practical salinity units (psu) to define the plume boundary (Center for Coastal Margin Observation and Prediction; db33 climatological atlas; http://www.stccmop.org/datamart/virtualcolumbiariver). We did not include salinity or temperature as covariates because a correlation matrix indicated that these variables were collinear with multiple predictors. Thin plate regression splines were used as smoothing functions, and spline shrinkage was used to perform automatic smoothness selection of covariates [64]. Backward variable selection was accomplished by first fitting models with all explanatory variables, and removing non-significant terms (p-value > 0.05). Model performance was evaluated by examining deviance explained, changes in Akaike information criterion for small sample sizes (AIC\(_c\)), and Akaike weights \((\omega_i)\). Final models were selected as those with \(\Delta\text{AIC}_c < 2\) and \(\omega_i > 0.5\). Normalized residuals were plotted to check for violations of model assumptions [65]. The partial effect of each covariate retained in each final model was plotted to examine the relationship between risk and individual physical factors.

The relationship between predation risk during early marine residence and salmon survival was evaluated across the three years by plotting mean predation risk of juvenile coho, yearling Chinook, and subyearling Chinook salmon against adult returns. Returning adult spring and fall Chinook salmon, represented by counts of fish from the corresponding juvenile year class at Bonneville Dam (the first dam on the Columbia River [river km 235] that salmon must pass during their return migration) were obtained from Columbia Basin Research DART data server (www.cbr.washington.edu/dart/adult_annual.html). The majority of yearling Chinook
salmon spend two years in the ocean prior to returning to natal rivers in the spring [66], so adult spring Chinook run counts were lagged by two years (i.e., adult spring Chinook salmon returning in 2012 were assumed to represent fish that entered the ocean during 2010). The majority of subyearling Chinook salmon spend three years at sea and return during the fall [67], so fall Chinook salmon run counts were lagged by three years. Adult coho typically return after one year at sea [68], and production is primarily below Bonneville Dam. Therefore, we used adult coho salmon returns to public hatcheries (Oregon Production Index Hatchery, OPIH) reported by the Pacific Fisheries Management Council [69], where ocean survival is estimated as the ratio of hatchery smolt release numbers to hatchery adult freshwater returns in the year following smolt entry into the ocean.

**Results**

Frequency of seabird co-occurrence with juvenile salmon at individual stations averaged 0.79 ± 0.41 (SD) across the six surveys, and was consistently high on all transects (mean > 0.75) except the southernmost transect (NH) where numbers of juvenile salmon were low (Fig 2, S1–S3 Figs). Mean co-occurrence was greater than 0.75 at all sampling stations along the Columbia River transect, and the majority of stations sampled on transects along the Washington coast (Fig 2).

Predation risk \( R \) of yearling Chinook salmon (1.08 ± 7.15) was significantly greater than predation risk of coho (0.150 ± 0.77) and subyearling Chinook salmon (0.048 ± 0.20; \( H_2 = 50.31, \) p-value < 0.005). Predation risk for coho was greatest near the Cape Meares transect (Fig 3A), whereas risk estimates for Chinook yearling salmon were greatest near Willapa Bay and La Push (Fig 3B). In comparison, risk for subyearling Chinook salmon was greatest near the mouth of the Columbia River (Fig 3C).

On average, juvenile salmon predation risk dropped by 70.3 ± 3.2% (SD) when densities of alternative prey were included in calculations. Predation risk declined significantly for juvenile coho (-69.0%; \( W = 16790, p = 0.0092 \)) and yearling Chinook salmon (-68.2%; \( W = 16144, p = 0.0018 \)). Despite a 73.7% decline in predation risk for subyearling Chinook salmon, the difference was not significant (\( W = 18912, p = 0.4402 \)). The lack of significance is attributed to the small sample size (\( n = 54 \)).

GAMM results indicate that latitude, distance from shore, water clarity, and plume surface area were retained in final models of predation risk for juvenile coho and yearling Chinook salmon, while only water clarity and plume surface area were retained in the final model for subyearling Chinook salmon (Table 1). Predation risk for juvenile coho salmon was greatest at around 45.5°N, whereas predation risk increased linearly with latitude for yearling Chinook salmon (Figs 4 and 5). The effect of distance from shore indicated greatest risk for juvenile coho salmon approximately 20 km from shore, whereas risk for yearling Chinook salmon was greatest in nearshore waters (<10 km from shore) and declined across the offshore range sampled (1.9–46.3 km). Predation risk for juvenile coho, yearling Chinook, and subyearling Chinook salmon was greatest in turbid waters, and decreased as waters became more clear (>85% beam transmittance; Figs 4–6). Juvenile coho and yearling Chinook salmon predation risk was highest during periods when plume surface areas were small (<15,000 km²), and declined across the range of surface areas observed (1,535–35,840 km²; Figs 4 and 5). In comparison, predation risk of subyearling Chinook salmon was greatest when plume surface areas were large (>15,000 km²; Fig 6).

Annual counts of adult coho salmon returns were positively related to predation risk of juvenile coho salmon (Fig 7A). In contrast, annual counts of adult spring Chinook salmon at Bonneville Dam were negatively related to yearling Chinook salmon predation risk (Fig 7B).
Fig 2. Mean co-occurrence of seabirds and juvenile salmon at sampling stations during May and June 2010–2012. The Cape Meares murre colony identified in the text is labeled.

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Fig 3. Mean predation risk (R) for juvenile coho, yearling Chinook salmon, and subyearling Chinook salmon sampled at trawl stations during May and June 2010–2012.

