

Trophic Relationships of Resident Chinook and Coho Salmon and the Influence of Artificial Light at Night (ALAN) on Predation Risk for During Early Marine Life Stages of Juvenile Salmon and Forage Fishes in Puget Sound

Interim Report to Long Live the Kings, Salish Sea Marine Survival Project

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INTRODUCTION

Predation is considered a major source of mortality for salmon during early marine life stages. Therefore, identifying the primary predators and the mechanisms that influence the efficacy of these predators can inform and prioritize restoration efforts for these species. Previous analyses by Beauchamp and Duffy (2011) suggested that resident Chinook salmon *Oncorhynchus tshawytscha* could potentially consume 10-50% of the subyearling hatchery and wild Chinook entering Puget Sound annually; however, the limited sample sizes, suboptimal timing and temporal resolution of sampling the predators' diets infused considerable uncertainty into the predation estimates. These potentially high mortality rates prompted the need for further analyses supported by additional sampling dedicated to addressing the key uncertainties identified for the previous predation estimates. In this study, we conducted frequent (twice weekly) sampling of resident Chinook and Coho salmon *O. kisutch* to enhance the temporal resolution of diet composition during the May-September period when juvenile salmon were considered most vulnerable to predation in Puget Sound.

Predation mortality can also increase if search or capture efficiency of predators improves due to increased detection capability by predators or longer exposure to prey under enhanced foraging conditions. Most aquatic vertebrates and some invertebrates rely on vision as the primary sensory mechanism for movement, feeding, and avoiding

predation, especially in pelagic environments. All major predators on juvenile salmon rely primarily on vision to search for and consume their prey. Therefore, understanding how the visual environment varies through time and space, and how these variations affect visually-based predation risk on juvenile salmon can provide considerable insight into marine survival trends through time and inform future restoration priorities.

This study addressed two primary topics in separate sections of the report: 1) the role of resident Chinook and Coho salmon as predators on subyearling Chinook, other salmon, and forage fish species; and 2) surveying the nocturnal light environment during the early marine life stages of Chinook salmon in Puget Sound and evaluating how artificial light at night (ALAN) influences predation risk of juvenile salmon and other prey fishes to visually-feeding predators. These topics are presented as separate sections of this report.

SECTION 1:
DIET AND PREDATION BY RESIDENT CHINOOK AND COHO
SALMON DURING EARLY MARINE LIFE OF CHINOOK SALMON IN
PUGET SOUND

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Abstract—Temporal diet composition and consumption by resident Chinook and Coho Salmon *Oncorhynchus tshawytscha* and *O. kisutch* were estimated during the growing season in 2018 and 2019 to evaluate the predation impact on subyearling Chinook salmon, other juvenile salmon, and forage fishes during the period when juvenile salmon were presumably most vulnerable to pelagic predators within Puget Sound. Resident salmon (age-1 and older Chinook and Coho) were sampled weekly via micro-trolling from mid-May through mid-September in the Central and Whidbey Basins of Puget Sound during 2018 and 2019. Temporal and size-specific diet composition, water temperature, size and incremental growth data for resident Chinook and Coho salmon were input into bioenergetics model simulations to estimate daily and monthly per capita and population-level consumption rates by resident salmon on juvenile Chinook, other juvenile salmon, forage fishes, and invertebrate prey groups. Consumption demand varied among size classes and species of predators, among months and between years. Little evidence was found for predation on juvenile Chinook or other salmon species. Coho predation on subyearling Chinook represented an estimated 1-1.5% of the hatchery smolts entering marine waters, whereas no cannibalism by resident Chinook was evident. Population-level predation on Pacific Herring was surprisingly comparable between resident Chinook and Coho in Puget Sound, despite considerable differences in monthly diet, growth, consumption, and survival of these consumers. The estimated consumption of 180-214 MT or 11-13 million yearling Herring consumed by resident Chinook during May-September 2018 and 2019 and another 212 MT or 13 million yearling Herring consumed by Coho during May-September 2018

represented a potentially significant source of mortality on Herring, especially since Herring represent an important fraction of the resident salmon diets during the other seven months of the year.

INTRODUCTION

Predation is considered a major source of mortality for salmon during early marine life stages. Therefore, identifying the primary predators and the mechanisms that influence the efficacy of these predators can inform and prioritize restoration efforts for these species. Previous analyses by Beauchamp and Duffy (2011) suggested that resident Chinook salmon could potentially consume 10-50% of the subyearling hatchery and wild Chinook entering Puget Sound annually.

The key uncertainties in these predation calculations involved small sample sizes, inadequate timing, and temporal resolution for diet composition data of resident salmon during the period when juvenile salmon first moved offshore from shoreline habitats and were presumed most vulnerable to pelagic predators. Beauchamp and Duffy (2011) had to pool over nine years (2001-2009) of midwater trawling surveys by Canada Department of Fisheries and Oceans (*R/V Ricker* cruises) to accumulate diet composition data from 119 non-empty stomach samples of age-1 and older resident Chinook salmon. These samples were concentrated during 1-3 day cruises in July (N=74 non-empty stomachs) and mid-September/mid-October (N=36). Since peak movement of subyearling Chinook from shoreline to epi-pelagic habitats occurred in early-mid June for most hatchery stocks (Gamble et al. 2018), there was a gap in diet data during the initial period when subyearlings were likely most vulnerable to predation. In this study, we conducted frequent (twice weekly) targeted sampling of resident Chinook and Coho salmon (FL > 200 mm) to enhance the temporal resolution of diet composition during the May-September period when juvenile salmon were considered most vulnerable to predation in Puget Sound.

The objectives of this study were to: 1) obtain diet data for resident Chinook and Coho salmon at relatively high temporal resolution salmon during spring-summer periods corresponding with early marine stages of juvenile salmon in epi-pelagic

habitats of Puget Sound; and 2) Estimate the predation impact of resident Chinook [and Coho] on juvenile Chinook salmon and other prey fishes as functions of predator size, month, and region during non-pink and pink salmon *O. gorbuscha* years.