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Table 1. Generalized additive mixed effects models of predation risk for each salmonid group.

| Salmon Group | Model | Description | Formulation | edf | Deviance explained | AIC<sub>c</sub> | ΔAIC<sub>c</sub> | ω<sub>i</sub> |
|--------------|-------|-------------|-------------|-----|--------------------|----------------|---------------|------------|
| Juvenile Coho | CO.1  | Full model  | Risk ~ s(Lat) + s(Distance from shore) + s(Water clarity) + s(Plume area) + s(Station, bs = ’re’) | 14  | 49.0 | 121.47 | 0.00 | 0.88 |
|              | CO.2  | Drop distance to shore | Risk ~ s(Lat) + s(Water clarity) + s(Plume area) + s(Station, bs = ’re’) | 15  | 48.3 | 125.40 | 3.93 | 0.12 |
|              | CO.3  | Drop latitude | Risk ~ s(Water clarity) + s(Plume area) + s(Station, bs = ’re’) | 20  | 50.5 | 136.01 | 14.54 | 0.00 |
|              | CO.4  | Drop water clarity | Risk ~ s(Plume Area) + s(Station, bs = ’re’) | 15  | 38.8 | 140.08 | 18.61 | 0.00 |
| Yearling Chinook | CY.1  | Full model  | Risk ~ s(Lat) + s(Distance from shore) + s(Water clarity) + s(Plume area) + s(Station, bs = ’re’) | 23  | 71.8 | 200.60 | 0.00 | 0.72 |
|              | CY.2  | Drop latitude | Risk ~ s(Distance from shore) + s(Water clarity) + s(Plume area) + s(Station, bs = ’re’) | 22  | 70.3 | 202.49 | 1.89 | 0.28 |
|              | CY.3  | Drop water clarity | Risk ~ s(Distance from shore) + s(Plume area) + s(Station, bs = ’re’) | 18  | 63.8 | 222.05 | 21.46 | 0.00 |
|              | CY.4  | Drop distance to shore | Risk ~ s(Plume Area) + s(Station, bs = ’re’) | 23  | 66.8 | 227.74 | 27.14 | 0.00 |
| Subyearling Chinook | SY.1  | Full model  | Risk ~ s(Lat) + s(Distance from shore) + s(Water clarity) + s(Plume area) + s(Station, bs = ’re’) | 7   | 36.1 | 50.08 | 3.55 | 0.09 |
|              | SY.2  | Drop latitude | Risk ~ s(Distance from shore) + s(Water clarity) + s(Plume area) + s(Station, bs = ’re’) | 5   | 30.5 | 47.11 | 0.57 | 0.39 |
|              | SY.3  | Drop distance to shore | Risk ~ s(Water clarity) + s(Plume area) + s(Station, bs = ’re’) | 4   | 26.7 | 46.54 | 0.00 | 0.52 |
|              | SY.4  | Drop water clarity | Risk ~ s(Plume area) + s(Station, bs = ’re’) | 3   | 11.9 | 62.21 | 15.67 | 0.00 |

For each model formulation tested, the corresponding effective degrees of freedom (edf), deviance explained, Akaike information criterion corrected for small sample size (AIC<sub>c</sub>) and differences (ΔAIC<sub>c</sub>), and Akaike weights (ω<sub>i</sub>) are presented. Selected final models are in bold.

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Similarly, the relationship between adult returns of fall Chinook and subyearling Chinook salmon predation risk was also negative (Fig 7C).

Discussion

Using co-occurrence of prey fish and seabirds and a Holling type II functional response, we found that for the three salmon groups examined, juvenile salmon predation risk is greatest in nearshore, turbid waters. Local densities of alternative prey reduced predation pressure on smolts by an average of 70%, indicating that coastal pelagic fish species such as northern anchovy have the potential to influence juvenile salmon mortality during early marine residence [2, 17, 18]. Our results also suggest that a larger Columbia River plume surface area reduces predation risk for juvenile coho and yearling Chinook salmon. Taken together, this study reinforces and expands on findings that the Columbia River plume influences predation.
Juvenile salmon co-occurred with seabirds at the majority of sampling stations in this study, indicating that potential encounters between predators and smolts during their seaward migration extends beyond the boundaries of the Columbia River estuary and plume. Smolt-seabird co-occurrence was greatest near the mouth of the Columbia River, which is not surprising given that juvenile salmon emigrate out of the Columbia River to an area where seabirds consistently occur [5–7]. The co-occurrence of smolts and seabirds at sampling stations in the northern portion of the survey area also indicates that juvenile salmon are exposed to avian predators throughout most of their northward migration along the Washington coast. In particular, yearling Chinook salmon may be more vulnerable to predators throughout Washington coastal waters, considering their consistent co-occurrence with seabirds and elevated risk estimates at greater latitudes relative to coho and subyearling Chinook salmon.

Fig 5. Plots of the partial effects of latitude, distance from shore, water clarity and plume surface area on predation risk of yearling Chinook salmon caught in surface trawls during May and June 2010–2012. Points on the plots are partial residuals of the full model without the effect of the term concerned (x-axis covariate). Gray shading around smooth fits represents 95% confidence intervals, and data availability is indicated by tic marks above x-axis.

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pressure experienced by juvenile salmon, and that early marine residence is a period of high mortality risk for ocean-going salmonids [2, 30, 70].
Despite consistent co-occurrence of seabirds and smolts throughout most of the study area, we demonstrate that predation risk to juvenile salmon can be reduced substantially when forage fish are available, supporting the alternative prey hypothesis [2, 17, 18]. Aggregation patterns of smolts and alternative prey led to an uneven spatial distribution of predation risk for juvenile coho, yearling Chinook, and subyearling Chinook salmon. Coastal pelagic fish densities are often greatest near the mouth of the Columbia River, and on the Washington coast near Grays Harbor and Willapa Bay [29, 71], where subyearling Chinook and yearling Chinook salmon predation risk was high. Increased risk estimates in this area may be explained by the strong influence of river plume dynamics on salmon and alternative prey densities [29]. Relatively greater predation risk estimates also occurred near Cape Meares for all three salmonids examined, even though co-occurrence estimates were not consistently high on this transect. Cape Meares is the site of a large murre colony [72], and these results suggest juvenile salmon occupying nearshore waters south of the Columbia River mouth [73] may experience greater predation risk in areas where fewer alternative prey occur adjacent to a seabird colony. Similarly, yearling Chinook salmon predation risk was greater in northern Washington waters near La Push, which may be related to greater densities of smolts and seabirds, and relatively fewer alternative prey.

Even when alternative prey densities are high, salmon may still be vulnerable to predation [16]. Greater densities of forage fish near productive plume waters attract large groups of foraging murres and shearwaters [6, 29], which could explain the increased predation risk to co-occurring smolts in nearshore and turbid waters (i.e., apparent competition) [74]. We assumed that shearwaters and murres do not exhibit prey selectivity, but acknowledge that predation risk estimates may vary in alternate models that include prey preference and switching [75–77]. There are no recent data on food habits of shearwaters and murres in the northern California Current, so knowledge of seabird prey selection when two or more prey co-occur is unknown. We also did not consider interference competition in this study, although seabirds are known to be attracted to aggregations of conspecifics [78–80]. While seabirds are generally thought to benefit from collective foraging [81], competition for prey at very high predator densities may alter predation rates [82, 83]. Additional research on seabird encounter, attack,
Fig 7. Boxplot of predation risk for (a) juvenile coho salmon, (b) yearling Chinook salmon, and (c) subyearling Chinook salmon. Dark line: median; box: interquartile range (IQR); error bars: max/min within 1.5 x IQR above/below IQR; outliers not shown. Total adult returns (lagged to correspond to predation risk during year of smolt entry) are shown as diamonds.

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and consumption rates under varying prey and predator community compositions, distributions, and aggregation sizes will expand our understanding of avian impacts on potential prey including juvenile salmon.

Plume surface area is an important factor influencing smolt predation risk, although we found contrasting relationships between plume area and smolt life history. Coho and yearling Chinook salmon rear in freshwater for one year before migrating to sea in May and June [84], when plume surface areas are typically at seasonal maxima [85]. We found that as plume surface area increased above 15,000 km\(^2\), predation risk for both juvenile coho and yearling Chinook salmon decreased, suggesting that migrating to sea during peaks in river discharge may reduce predation mortality. Increasing freshwater discharge enhances overall production of coastal waters [86], thereby increasing local abundances of multiple trophic levels including zooplankton and larval fish that serve as prey for forage fish and juvenile salmon. Northern anchovy densities are positively correlated with increases in river discharge [87], and anchovy aggregate and spawn near Columbia River plume boundaries in spring and summer [88, 89]. Both shearwaters and murres concentrate in the Columbia River plume when surface areas are low [29] and move towards plume boundary waters when surface areas exceed approximately 1,500–4,000 km\(^2\) [90]. As plume surface areas become larger, shearwaters and murres track the plume boundary waters and appear to expand their foraging area [29, 90]. This movement of seabirds to the plume boundary may be due to enhanced biophysical coupling [91, 92] that increases foraging opportunities. Therefore, greater plume surface areas may lower juvenile coho and yearling Chinook salmon predation risk by increasing the foraging area for seabirds that are attracted to the Columbia River plume [6, 29, 93], and aggregating alternative prey near plume boundaries, where juvenile salmon do not congregate [94].

In contrast to risk estimates for coho and yearling Chinook salmon, predation risk for subyearling Chinook salmon was higher with greater plume surface areas. Subyearling Chinook salmon migrate to sea after residing for only a few months in freshwater and are therefore smaller in size than yearling salmon [84]. Most subyearling Chinook salmon typically enter the ocean later in the summer, when river discharge is often lower [95]. During periods of above average river flows in spring, however, greater densities of subyearling Chinook salmon can be found in the Columbia River plume and surrounding coastal waters, indicating that these smaller fish may not be able to swim against increased outgoing river flow [55]. Subyearling Chinook salmon also occupy nearshore waters near the mouth of the Columbia River longer than juvenile coho and yearling Chinook salmon [33, 48], making them more vulnerable to seabirds foraging near the mouth of the Columbia River. The observed relationship between subyearling Chinook salmon predation risk and plume surface area could also be related to survey timing and small sample sizes, as we only used samples from spring (May and June) and greater numbers of subyearling Chinook salmon are usually caught in fall (September) surveys when they are more abundant in coastal waters [30, 94].

Predation risk was highest for smolts when water clarity was at low or intermediate values, indicating that turbidity does not provide smolts a refuge from avian predators in the ocean. This is not unexpected given that shearwaters and murres are attracted to turbid plume waters [6, 29, 90], but contrasts to studies of juvenile salmon consumption by piscivorous fish in lakes and rivers [26, 28, 96]. Water clarity measurements used in this study represent a mix of suspended sediment and phytoplankton concentrations associated with the nutrient-rich recirculating plume waters, whereas turbidity in freshwater habitats may be driven by different mechanisms. Despite these differences, previous research has found that seabirds can effectively forage in highly turbid freshwater and saltwater habitats [97–99], which suggests that smolts are vulnerable to avian predators when water clarity is low regardless of the habitat type. Turbidity values in the Columbia River plume are typically highest in near-surface waters.
(< 5 m), with clarity increasing beneath the surface lens of the plume [100]. Thus, the large footprint of the plume may serve as a predictable surface feature for aerial avian predators to locate before pursuing prey in deeper waters [90].