METHODS

We collected resident sub-adult and adult Chinook and Coho salmon and adult Pink salmon from the Central and Whidbey Basins of Puget Sound during late May through mid-September in 2018 and 2019 to determine their diet composition and consumption demand on juvenile Chinook salmon, other salmon, forage fishes, and key invertebrate prey during years when juvenile pink salmon were present (2018) and absent (2019). The sampling periods were selected to bracket the critical early marine growth period for subyearling Chinook salmon after they transition from shoreline to openwater (epi-pelagic) habitats within Puget Sound (Duffy et al. 2005; Duffy and Beauchamp 2011). Empirical size-specific monthly diet, growth, and thermal experience data were used as inputs in bioenergetics simulations of temporal consumption demand for each age class and species of consumer. The monthly consumption rates of prey fish species and key invertebrates were used to evaluate the relative importance of resident and returning adult Chinook, Coho, and adult Pink salmon on juvenile salmon and other forage fishes and to identify the primary prey sources that fueled the energy budgets of these consumers during the peak spring-summer growing period. For the purposes of this study, sub-adult Chinook and Coho were defined as individuals that remained in Puget Sound past their first summer in marine waters. By the following spring, these sub-adult residents exceeded 200 mm FL and were becoming increasingly piscivorous (Duffy et al. 2010; Beauchamp and Duffy 2011).

Field Sampling

We used micro-trolling (Duguid and Juanes 2017) for sampling sub-adult and adult salmon in order to economically and nonlethally capture, process, and release ESA-listed

Puget Sound Chinook Salmon. Micro-trolling has been successfully applied to sampling epi-pelagic juvenile and sub-adult Chinook and Coho salmon in the Strait of Georgia (Duguid and Juanes 2017) and has been previously used to sample pelagic piscivorous trout in lakes (Cartwright et al. 1998). Micro-trolling is a scaled-down version of commercial trolling, wherein multiple leaders with lures and attractors are attached directly to a downrigger cable with commercial trolling clips and fished simultaneously at various depths (See **Appendix 1** for representative combinations of lures, flashers and hook sizes). One downrigger was deployed on each side of a 7-m motorboat. Trolling speeds ranged 2.4-3.2 kph (1.5-2.0 mph).

Microtrolling was conducted two days per week from late-May through mid-September in 2018 and 2019, generally sampling one day in the Central Basin (Duwamish Head, Shilshole, or Jefferson Head) and the other day in the Whidbey Basin (Possession Bar). On-site sampling typically spanned a 5-h period (2-3 h before-after slack tides) during daylight.

Capture and handling was conducted in a manner to avoid mortality and minimize stress of both target and non-target species and size groups. Unless a fish was detected sooner, the lures on each downrigger were checked every 10 minutes from the time that the selected depths were reached until retrieval began. Hooked fish were retrieved from the water with a knotless rubberized landing net, unhooked, and put in an aerated holding tank. Individual fish were anesthetized in a separate container using CO₂, examined for adipose fin clips or magnetized coded-wire tags (CWT), then measured (FL-mm) and weighed (g). Stomach contents were collected by gastric lavage, scales were removed from the preferred area, and a clip of caudal fin tissue was taken for genetic analysis. Fish recovered in an aerated live well before release in proximity to the location of capture. All fish capture and handling procedures were conducted under the auspices of IACUC protocol #2008-57 approved by the Institutional Animal Care and Use Committee of the Western Fisheries Research Center, U.S. Geological Survey.

Genetic Species Identification of Resident Sub-Adult Salmon

Because field identifications of subadult salmon can be inaccurate, species identifications of the microtroll-caught salmon were subsequently determined genetically. Genomic DNA from fin clip tissue samples was extracted using Invitrogen PureLink Pro96 extraction kits. DNA was quantified and diluted to 1 ng/μl for subsequent analysis. Species were assigned via qPCR analysis using the Chinook-specific assay CKCO3_464-534 and the Coho-specific assay COCyb_980-1093 (M. Hoy, unpublished data; Pilliod and Laramie 2016). Both are TaqMan assays with FAM-labeled MGB probes. COCO3_464-534 amplifies a region of the CO3 gene and COCyb_980-1093 amplifies a region of the Cytochrome b gene (both mtDNA).

Size, Age, and Growth

We estimated age and growth patterns for Chinook and Coho salmon by combining fork length (FL, mm) and weight (Wt, g) at capture with scale-based ages and back-calculated FL at age (Gamble et al. 2018). Scales taken from the preferred area of the fish were cleaned, mounted, and pressed into acetate impressions. Digital images of the acetate impressions were captured with a digital camera mounted to a compound microscope and analyzed using Image-Pro Premier software. Radii of the scale impressions were measured at every circulus up to the first ocean annulus and then to each subsequent annulus and to the outer margin of the scale. Two scale readers interpreted scale patterns and identified annuli for each sample. Scale radius SR (mm) was highly correlated with FL (mm) for Chinook in 2018 ($r^2 = 0.972$, $N = 22$):

$$FL = 200.0 \cdot SR + 27.9,$$

and for Chinook in 2019 ($r^2 = 0.976$, $N = 23$):

$$FL = 204.5 \cdot SR + 20.0.$$

Scale radius SR (mm) was also highly correlated with FL (mm) for Coho in 2018 ($r^2 = 0.966$, $N = 13$):

$$FL = 149.4 \cdot SR + 60.6,$$

and for Coho in 2019 ($r^2 = 0.937$, $N = 16$):

$$FL = 215.7 \cdot SR + 4.6.$$

The relationships above were applied to scale-based growth trajectories to back-calculate FL at annuli or various circuli associated with ecologically-relevant periods in the life history of resident Chinook and Coho salmon. The lengths at these time points were converted to weight using length-weight regressions specific to each combination of species and year. Fork length to weight Wt (g) regressions also exhibited high correlations for Chinook in 2018 ($r^2 = 0.990$, $N = 125$, 146-715 mm FL):

$$Wt = 0.0000046 \cdot FL^{3.179},$$

and for Chinook in 2019 ($r^2 = 0.976$, $N = 95$, 153-736 mm FL):

$$Wt = 0.0000141 \cdot FL^{2.987}.$$

For Coho, the fork length to weight Wt (g) regressions showed somewhat lower correlations in 2018 ($r^2 = 0.837$, $N = 54$, 145-580 mm FL):

$$Wt = 0.0000502 \cdot FL^{2.777},$$

and for Coho in 2019 ($r^2 = 0.918$, $N = 97$, 145-648 mm FL):

$$Wt = 0.0000161 \cdot FL^{2.964}.$$

Diet Analysis

Diet samples were processed separately for each stomach and analyzed in terms of the proportional wet-mass dietary contributions of each prey fish species and functional groups of invertebrates, stratified by size and species of consumer, month, and year. Prey were identified and separated into functional groups and blotted-dry wet weights were recorded for each group. Whenever possible, lengths of prey fishes in the diet were measured and recorded (standard length, vertebral counts and lengths with or without the head capsule, etc.) to reconstruct prey size at time of consumption to examine the relationships between predator size and prey size.

Bioenergetic Simulations for Estimating Prey Consumption

Age-specific size and incremental growth data for resident Chinook and Coho salmon were used to estimate consumption rates given the observed estimates of incremental growth during 2018 and 2019 (**Table 1**), given temporal changes in thermal experience (**Table 2**), size-specific monthly diet composition (**Tables 3 and 4**), and the associated energy density and indigestible fraction of key prey (**Table 5**). These inputs for the bioenergetics model simulations were used to estimate daily and monthly consumption rates by individuals within each age/size class of resident Chinook and Coho salmon on juvenile Chinook, other juvenile salmon, forage fishes, and invertebrate prey groups (Beauchamp and Duffy 2011). These per capita consumption rates could then be combined with different population scenarios for resident Chinook and Coho to estimate their population-level predation rates on juvenile Chinook, other salmonid species, other prey fishes and key invertebrates, and identify specific periods associated with high predation, and the sizes or species of predators responsible for the heaviest predation pressure.

To expand per capita consumption to population-level consumption rates, hatchery smolt releases, stage-specific survival rates, and assumed proportions of Chinook and Coho that adopt the resident life history strategy were used to estimate the abundance of resident salmon at large in Puget Sound. Hatchery smolt releases were multiplied by an assumed survival to marine entry (50% for subyearling Chinook smolts and 100% for yearling Coho smolts). An abundance-weighted pooled SAR estimate, based on HGMP release numbers and adjusted by the assumed survival to marine entry, was converted to an instantaneous daily mortality rate. Resident salmon abundance was reduced daily by the instantaneous mortality rate, and daily consumer abundance was multiplied by the daily per capita consumption rate on each prey group for the corresponding species and age/size class of resident Chinook or Coho.

For Chinook salmon, the annual subyearling smolt release goals were approximately 40,000,000 for hatcheries in Puget Sound according to HGMP summaries.

The abundance-weighted SAR for age 0.2 hatchery Chinook was 0.5%. We partitioned the average SAR of 0.5% into an assumed 50% survival of Chinook smolts from hatchery to marine entry, followed by 1% survival for the marine-rearing portion of SAR. Thus, 1% survival over a 27-month marine rearing period translated into an instantaneous daily mortality rate of $Z = 0.0057$. We assumed that 30% of subyearling Chinook smolts adopted a resident life history strategy based on estimates of 29% reported by O'Neill and West (2009) based on PCB accumulation and FRAM estimates of ocean-rearing versus resident Chinook; similar percentages (24%) were reported by Chamberlin et al. (2011) for mid Puget Sound stocks, based on CWT recovery data.

For Coho salmon, the annual yearling smolt release goals were approximately 14,000,000 for hatcheries in Puget Sound according to HGMP summaries. The abundance-weighted SAR for hatchery Coho was 3.9% which translated into an instantaneous daily mortality rate of $Z = 0.00593$, assuming an 18-month period of marine rearing. Rohde et al. (2014) reported a conservative estimate of 5.3% residency by hatchery Coho, based on CWT recoveries. Consequently, a conservative estimate of hatchery smolts that resident would revert to residency would be 742,000. For the purposes of this analysis, we assumed that 1,000,000 Coho smolts adopted a resident life history strategy to account for a less-conservative estimate of residency and to include some contribution from wild smolts.

RESULTS

Size, Age, and Growth

Microtrolling yielded catches of 232 Chinook (136 in 2018 and 96 in 2019), 167 Coho (70 in 2018 and 97 in 2019), 22 adult Pink (2019), and 3 adult Sockeye (2019) over the late May through mid-September sampling periods of 2018 and 2019. The size distributions of Chinook spanned a range of 146-736 mm FL representing multiple size modes associated with up to four age classes of marine growth during each of the two sampling years (**Figure 1**). Coho spanned a size range of 145-648 mm FL and exhibited

two distinct size modes during each sampling year with the first mode representing yearling Coho during their first summer of marine growth and the second mode reflecting the prevalent size distribution of subadults during their second and final year of marine growth (**Figure 1**). The mean size at age (annulus formation) for Chinook salmon appeared larger, but not significantly so, in 2019 than 2018, whereas yearling Coho from 2018 were slightly larger after the first year of freshwater growth but converged to a similar size as the 2019 samples at age-2 after their first year of marine growth (**Figure 2**).

Diet Composition

Diet composition varied considerably among size classes and months for Chinook salmon (**Figure 3**). A small sample size of subyearling Chinook with non-empty stomachs (130-199 mm FL; N = 6 in 2018 and N = 7 in 2019) fed predominantly on crustacean invertebrates including larval crab and Hyperiid or Gammarid amphipods, then included herring or sandlance by August or September. Sample sizes for yearling resident Chinook were also relatively small (N = 14 non-empty stomachs in 2018 and N = 35 in 2019). Yearling resident Chinook (200-299 mm FL) also fed heavily on different types of invertebrates through July each year before adding Hyperiid amphipods in August and Herring in August and September both years. In 2019, crab larvae dominated the yearling Chinook diets during May-July but were not evident during 2018. Piscivory was considerably higher for Chinook larger than 300 mm FL both years but was much higher in 2018 than 2019. Herring followed by sandlance and other fishes contributed to more than 90% of the diets each month in 2018. In contrast, prey fish represented less than 45% of the diet during most of 2019, except in August when the only non-empty stomach contained entirely herring. No evidence of predation on subyearling Chinook or other species of juvenile salmon was observed by any size class of Chinook during either 2018 or 2019.

All sizes of Coho salmon relied more heavily on invertebrates throughout the growing season compared to Chinook (**Figure 4**). For all size classes, diets during the

earlier months contained large proportions of larval crab, then shifted to increasing fractions of Gammarid or Hyperiid amphipods. As with the larger Chinook, Coho > 300 mm FL exhibited higher piscivory than smaller conspecifics with much higher fractions of prey fish found in the diets during 2018 than 2019. Herring represented 30-40% of the diet by mass during June-September 2018, whereas prey fish were virtually undetectable in the diets of large Coho in 2019. Sandlance were also eaten by large Coho in July 2018. One case of predation on subyearling Chinook by a 494-mm FL Coho was observed during early July 2018.