Our comparison of risk to adult salmon returns indicates that potential predation risk experienced by juvenile salmon during early marine residence may relate to adult returns 2 to 3 years later. However, our results were inconsistent; we found a positive relationship between risk and coho returns, in contrast to a negative relationship for subyearling Chinook and yearling Chinook salmon adult returns. This may relate to the interactive effects of freshwater discharge and ocean conditions on salmon survival, or to our use of only three years of aggregated adult salmon data. The relationships between adult returns and predation risk for each salmon group are likely to change with additional years of data. We also assumed that return timing for salmon in this study was concentrated within a single year, although individuals from the same cohort, particularly for Chinook salmon, return between 2 to 6 years after ocean entry [66, 101]. To increase the utility of a survival index, additional effort using a longer timeline for returning adults may elucidate relationships between predation risk and survival to adulthood. A longer time series to calculate stock-specific juvenile salmon predation risk may also increase precision of risk estimates for threatened and endangered species such as upper Columbia River and Snake River wild spring/summer Chinook salmon.

This study demonstrates that predictions of juvenile salmon early marine survival may be informed by knowledge of river discharge, plume surface area, forage fish abundance, and associated estimates of predation risk. Plume surface area is correlated to river discharge [34], and both metrics are available from monitoring stations on the river and from hydrodynamic model outputs [102]. To reduce juvenile salmon predation risk, springtime river flows and spill regimes could be coordinated to manage river discharge so that plume surface areas during downstream smolt migration remain greater than ~15,000 km\(^2\). Data from the SELFE model (Center for Coastal Margin Observation and Prediction; db33 climatological atlas; http://www.stccmop.org/datamart/virtualcolumbiariver) suggest that this may not be a difficult goal to achieve. While daily average river plume surface areas for the months of April to July during 1999–2016 exceeded 15,000 km\(^2\) only 7% of time, plume surface areas were greater than 10,000 km\(^2\) approximately 22% of the time. Even if spill modification is impractical, knowledge of plume surface areas may be a useful proxy index of smolt early marine mortality that could be incorporated into models of adult salmon survival. Further, river discharge or plume surface area could be used by hatchery managers considering varying smolt release timing in an effort to maximize early marine survival of juvenile salmon. Similarly, knowledge of ocean conditions that influence the abundance and distribution of forage fish may also inform estimates of juvenile salmon survival.

This study used predator-prey theory to estimate predation risk of Columbia River salmon and to examine environmental conditions that affect predation risk. Results suggest that predation on juvenile salmon is greatest nearshore, in turbid waters, and when river discharge is relatively low. We also demonstrated that alternative prey can mediate predation risk to juvenile salmon. This approach is applicable to other studies focused on aquatic predator-prey interactions where direct observations of predation events are difficult to obtain. To validate our results and to enable computation of juvenile salmon predation mortality, however, diet samples of seabirds under varying environmental conditions, particularly during periods of increased or decreased plume surface areas, are required. Evidence of salmon consumption by other predator groups including marine mammals and piscivorous fish has been compiled [46, 103], but without empirical data on seabird consumption of juvenile salmon and alternative prey, the cumulative impact and relative importance of avian predators on juvenile salmon predation mortality remains unresolved.
Supporting information

S1 Fig. Distribution of juvenile coho salmon (fish km\(^{-2}\)) caught in surface trawls during a) May 2010, b) May 2011, c) May 2012, d) June 2010, e) June 2011, and f) June 2012. (TIF)

S2 Fig. Distribution of yearling Chinook salmon (fish km\(^{-2}\)) caught in surface trawls during a) May 2010, b) May 2011, c) May 2012, d) June 2010, e) June 2011, and f) June 2012. (TIF)

S3 Fig. Distribution of subyearling Chinook salmon (fish km\(^{-2}\)) caught in surface trawls during a) May 2010, b) May 2011, c) May 2012, d) June 2010, e) June 2011, and f) June 2012. (TIF)

S4 Fig. Distribution of alternative prey (surface trawl and acoustic measurements combined, fish km\(^{-2}\)) during a) May 2010, b) May 2011, c) May 2012, d) June 2010, e) June 2011, and f) June 2012. (TIF)

S5 Fig. Distribution of seabirds (common murre and sooty shearwater, birds km\(^{-2}\)) during a) May 2010, b) May 2011, c) May 2012, d) June 2010, e) June 2011, and f) June 2012. (TIF)

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References

1. Northwest Fisheries Science Center. Status review update for Pacific salmon and steelhead listed under the Endangered Species Act: Pacific Northwest. 2015 [cited 24 Jun 2019]. Available: https://wwwnwfsccnoaa.gov/assets/11/8623_03072016_124156_Ford-NWSalmonBioStatusReviewUpdate-Dec%202015%20v2.pdf

2. Pearcy WG. Ocean ecology of north Pacific salmonids. Seattle: Washington Sea Grant Program; Distributed by the University of Washington Press; 1992.

3. Beamish RJ, Mahnken C. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Prog Oceanogr. 2001; 49: 423–437. https://doi.org/10.1016/0079-6611(01)00034-9

4. Collis K, Roby DD, Craig DP, Adamany S, Adkins JY, Lyons DE. Colony size and diet composition of piscivorous waterbirds on the lower Columbia River: Implications for losses of juvenile salmonids to avian predation. Trans Am Fish Soc. 2002; 131: 537–550.

5. Adams J, MacLeod C, Suryan RM, Hyrenbach KD, Harvey JT. Summer-time use of west coast US National Marine Sanctuaries by migrating sooty shearwaters (Puffinus griseus). Biol Conserv. 2012; 156: 105–116. https://doi.org/10.1016/j.biocon.2011.12.032

6. Zamon JE, Phillips EM, Guy TJ. Marine bird aggregations associated with the tidally-driven plume and plume fronts of the Columbia River. Deep Sea Res Part II Top Stud Oceanogr. 2014; 107: 85–95. https://doi.org/10.1016/j.dsr2.2013.03.031

7. Menza C, Leimess J, White T, Winship AJ, Kinlan B, Kracker L, et al. Predictive mapping of seabirds, pinnipeds and cetaceans off the Pacific coast of Washington. NOAA Tech Memo NOS NCCOS 210. 2016; 96.