Both resident Chinook and Coho salmon ate predominantly age-1 Pacific Herring that were < 150 mm FL (**Figure 5**). Resident salmon consumed Pacific Herring that were up to 50% of their own body length, but aside from the minimum size that a predator would be competent to feed on herring of a specific size, no further relationship existed between predator and prey size.

Population-level Consumption

For both resident Chinook (**Figure 6**) and Coho Salmon (**Figure 7**), consumption demand varied considerably among major prey types between years and among size classes of predators. Total consumption declined year classes from month to month through the growing season, indicating that the abundance of both resident Chinook and Coho declined faster than per capita growth and consumption. In addition, both species exhibited lower monthly consumption rates, but considerably higher levels of piscivory in 2018 than 2019, and older year classes were more piscivorous than the youngest year class of resident salmon.

Chinook Consumption-For resident Chinook, lower growth rates and higher contributions of high-energy prey fish in the energy budget resulted in lower consumption rates in 2018 than 2019 (**Table 1**). Bioenergetic simulations indicated that per capita feeding rates were lower for all ages of Chinook in 2018 (42-49% C_{max}) compared to 2019 (57-65% C_{max}). Growth efficiencies were higher in 2018 (13.7% for age 0.1 declining to 10.5% for age 0.3) than in 2019 (12.2% for age 0.1 declining to 6.6%

for age 0.3). The lower consumption rate and higher growth efficiencies were consistent with the higher contribution of herring to the energy budget in 2018.

Monthly population-level consumption rates of key prey by resident Chinook varied between years and among size classes (**Figure 6**). Age 0.1 Chinook fed predominantly on invertebrates, especially during May-July, but consumed increasing biomass Herring and other prey fishes during August-September both years. Herring, followed distantly by sandlance, were the primary prey fishes consumed by all sizes of resident Chinook. In 2018, the age 0.2 and older resident Chinook ($FL \geq 300$ mm) primarily consumed Herring during all months, followed by lower biomasses of sandlance and other prey fishes with very little contribution of invertebrate prey. In 2019, larval crab contributed most of the energy budget for all sizes of resident Chinook through June or July consumption, then shifted toward Herring, amphipods, and miscellaneous invertebrates during July through September.

During May through September, resident Chinook population consumed an estimated 618 metric tons (MT) of total prey biomass in 2018 and 1,030 MT of prey in 2019 (**Table 6**). No evidence of predation by resident Chinook on juvenile Chinook or other salmon species was observed. The biomass of notable prey groups consumed during these months included 180 MT of Herring, 21 MT of sandlance, 35 MT of other fish, 52 MT of gammarid amphipods, and 7 MT of larval crab during 2018, whereas consumption during 2019 included 214 MT of Herring, 40 MT of sandlance, 12 MT of other fish, 119 MT of gammarid amphipods, and 430 MT of larval crab. Predation on Herring was focused almost exclusively on age-1 prey with a modal body mass of 16 g; therefore, an estimated 11,000,000 age-1 Herring were consumed during May-September by the resident Chinook population (age 0.1 to age 0.3) in 2018 and an estimated 13,000,000 were consumed during the same period in 2019.

Coho Consumption--For resident Coho, bioenergetics simulations for growth and consumption during 2018 indicated that both age classes were feeding at relatively high rates (63% C_{max} for age 1.0 and 89% C_{max} for age 1.1) and experienced good growth

efficiency (10.8% for age 1.0 and 13.0% for age 1.1; **Table 1**). The absence of prey fish in the diets of age 1.1 Coho during 2019 was suspect and likely caused anomalous results in bioenergetics simulations for this cohort. Although the same age-specific initial-final weights and growth rates were assigned to bioenergetic simulations for both years, the older age class in 2019 could not reach the assigned final weight over the 150-day simulation period when feeding on the observed invertebrate-only diet. In fact, when assigned the theoretical maximum feeding rate of 100% C_{max} , the older age class only grew from 860 g to 1439 g, far short of the targeted final weight of 1741 g. However, when 20-40% of the invertebrate diet was substituted with Herring, in relatively parallel but lower proportions as the observed diet in 2018 (Herring represented 30-50% of the monthly diet of older Coho in 2018), Coho hit the final target weight of 1741 g while feeding 96% C_{max} . Similar simulations using 10-20% Herring failed to achieve the target final weight without exceeding 100% C_{max} . As a result of the dietary discrepancies and inability to fit consumption to observed growth for the older Coho in 2019 as described above, we believe that the observed diets erroneously failed to observe piscivory, either as a consequence of the sampling method or timing. Specifically, diet samples were only collected during daylight rather than extending through twilight and early night periods. A modest attempt at fishing through twilight caught several resident Chinook, but not Coho, and was thus inadequate to resolve the potential importance of diel feeding chronology.

Monthly population-level consumption rates of key prey by resident Coho varied between years and among size classes (**Figure 7**). In both years, age 1.0 Coho (130-299 mm FL) recruited to the epi-pelagic zone by June and fed predominantly on larval crab during June-July, then shifted to progressively more amphipods (primarily Gammarids but also a considerable amount of Hyperiid) from July through September. For the age 1.1 Coho, larval crab (May-June) and Gammarid amphipods (all months) were important contributors to the energy budget both years, whereas prey fishes were only measurably important during 2018. Herring were the predominant prey fish consumed from May through September, followed secondarily by Sandlance. One instance of

predation on subyearling Chinook salmon recorded in the diet of an age 1.1 Coho during July translated into a measurable level of predation when expanded conservatively to population-level consumption.

Bioenergetic simulations of predation by resident Coho estimated that 7,127 kg of subyearling Chinook were consumed during summer 2018 with nearly 4,000 Kg of consumption concentrated in July (**Table 7**). Concurrent body mass data were not available for juvenile Chinook during 2018 or 2019; therefore, the monthly mean body mass estimates from 2014 and 2015 for subyearling Chinook in offshore habitats of Puget Sound were used to convert the monthly biomass of Chinook consumed into numerical estimates of predation loss. Monthly mean body mass of offshore subyearling Chinook differed significantly between years with June, July, August, and September means equaling 8.6 g, 10.2 g, 16.8 g, and ~40 g in 2014 versus 9.9 g, 17.6 g, 25.2 g, and ~60 g, respectively. When monthly mean body mass was divided into the monthly biomass of Chinook consumed, this yielded numerical predation estimates of 601,000 eaten based on prey sizes from 2014 and 383,000 eaten based on prey sizes in 2015. Based on the HGMP goals of 40,000,000 subyearling hatchery Chinook released per year, these predation estimates would equate to 1.5% predation mortality when subyearling Chinook growth was slower as in 2014, or 1.0% mortality when subyearlings grew faster as in 2015.

Population-level consumption by resident Coho during May through September translated into an estimated 1,157 MT of total prey biomass in 2018 and 1,205 MT of prey in 2019 (**Table 7**). The biomass of other notable prey groups consumed during these months included 212 MT of Herring, 23 MT of sandlance, 34 MT of other fish, 455 MT of Gammarid and Hyperiid amphipods, and 322 MT of larval crab during 2018, whereas consumption during 2019 included minimal fish predation: 10 MT of Herring and 1 MT of sandlance, but 661 MT of Gammarid and Hyperiid amphipods, and 424 MT of larval crab. Predation on Herring was focused almost exclusively on age-1 prey with a modal body mass of 16 g; therefore, an estimated 13,000,000 age-1 Herring would be consumed annually during May-September for every 1,000,000 Coho smolts that

adopted a resident life history strategy. This predation impact was very similar to the estimates of 11,000,000-13,000,000 herring consumed annually by the resident Chinook population during 2018 or 2019. While the similarity in impact might seem surprising, given the apparent lower initial abundance of resident Coho than Chinook, the annual marine survival estimates for Coho are much higher than for Chinook, and per capita feeding rate for the most piscivorous size class of Coho (age 1.1, 89% C_{max}) was considerably higher than for the more piscivorous age classes of Chinook (42-49% C_{max} for ages 0.2 and 0.3 in 2018 and 62-65% C_{max} in 2019 when lower proportions of herring were eaten).

DISCUSSION

Little evidence was found for predation on juvenile Chinook Salmon by resident salmon in Puget Sound in contrast to an earlier study which was based on composite diet and growth data for resident Chinook salmon collected during midwater trawl surveys in July and September during 2001-2009 and reported a conservative estimate of 6% mortality on subyearling Chinook with concern that mortality could reach as high as 50-60% if higher temporal resolution data revealed higher proportions of subyearling Chinook in the diet when presumably most vulnerable as they initially transitioned to the epi-pelagic habitat in June (Beauchamp and Duffy 2011). The one observed incidence of predation involved resident Coho Salmon feeding on subyearling Chinook, whereas no cannibalism by resident Chinook on younger conspecifics was found. Population-level predation on Pacific Herring was surprisingly comparable between resident Chinook and Coho in Puget Sound, despite considerable differences in monthly diet, growth, consumption, and survival of these consumers. We observed considerable interannual variability in consumption of fish and invertebrates by resident salmon, and a much higher reliance on invertebrates than expected. The population-level consumption rates by resident Chinook and Coho on major prey like Herring, Amphipods, and larval crab have implications for epi-pelagic food web interactions in Puget Sound and help identify some significant sources of uncertainty.

The estimated predation mortality imposed by resident Coho on subyearling Chinook salmon ranged between 383,000 and 601,000 depending on the average growth rate and body mass achieved by juvenile Chinook during the critical June-July growth period which corresponds with their initial month(s) of rearing in epi-pelagic habitats. These numerical predation rates by resident Coho equated to 1.0-1.5% mortality of subyearling Chinook smolt production within Puget Sound and was very similar to the estimated mortality imposed by the sea-run Cutthroat trout population (Duffy and Beauchamp 2008).

Estimates of predation mortality involving extremely rare prey are fraught with potential sources of uncertainty. Sample sizes within temporal and consumer size-based cells in diet analysis certainly influence the detection of rare prey. For context, sample sizes of 8-10 non-empty stomachs are typically needed within each size x period analysis cell before the percentages of major prey groups (e.g., % fish versus % invertebrate prey) stabilize (Beauchamp et al. 2007), whereas the percentage contributions of rare prey would still remain elusive. Extrapolation error associated with the actual versus estimated duration of predation and the abundance of predators account for major sources of potential variability in predation estimates. Collectively, after accounting for these sources of uncertainty, we conclude that predation by resident Chinook Salmon on subyearling Chinook was low or absent during the conditions encountered in May-September 2018 and 2019 within the regions sampled in the Central and Whidbey Basins of Puget Sound. However, additional uncertainty remains regarding predation by resident Coho.

The heavy reliance on invertebrate prey, especially by resident Coho Salmon, and the inability of bioenergetic model simulations to achieve the observed annual growth rates for Coho without a significant contribution of fish prey in the diet created significant uncertainty about whether piscivory in general was being underestimated as a consequence of how and when predators were sampled, especially with respect to diel feeding chronology. Twilight during dawn or dusk is often associated with peaks in piscivory as prey fish schools disperse into more randomly distributed prey fields that

increase encounters with predators and increase the capture success associated with these encounters (Beauchamp et al. 1999; Schoen et al. 2012). Because effective sampling during twilight-night periods could not be sustained, uncertainty related to the influence of feeding chronology on the accuracy of the relative importance of prey fish in the diet remains unresolved, especially for Coho but is also a concern for Chinook. We are currently evaluating if sufficient frozen whole-body samples of resident and first-marine season Coho and Chinook remain in the archive to enable some stable isotope-based comparisons of these species, size classes and years (2018 and 2019) to determine whether piscivory was underestimated for either species.