8. Enstipp MR, Gremillet D, Jones DR. Investigating the functional link between prey abundance and seabird predatory performance. Mar Ecol Prog Ser. 2007; 331: 267–279.

9. Crook KA, Davoren GK. Underwater behaviour of common murres foraging on capelin: influences of prey density and antipredator behaviour. Mar Ecol Prog Ser. 2014; 501: 279–290. https://doi.org/10.3354/meps10696

10. Piatt JF, Harding AMA, Shultz M, Speckman SG, VanPelt TI, Drew GS, et al. Seabirds as indicators of marine food supplies: Cairns revisited. Mar Ecol Prog Ser. 2007; 352: 221–234. https://doi.org/10.3354/meps07078

11. Holling CS. Some characteristics of simple types of predation and parasitism. Can Entomol. 1959; 91: 385–398. https://doi.org/10.4039/Ent9138-7

12. Wiens JA, Scott JM. Model estimation of energy flow in Oregon coastal seabird populations. The Condor. 1975; 77: 439–452. https://doi.org/10.2307/1366091

13. Varoujean D, Matthew D. Distribution, abundance, and feeding habits of seabirds off the Columbia River, May-June, 1982. Charleston, OR: University of Oregon Institute of Marine Biology; 1983 p. 25 pp.

14. Litz MNC, Heppell SS, Emmett RL, Brodeur RD. Ecology and distribution of the northern subpopulation of northern anchovy (Engraulis mordax) off the US west coast. Calif Coop Ocean Fish Invest Rep. 2008; 49: 167–182.

15. Montevechi WA, Cairns DK, Myers RA. Predation on marine-phase Atlantic salmon (Salmo salar) by gannets (Morus bassanus) in the Northwest Atlantic. Can J Fish Aquat Sci. 2002; 59: 602–612. https://doi.org/10.1139/f02-033

16. Wells BK, Santora JA, Henderson MJ, Warzybok P, Jahncke J, Bradley RW, et al. Environmental conditions and prey-switching by a seabird predator impact juvenile salmon survival. J Mar Syst. 2017; 174: 54–63. https://doi.org/10.1016/j.jmarsys.2017.05.008

17. Fisher JP, Pearcy WG. Growth of juvenile coho salmon (Oncorhynchus kisutch) off Oregon and Washington, USA, in years of differing coastal upwelling. Can J Fish Aquat Sci. 1988; 45: 1036–1044. https://doi.org/10.1139/f88-127
18. Emmett RL, Sampson DB. The relationships between predatory fish, forage fishes, and juvenile salmonid marine survival off the Columbia River: A simple trophic model analysis. CalCOFI Rep. 2007; 48: 92–105.

19. Petersen JH, DeAngelis DL. Dynamics of prey moving through a predator field: a model of migrating juvenile salmon. Math Biosci. 2000; 165: 97–114. https://doi.org/10.1016/s0025-5564(00)00017-1 PMID: 10854613

20. Furey NB, Hinch SG, Bass AL, Middleton CT, Minke-Martin V, Lotto AG. Predator swamping reduces predation risk during nocturnal migration of juvenile salmon in a high-mortality landscape. J Anim Ecol. 2016; 85: 948–959. https://doi.org/10.1111/1365-2656.12528 PMID: 27159553

21. Leopold LB, Langbein WB. A primer on water. Washington, D.C.: U.S. Government Printing Office; 1960. Available: http://pubs.er.usgs.gov/publication/7000045

22. Mulder T, Syvitski JPM. Turbidity currents generated at river mouths during exceptional discharges to the world oceans. J Geol. 1995; 103: 285–299. https://doi.org/10.1086/629747

23. Petersen JH, Gadomski DM. Light-mediated predation by northern squawfish on juvenile chinook salmon. J Fish Biol. 1994; 45: 227–242. https://doi.org/10.1111/j.1095-8649.1994.tb01095.x

24. Vogel JL, Beauchamp DA. Effects of light, prey size, and turbidity on reaction distances of lake trout (Salvelinus namaycush) to salmonid prey. Can J Fish Aquat Sci. 1999; 56: 1293–1297. https://doi.org/10.1139/f99-071

25. Mazur MM, Beauchamp DA. A comparison of visual prey detection among species of piscivorous salmonids: effects of light and low turbidities. Environ Biol Fishes. 2003; 67: 397–405. https://doi.org/10.1023/A:1025807711512

26. Gregory RS, Levings CD. Turbidity reduces predation on migrating juvenile Pacific salmon. Trans Am Fish Soc. 1998; 127: 275–285.

27. De Robertis A, Ryer CH, Veloza A, Brodeur RD. Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. Can J Fish Aquat Sci. 2003; 60: 1517–1526. https://doi.org/10.1139/F03-123

28. Hansen AG, Beauchamp DA, Schoen ER. Visual prey detection responses of piscivorous trout and salmon: Effects of light, turbidity, and prey size. Trans Am Fish Soc. 2013; 142: 854–867. https://doi.org/10.1080/0028487.2013.8475978

29. Phillips EM, Horne JK, Zamon JE. Predator–prey interactions influenced by a dynamic river plume. Can J Fish Aquat Sci. 2017; 74: 1375–1390. https://doi.org/10.1139/cjfas-2016-0302

30. Miller JA, Teel DJ, Baptista A, Morgan CA, Bradford M. Disentangling bottom-up and top-down effects on survival during early ocean residence in a population of Chinook salmon (Oncorhynchus tshawytscha). Can J Fish Aquat Sci. 2013; 70: 617–629. https://doi.org/10.1139/cjfas-2012-0354