This analysis highlighted the importance of Pacific Herring, larval crab and amphipods (mostly Gammarids, but also Hyperiid) in the energy budget of resident Chinook and Coho, and provided consumption biomass estimates that can be compared to other life stages and species of consumers both to evaluate relative consumption demand for shared prey resources and also as agents of mortality for important prey like Herring. The estimated consumption of 180-214 MT or 11-13 million yearling Herring consumed by resident Chinook during May-September 2018 and 2019 and another 212 MT or 13 million yearling Herring consumed by Coho during May-September 2018 represent a potentially significant source of mortality on Herring, especially when considering that Herring represent an important fraction of the resident diets during the other seven months of the year (Beauchamp and Duffy 2011; J. Chamberlin unpublished data). This predation demand focuses almost entirely on age-1 subadults, the year before most Puget Sound stocks mature to spawn as age-2 and older adults. Population-level consumption demand on larval crab by Resident Chinook (7-430 MT) and Coho (322-424 MT) was similar to the demand of subyearling Chinook (252-488 MT) during the latter's critical growth period (Connelly et al. 2018), especially in years of lower piscivory by the resident salmon. The importance of Gammarid and Hyperiid amphipods to the mid-late summer energy budget of resident Chinook and Coho is also notable in terms of identifying significant trophic linkages in the epi-pelagic food web of Puget Sound, but we need more information about the dynamics of these prey and their

importance to other consumers before the implications of amphipod consumption can be placed within the appropriate context.

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REFERENCES

- Beauchamp, D.A., C.M. Baldwin, J.L. Vogel, and C.P. Gubala. 1999. Estimating diel, depth-specific foraging with a visual encounter rate model for pelagic piscivores. *Canadian Journal of Fisheries and Aquatic Sciences* 56(Supplement 1):128-139.
- Beauchamp, D. A., D. Wahl, and B. M. Johnson. 2007. Predator-Prey Interactions. Pages 765-842. *In* C.S. Guy and M.J. Brown, editors, *Analysis and interpretation of inland fisheries data*. American Fisheries Society. Bethesda, Maryland.
- Beauchamp, D. A. 2009. Bioenergetic Ontogeny: Linking climate and mass-specific feeding to life-cycle growth and survival of salmon. Pages 53-72 *In* C. Zimmerman and C. C. Krueger, editors. *Pacific Salmon: Ecology and Management of Western Alaska's Populations*. American Fisheries Society Symposium 70. Bethesda, Maryland.
- Beauchamp, D.A., and E.J. Duffy. 2011. Stage-specific growth and survival during early marine life of Puget Sound Chinook salmon in the context of temporal-spatial environmental conditions and trophic interactions. Final Report to the Pacific Salmon Commission. Report # WACFWRU-11-01.
- Beauchamp, D.A., N. Elder, M. Wittmond, L. Wetzel, M. Hoy, K. Stenberg, A. Lind-Null, and K.A. Larsen. 2018. Effects of seasonal availability and energy content of key prey on growth performance during critical periods for juvenile Chinook Salmon. Salish Sea Marine Survival Project. Long Live the Kings. Final Report #LLTK-SSMSP-35. 28 pages.
- Chamberlin, J.W., T.E. Essington, J.W. Ferguson, and T.P. Quinn. 2011. The influence of hatchery rearing practices on salmon migratory behavior: is the tendency of Chinook

salmon to remain within Puget Sound affected by size and date of release?
Transactions of the American Fisheries Society 140:198-1408.

Connelly, K.A., J.R. Gardner, M.M. Gamble, J.W. Chamberlin, A. Winans, J. Keister, and D.A. Beauchamp. 2018 Marine survival of Puget Sound Chinook: Size-selective mortality, growth limitation, and bioenergetics of sub-yearling Chinook salmon in Puget Sound, Washington. Salish Sea Marine Survival Project. Long Live the Kings. Final Report #LLTK-SSMSP-9. 103 pages.

Duffy, E. J., D. A. Beauchamp, R. M. Buckley. 2005. Early marine life history of juvenile Pacific salmon in two regions of Puget Sound. Estuarine Coastal and Shelf Science 64:94-107.

Duffy, E.J. and D.A. Beauchamp. 2008. Seasonal piscivory by coastal cutthroat trout (*Oncorhynchus clarki clarki*) in Puget Sound: implications for juvenile salmon. Transactions of the American Fisheries Society 137:165-181.

Duffy, E.J., D.A. Beauchamp, R. Sweeting, R. Beamish, and J. Brennan. 2010. Ontogenetic diet shifts of juvenile Chinook salmon in nearshore and offshore habitats of Puget Sound. Transactions of the American Fisheries Society. 139:803-823.

Duffy, E.J., and D.A. Beauchamp. 2011. Rapid growth in the early marine period improves marine survival of Puget Sound Chinook salmon. Canadian Journal of Aquatic and Fisheries Sciences 68:232-240.

Duguid, W.D.P., and F. Juanes. 2017. Microtrolling: an economical method to nonlethally sample and tag juvenile Pacific salmon at sea. Transactions of the American Fisheries Society 146:359-369.

O'Neill, S.M., and J.E. West. 2009. Marine distribution, life history traits, and the accumulation of polychlorinated biphenyls in Chinook salmon from Puget Sound, Washington. Transactions of the American Fisheries Society 138:616-632.

Pilliod, D.S., and M.B. Laramie. 2016. Salmon redd identification using environmental DNA (eDNA): U.S. Geological Survey Open-File Report 2016–1091. 25 pages.
<http://dx.doi.org/10.3133/ofr20161091>.

Rohde, J., K.L. Fresh, and T.P. Quinn. 2014. Factors affecting partial migration in Puget Sound Coho Salmon. North American Journal of Fisheries Management 34:559-570.

Schoen, E.R., D.A. Beauchamp, and A.G. Hansen. 2012. Effects of turbidity on foraging behavior and capture success of piscivorous juvenile Chinook Salmon. Interim Report to the Cooperative Research Units Program. November 2012. 17 pages.

Table 1a. Bioenergetics model inputs and summary outputs for age-specific simulations for resident Chinook in Puget Sound during May-September in 2018 and 2019. May 1st represents day 1 of simulations each year.

Year/Age	AvgFL	Diet Size Class	Initial Wt (g)	Final Wt (g)	Growth (g)	Total		Growth Efficiency	Predator energy density
						%Cmax (P-val)	Consumption (g/y)		
2018									
1	216.1	200-299	122.3	451.2	329.0	0.463	2396	13.7%	default eqn.
2	325.8	>300	451.2	1084.6	633.4	0.422	5015	12.6%	default eqn.
3	429.3	>300	1084.6	2151.6	1067.0	0.490	10114	10.5%	default eqn.
2019									
1	219.8	200-299	138.9	588.4	449.5	0.571	3688	12.2%	default eqn.
2	356.4	>300	588.4	1889.9	1301.5	0.646	10849	12.0%	default eqn.
3	526.8	>300	1889.9	3054.4	1164.5	0.623	17644	6.6%	default eqn.