31. Burke BJ, Liermann MC, Teel DJ, Anderson JJ. Environmental and geospatial factors drive juvenile Chinook salmon distribution during early ocean migration. Can J Fish Aquat Sci. 2013; 70: 1167–1177. https://doi.org/10.1139/cjfas-2012-0505

32. Fisher JP, Wettkamp LA, Teel DJ, Hinton SA, Orsi JA, Farley EV, et al. Early ocean dispersal patterns of Columbia River Chinook and coho salmon. Trans Am Fish Soc. 2014; 143: 252–272. https://doi.org/10.1080/00284847.2013.847862

33. Teel DJ, Burke BJ, Kuligowski DR, Morgan CA, Doornik DMV. Genetic identification of Chinook salmon: Stock-specific distributions of juveniles along the Washington and Oregon coasts. Mar Coast Fish. 2015; 7: 274–300. https://doi.org/10.1080/19425120.2015.1054961

34. Burla M, Baptista AM, Zhang YL, Frolov S. Seasonal and interannual variability of the Columbia River plume: A perspective enabled by multiyear simulation databases. J Geophys Res-Oceans. 2010; 115: C00B16. https://doi.org/10.1029/2008jc004964

35. Hebblewhite M, Merrill EH, McDonald TL. Spatial decomposition of predation risk using resource selection functions: an example in a wolf–elk predator–prey system. Oikos. 2005; 111: 101–111. https://doi.org/10.1111/j.0030-1299.2005.13858.x

36. Ward EJ, Levin PS, Lance MM, Jeffries SJ, Acevedo-Gutiérrez A. Integrating diet and movement data to identify hot spots of predation risk and areas of conservation concern for endangered species. Conserv Lett. 2012; 5: 37–47. https://doi.org/10.1111/j.1755-263X.2011.00210.x

37. Swain DP, Benoit HP, Hammill MO. Spatial distribution of fishes in a Northwest Atlantic ecosystem in relation to risk of predation by a marine mammal. J Anim Ecol. 2015; 84: 1286–1298. https://doi.org/10.1111/1365-2656.12391 PMID: 25976520

38. Bradford MJ. Comparative review of Pacific salmon survival rates. Can J Fish Aquat Sci. 1995; 52: 1327–1338. https://doi.org/10.1139/f95-129
39. Emmett RL, Schiewe MH. Estuarine and ocean survival of Northeastern Pacific salmon: Proceedings of the workshop. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-NWFSC-29; 1997 p. 313 pp. Available: internal-pdf://tm29-360863232/tm29.pdf

40. Brodeur RD, Myers KW, Helle JH. Research conducted by the United States on the early ocean life history of Pacific salmon. North Pac Anadromous Fish Comm Bull. 2003; 3: 89–131.

41. Tasker ML, Jones PH, Dixon T, Blake BF. Counting seabirds at sea from ships: A review of methods employed and a suggestion for a standardized approach. The Auk. 1984; 101: 567–577. https://doi.org/10.2307/4086610

42. Baltz DM, Morejohn GV. Food habits and niche overlap of seabirds wintering on Monterey Bay, California. The Auk. 1977; 94: 526–543. https://doi.org/10.2307/4085219

43. Chu EW. Sooty shearwaters off California: diet and energy gain. Special publication of the Canadian Wildlife Service. Marine Birds: Their feeding ecology and commercial fisheries relationships. Special publication of the Canadian Wildlife Service. Ottawa.; 1984. pp. 64–71.

44. Nevins HM. Diet, demography, and diving behavior of the Common Murre (Uria aalge) in central California. MS Thesis, San Francisco State University, Moss Landing Marine Laboratories. 2004.

45. Lance MM, Thompson CW. Overlap in diets and foraging of common murres (Uria aalge) and rhinoceros auklets (Cerorhinca monocerata) after the breeding season. The Auk. 2005; 122: 887–901.

46. Szoboszlai AI, Thayer JA, Wood SA, Sydeman WJ, Koehn LE. Forage species in predator diets: Synthesis of data from the California Current. Ecol Inform. 2015; 29: 45–56. https://doi.org/10.1016/j.ecoinf.2015.07.003

47. Pearcy WG, Fisher JP. Distribution and abundance of juvenile salmonids off Oregon and Washington, 1981–1985. NOAA Tech Rep NMFS 93. 1990; 83.

48. Fisher JP, Pearcy WG. Distribution, migration, and growth of juvenile Chinook salmon, Oncorhynchus tshawystcha, off Oregon and Washington. Fish Bull. 1995; 93: 274–289.

49. MacLennan DN, Fernandes PG, Dalen J. A consistent approach to definitions and symbols in fisheries acoustics. ICES J Mar Sci J Cons. 2002; 59: 365–369. https://doi.org/10.1006/jmsc.2001.1158

50. Platt JF, Nettleship DN. Diving depths of four alcid genera. The Auk. 1985; 102: 293–297.

51. Weimerskirch H, Sagar PM. Diving depths of sooty shearwaters Puffinus griseus. Ibis. 1996; 138: 786–788. https://doi.org/10.1111/j.1474-919X.1996.tb08837.x

52. Shaffer SA, Weimerskirch H, Scott D, Pinaud D, Thompson DR, Sagar PM, et al. Spatiotemporal habitat use by breeding sooty shearwaters Puffinus griseus. Mar Ecol Prog Ser. 2009; 391: 209–220. https://doi.org/10.3354/meps07932

53. Parker-Stetter SL, Rudstam LG, Sullivan PJ, Warner DM. Standard operating procedures for fisheries acoustic surveys in the Great Lakes. Ann Arbor, MI; 2009 p. 168.