Table 1b. Bioenergetics model inputs and summary outputs for age-specific simulations for resident Coho in Puget Sound during May-September in 2018 and 2019. May 1st represents day 1 of simulations each year.

Year/Age	AvgFL	Diet Size Class	Initial Wt (g)	Final Wt (g)	Growth (g)	Total		Growth Efficiency	Predator energy density	Comments
						%Cmax (P-val)	Consumption (g/y)			
2018										
1	197.0	130-299	101.2	187.8	86.6	0.635	804	10.8%	default eqn.	
2	405.0	≥300	860.0	1741.4	881.4	0.894	6805	13.0%	default eqn.	
2019										
1	197.0	130-299	101.2	187.8	86.6	0.681	850	10.2%	default eqn.	
2	405.0	≥300	860.0	1438.6	578.6	1.000	7037	8.2%	default eqn.	Final wt not achieved
2a	405.0	≥300	860.0	1741.4	881.4	0.959	7369	12.0%	default eqn.	20-40% herring in diet

Table 2. Thermal experience inputs for all sizes of resident Chinook and Coho based on depth-averaged epi-pelagic (0-30 m) temperatures.
May 1st = day 1 of the simulations.

Day	Temp
1	11.5
31	12.1
61	12.6
91	12.9
121	12.7
151	10.8
181	9.6
211	9.9
241	10.1
271	10.4
301	10.7
331	11.0
365	11.5

Table 3. Temporal diet composition for specific size classes of resident Chinook in Puget Sound during 2018 and 2019. Diets for May 1-September 30 were used as inputs for bioenergetics model simulations (simulation days 1-150).

2018 Chinook 200-299

Day	Chinook	Other Salmon	Herring	Sand lance	Other Fish	Unid Fish	Gammarid Amphipod	Hyperiid Amphipod	Crab Larvae	Other Invert	Unid Food
1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
31	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
105	0.00	0.00	0.33	0.00	0.01	0.00	0.33	0.04	0.00	0.29	0.00
135	0.00	0.00	0.67	0.00	0.12	0.00	0.11	0.03	0.01	0.06	0.00
150	0.00	0.00	0.67	0.00	0.12	0.00	0.11	0.03	0.01	0.06	0.00
365	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00

2018 Chinook
300+

Day	Chinook	Other Salmon	Herring	Sand lance	Other Fish	Unid Fish	Gammarid Amphipod	Hyperiid Amphipod	Crab Larvae	Other Invert	Unid Food
1	0.00	0.00	0.92	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00
31	0.00	0.00	0.52	0.18	0.00	0.00	0.19	0.00	0.10	0.00	0.01
45	0.00	0.00	0.52	0.18	0.00	0.00	0.19	0.00	0.10	0.00	0.01
75	0.00	0.00	0.40	0.17	0.34	0.00	0.00	0.00	0.00	0.09	0.00
105	0.00	0.00	0.78	0.07	0.06	0.00	0.07	0.02	0.00	0.00	0.00
135	0.00	0.00	0.46	0.00	0.35	0.00	0.19	0.00	0.00	0.00	0.00
150	0.00	0.00	0.46	0.00	0.35	0.00	0.19	0.00	0.00	0.00	0.00
365	0.00	0.00	0.46	0.00	0.35	0.00	0.19	0.00	0.00	0.00	0.00

Table 3-
continued

2019 Chinook 200-299

Day	Chinook	Other Salmon	Herring	Sand lance	Other Fish	Unid Fish	Gammarid Amphipod	Hyperiid Amphipod	Crab Larvae	Other Invert	Unid Food
1	0.00	0.00	0.00	0.14	0.00	0.00	0.01	0.03	0.72	0.10	0.00
31	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.99	0.00	0.01
45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.99	0.00	0.01
75	0.00	0.00	0.00	0.15	0.02	0.00	0.19	0.04	0.48	0.06	0.06
105	0.00	0.00	0.38	0.00	0.00	0.00	0.47	0.01	0.00	0.02	0.12
135	0.00	0.00	0.17	0.00	0.00	0.17	0.00	0.17	0.00	0.31	0.18
150	0.00	0.00	0.17	0.00	0.00	0.17	0.00	0.17	0.00	0.31	0.18
365	0.00	0.00	0.17	0.00	0.00	0.17	0.00	0.17	0.00	0.31	0.18

2019 Chinook 300+

Day	Chinook	Other Salmon	Herring	Sand lance	Other Fish	Unid Fish	Gammarid Amphipod	Hyperiid Amphipod	Crab Larvae	Other Invert	Unid Food
1	0.00	0.00	0.37	0.00	0.00	0.10	0.05	0.00	0.40	0.08	0.00
31	0.00	0.00	0.24	0.07	0.07	0.00	0.08	0.07	0.42	0.05	0.00
45	0.00	0.00	0.24	0.07	0.07	0.00	0.08	0.07	0.42	0.05	0.00
75	0.00	0.00	0.00	0.00	0.00	0.35	0.28	0.00	0.28	0.09	0.00
105	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
120	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
150	0.00	0.00	0.26	0.04	0.03	0.09	0.11	0.04	0.37	0.06	0.00
365	0.00	0.00	0.26	0.04	0.03	0.09	0.11	0.04	0.37	0.06	0.00

Table 4. Temporal diet composition for specific size classes of resident Coho in Puget Sound during 2018 and 2019. Diets for May 1-September 30 were used as inputs for bioenergetics model simulations (simulation days 1-150).