54. Barange M, Hampton I, Soule M. Empirical determination of in situ target strengths of three loosely aggregated pelagic fish species. ICES J Mar Sci J Cons. 1996; 53: 225–232. https://doi.org/10.1006/jmsc.1996.0026

55. Emmett RL, Brodeur RD, Orton PM. The vertical distribution of juvenile salmon (Oncorhynchus spp.) and associated fishes in the Columbia River plume. Fish Oceanogr. 2004; 13: 392–402. https://doi.org/10.1111/j.1365-2419.2004.00294.x

56. Smith JM, Fresh KL, Kagley AN, Quinn TP. Ultrasonic telemetry reveals seasonal variation in depth distribution and diel vertical migrations of sub-adult Chinook and coho salmon in Puget Sound. Mar Ecol Prog Ser. 2015; 532: 227–242. https://doi.org/10.3354/meps11360

57. Fauchald P. Spatial interaction between seabirds and prey: review and synthesis. Mar Ecol-Prog Ser. 2009; 391: 139–151. https://doi.org/10.3354/meps07818

58. Ahrens R, Walters CJ, Christensen V. Foraging arena theory. Fish Fish. 2012; 13: 41–59. https://doi.org/10.1111/j.1467-2979.2011.00432.x

59. Ainley DG, Spear LB, Allen SG, Ribic CA. Temporal and spatial patterns in the diet of the common murre in California waters. The Condor. 1996; 98: 691–705. https://doi.org/10.2307/1369852

60. Ainley DG, Ford RG, Brown ED, Suryan RM, Irons DB. Prey resources, competition, and geographic structure of kittiwake colonies in Prince William Sound. Ecology. 2003; 84: 709–723. https://doi.org/10.1890/0012-9658(2003)084[0709:PRCAGS]2.0.CO;2

61. Zar JH. Biostatistical analysis. 4th ed. Upper Saddle River, N.J: Prentice Hall; 1999.

62. Wood S. Mixed GAM Computation Vehicle with Automatic Smoothness Estimation. 2016.

63. R Core Team. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; 2016. Available: http://www.R-project.org/
Juvenile salmon predation risk

64. Wood SN. Generalized Additive Models: An Introduction with R. Chapman & Hall/CRC; 2006. Available: https://www.crcpress.com/Generalized-Additive-Models-An-Introduction-with-R/Wood/9781584884743

65. Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM. Mixed effects models and extensions in ecology with R. New York, NY: Springer New York; 2009. Available: http://link.springer.com/10.1007/978-0-387-87458-6

66. Quinn TP. The behavior and ecology of Pacific salmon and trout. Bethesda, MD: Seattle: American Fisheries Society; University of Washington Press; 2005.

67. Myers JM, Kope RG, Bryant GJ, Teel D, Lierheimer LJ, Wainwright TC, et al. Status review of Chinook salmon from Washington, Idaho, Oregon, and California. US Dept Commer NOAA Tech Memo NMFS-NWFC-35. 1998; 443.

68. Sandercock FK. Life history of coho salmon (Onchorhynchus kisutch). In: Groot C, Margolis L, editors. Pacific salmon life histories. Vancouver, BC: UBC Press; 1991. pp. 397–445.

69. PFMC (Pacific Fishery Management Council). Pacific Coast Fishery Ecosystem Plan for the U.S. Portion of the California Current Large Marine Ecosystem–Public Review Draft, February 2013. Portland, OR: Pacific Fishery Management Council; 2013.

70. Brosnan IG, Welch DW, Rechisky EL, Porter AD. Evaluating the influence of environmental factors on yearling Chinook salmon survival in the Columbia River plume (USA). Mar Ecol Prog Ser. 2014; 496: 181–196. https://doi.org/10.3354/meps10550

71. Litz MNC, Emmett RL, Bentley PJ, Claibore AM, Barceló C. Biotic and abiotic factors influencing forage fish and pelagic nekton community in the Columbia River plume (USA) throughout the upwelling season 1999–2009. ICES J Mar Sci. 2013; 71: 5–18. https://doi.org/10.1093/icesjms/fsst082

72. Naughton MB, Pitkin DJ, Lowe RW, So KJ, Strong CS. Catalog of Oregon seabird colonies. USFWS Biol Tech Publ BTP-R1009-2007. 2007.

73. McMichael GA, Hansson AC, Hamish RA, Trott DM. Juvenile salmonid migratory behavior at the mouth of the Columbia River and within the plume. Anim Biotelemetry. 2013; 1: 14. https://doi.org/10.1186/2050-3385-1-14

74. Holt RD. Predation, apparent competition, and the structure of prey communities. Theor Popul Biol. 1977; 12: 197–229. https://doi.org/10.1016/0040-5809(77)90042-9 PMID: 929457

75. Murdoch WW. Switching in general predators: experiments on predator specificity and stability of prey populations. Ecol Monogr. 1969; 39: 335–354. https://doi.org/10.2307/1942352

76. Oaten A, Murdoch WW. Switching, functional response, and stability in predator-prey systems. Am Nat. 1975; 109: 299–318. https://doi.org/10.2307/2459696

77. Chesson PL. Variable predators and switching behavior. Theor Popul Biol. 1984; 26: 1–26. https://doi.org/10.1016/0040-5809(84)90021-2

78. Hoffm an W, Heinemann D, Wiens JA. The ecology of seabird foraging flocks in Alaska. The Auk. 1981; 98: 437–456.

79. Haney JC, Fromstrup KM, Lee DS. Geometry of visual recruitment by seabirds to ephemeral foraging flocks. Osm Sciand. 1992; 23: 49–62. https://doi.org/10.2307/3676427

80. Bairos-Novak KR, Crook KA, Davoren GK. Relative importance of local enhancement as a search strategy for breeding seabirds: an experimental approach. Anim Behav. 2015; 106: 71–78. https://doi.org/10.1016/j.anbehav.2015.05.002

81. Veit RR, Harrison NM. Positive interactions among foraging seabirds, marine mammals and fishes and implications for their conservation. Front Ecol Evol. 2017; 5. https://doi.org/10.3389/fevo.2017.00121

82. Shealer DA, Burger J. Effects of interference competition on the foraging activity of tropical roseate terns. The Condor. 1993; 95: 322–329. https://doi.org/10.2307/1369355

83. Skalski GT, Gilliam JF. Functional responses with predator interference: Viable alternatives to the Holling type II model. Ecology. 2001; 82: 3083–3092. https://doi.org/10.1890/0012-9658(2001)082[3083:FRPIIV]2.0.CO;2

84. Weltkamp LA, Bentley PJ, Litz MNC. Seasonal and interannual variation in juvenile salmonids and associated fish assemblage in open waters of the lower Columbia River estuary. Fish Bull. 2012; 110: 426–450.

85. Hickey BM, Kudela RM, Nash JD, Bruland KW, Peterson WT, MacCready P, et al. River influences on shelf ecosystems: Introduction and synthesis. J Geophys Res. 2010; 115: C00B17. https://doi.org/10.1029/2009jc005452

86. Hickey B, Banas N. Why is the northern end of the California Current system so productive? Oceanography. 2008; 21: 90–107. https://doi.org/10.5670/oceanog.2008.07
87. Kaltenberg A, Emmett R, Benoit-Bird K. Timing of forage fish seasonal appearance in the Columbia River plume and link to ocean conditions. Mar Ecol Prog Ser. 2010; 419: 171–184. https://doi.org/10.3354/meps08848

88. Richardson SL. Abundance and distribution of larval fishes in waters off Oregon, May-October 1969, with special emphasis on the northern anchovy, *Engraulis mordax*. Fish Bull. 1973; 71: 697–711.

89. Richardson SL. Spawning biomass and early life of northern anchovy, *Engraulis mordax*, in the northern sub-population off Oregon and Washington. Fish Bull. 1981; 78: 855–876.

90. Phillips EM, Horne JK, Adams J, Zamor JE. Selective occupancy of a persistent yet variable coastal river plume by two seabird species. Mar Ecol Prog Ser. 2018; 594: 245–261. https://doi.org/10.3354/meps12534

91. Mackas DL, Louttit GC. Aggregation of the copepod *Neocalanus plumchrus* at the margin of the Fraser River plume in the Strait of Georgia. Bull Mar Sci. 1988; 43: 810–824.

92. St. John MA, Macdonald JS, Harrison PJ, Beamish RJ, Choromanski E. The Fraser River plume: some preliminary observations on the distribution of juvenile salmon, herring, and their prey. Fish Oceanogr. 1992; 1: 153–162.

93. Loredo SA, Orben RA, Suryan RM, Lyons DE, Adams J, Stephens SW. Spatial and temporal diving behavior of non-breeding common murres during two summers of contrasting ocean conditions. J Exp Mar Biol Ecol. 2019; 517: 13–24. https://doi.org/10.1016/j.jembe.2019.05.009

94. De Robertis A, Morgan CA, Schabetsberger RA, Zabel RW, Brodeur RD, Emmett RL, et al. Columbia River plume fronts II. Distribution, abundance, and feeding ecology of juvenile salmon. Mar Ecol Prog Ser. 2005; 299: 33–44. https://doi.org/10.3354/meps299033

95. Dawley EM, Ledgerwood RD, Blahm TH, et al. Migrational characteristics, biological observations, and relative survival of juvenile salmonids entering the Columbia River estuary, 1966–1983. Portland, OR: Bonneville Power Administration; 1986 p. 256. Report No.: Project 81–102. Available: http://columbiaestuary.org/services/resource-library/beach-and-purse-seine-sampling-juvenile-salmonids-volume-1

96. Hansen AG, Beauchamp DA. Latitudinal and photic effects on diel foraging and predation risk in freshwater pelagic ecosystems. J Anim Ecol. 2015; 84: 532–544. https://doi.org/10.1111/1365-2656.12295 PMID: 25266197

97. Haney JC, Stone AE. Seabird foraging tactics and water clarity: Are plunge divers really in the clear?. Mar Ecol Prog Ser. 1988; 49: 1–9.

98. Lovvorn JR, Baduini CL, Hunt GL Jr. Modeling underwater visual and filter feeding by planktivorous shearwaters in unusual sea conditions. Ecology. 2001; 82: 2342–2356. https://doi.org/10.2307/2680236

99. Grémillet D, Nazirides T, Nikolau H, Crivelli AJ. Fish are not safe from great cormorants in turbid water. Aquat Biol. 2012; 15: 187–194. https://doi.org/10.3354/ab00430

100. Horner-Devine AR, Jay DA, Orton PM, Spahn EY. A conceptual model of the strongly tidal Columbia River plume. J Mar Syst. 2009; 78: 460–475. https://doi.org/10.1016/j.jmarsys.2008.11.025

101. Greene CM, Jensen DW, Pess GR, Steel EA, Beamer E. Effects of environmental conditions during stream, estuary, and ocean residency on Chinook salmon return rates in the Skagit River, Washington. Trans Am Fish Soc. 2005; 134: 1562–1581. https://doi.org/10.1577/T05-037.1

102. Zhang Y, Baptista AM. SELFE: A semi-implicit Eulerian–Lagrangian finite-element model for cross-scale ocean circulation. Ocean Model. 2008; 21: 71–96. https://doi.org/10.1016/j.ocemod.2007.11.005

103. Adams J, Kaplan IC, Chasco B, Marshall KN, Acevedo-Gutiérrez A, Ward EJ. A century of Chinook salmon consumption by marine mammal predators in the Northeast Pacific Ocean. Ecol Inform. 2016; 34: 44–51. https://doi.org/10.1016/j.ecoinf.2016.04.010