2018 Coho 130-299

Day	Chinook	Other Salmon	Herring	Sand lance	Other Fish	Unid Fish	Gammarid Amphipod	Hyperiid Amphipod	Crab Larvae	Other Invert	Unid Food
1	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.03	0.73	0.09	0.00
31	0.00	0.00	0.00	0.00	0.12	0.00	0.02	0.03	0.76	0.08	0.00
45	0.00	0.00	0.00	0.00	0.12	0.00	0.02	0.03	0.76	0.08	0.00
75	0.00	0.00	0.03	0.00	0.08	0.00	0.04	0.18	0.67	0.01	0.00
105	0.00	0.00	0.03	0.00	0.02	0.00	0.39	0.13	0.14	0.29	0.00
135	0.00	0.00	0.00	0.00	0.00	0.00	0.43	0.36	0.01	0.16	0.04
150	0.00	0.00	0.00	0.00	0.00	0.00	0.43	0.36	0.01	0.16	0.04
365	0.00	0.00	0.03	0.00	0.04	0.00	0.30	0.15	0.29	0.18	0.01

2018 Coho 300+

Day	Chinook	Other Salmon	Herring	Sand lance	Other Fish	Unid Fish	Gammarid Amphipod	Hyperiid Amphipod	Crab Larvae	Other Invert	Unid Food
1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
31	0.00	0.00	0.50	0.00	0.00	0.00	0.40	0.00	0.10	0.00	0.00
45	0.00	0.00	0.50	0.00	0.00	0.00	0.40	0.00	0.10	0.00	0.00
75	0.04	0.00	0.32	0.13	0.01	0.00	0.50	0.00	0.00	0.00	0.00
135	0.00	0.00	0.33	0.00	0.00	0.00	0.50	0.00	0.00	0.17	0.00
150	0.00	0.00	0.33	0.00	0.00	0.00	0.50	0.00	0.00	0.17	0.00
365	0.00	0.00	0.34	0.06	0.00	0.00	0.46	0.00	0.08	0.06	0.00

**Table 4-
continued
2019 Coho 130-
299**

Day	Chinook	Other Salmon	Herring	Sand lance	Other Fish	Unid Fish	Gammarid Amphipod	Hyperiid Amphipod	Crab Larvae	Other Invert	Unid Food
1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.99	0.00	0.00
31	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.99	0.00	0.00
45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.99	0.00	0.00
75	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.40	0.36	0.10	0.00
105	0.00	0.00	0.07	0.00	0.01	0.00	0.46	0.17	0.14	0.05	0.10
135	0.00	0.00	0.00	0.00	0.00	0.00	0.61	0.13	0.05	0.17	0.03
150	0.00	0.00	0.00	0.00	0.00	0.00	0.61	0.13	0.05	0.17	0.03
365	0.00	0.00	0.01	0.00	0.00	0.00	0.30	0.24	0.03	0.43	0.02

2019 Coho 300+

Day	Chinook	Other Salmon	Herring	Sand lance	Other Fish	Unid Fish	Gammarid Amphipod	Hyperiid Amphipod	Crab Larvae	Other Invert	Unid Food
1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.98	0.02	0.00
31	0.00	0.00	0.00	0.00	0.00	0.00	0.47	0.00	0.51	0.00	0.02
45	0.00	0.00	0.00	0.00	0.00	0.00	0.47	0.00	0.51	0.00	0.02
75	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
105	0.00	0.00	0.00	0.00	0.00	0.00	0.99	0.00	0.00	0.01	0.00
135	0.00	0.00	0.00	0.00	0.00	0.00	0.49	0.01	0.00	0.50	0.00
150	0.00	0.00	0.00	0.00	0.00	0.00	0.49	0.01	0.00	0.50	0.00
365	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.27	0.72	0.01

Table 5. Prey energy density (J/g wet weight, upper table) and indigestible fractions (lower table) associated with diet inputs used for all sizes of Chinook and Coho for all years.

Prey energy density

Day	Chinook	Other Salmon	Herring	Sand lance	Other Fish	Unid Fish	Gammarid Amphipod	Hyperiid Amphipod	Crab Larvae	Other Invert	Unid Food
1	4480	4480	5543	5315	5260	5260	3100	2464	3384	3200	3400
365	4480	4480	5543	5315	5260	5260	3100	2464	3384	3200	3400

Indigestible fraction of prey

Day	Chinook	Other Salmon	Herring	Sand lance	Other Fish	Unid Fish	Gammarid Amphipod	Hyperiid Amphipod	Crab Larvae	Other Invert	Unid Food
1	0.03	0.03	0.03	0.03	0.03	0.03	0.1	0.1	0.1	0.1	0.1
365	0.03	0.03	0.03	0.03	0.03	0.03	0.1	0.1	0.1	0.1	0.1

Table 6. Monthly population-level consumption estimates (kg/mo) for resident Chinook by age during May-September 2018 and 2019.

2018												
Age												Total
0.1	Nt	Chinook	Herring	Sand-lance	Other Fish	Unid. Fish	Gammarid Amphipod	Hyperiid Amphipod	Crab Larvae	Other Inverts	Unid. Food	Consumption kg/mo
May	843,992	-	-	-	-	-	-	-	-	112,149	-	112,149
Jun	711,257	-	-	-	-	-	-	-	-	95,972	-	95,972
Jul	599,493	-	4,498	-	136	-	4,498	545	-	76,884	-	86,562
Aug	503,836	-	27,683	-	2,200	-	20,040	2,657	136	23,779	-	76,493
Sep	424,598	-	43,176	-	7,477	-	8,492	2,061	619	5,223	-	67,047
Subtotal		-	75,357	-	9,813	-	33,030	5,262	755	314,007	-	438,224
Age 0.2												
May	109,006	-	25,177	4,509	-	-	3,270	-	1,721	-	172	34,848
Jun	91,862	-	15,479	5,500	1,532	-	4,997	-	2,630	406	263	30,807
Jul	77,427	-	13,576	4,455	7,494	-	874	91	291	1,911	29	28,722
Aug	65,073	-	17,706	1,703	3,487	-	2,184	377	-	202	-	25,660
Sep	54,839	-	10,316	117	6,959	-	3,840	33	-	-	-	21,266
Subtotal		-	82,254	16,283	19,472	-	15,165	502	4,642	2,519	464	141,302

Table 6-continued

Age 0.3	Nt	Chinook	Herring	Sand- lance	Other Fish	Unid. Fish	Gammarid Amphipod	Hyperiid Amphipod	Crab Larvae	Other Inverts	Unid. Food	Total Consump- tion kg/mo
May	14,079	-	7,073	1,264	-	-	915	-	481	0	48	9,781
Jun	11,864	-	4,280	1,521	422	-	1,383	-	728	112	73	8,517
Jul	10,000	-	3,701	1,216	2,044	-	239	25	80	521	8	7,834
Aug	8,404	-	4,763	459	937	-	587	102	-	55	-	6,902
Sep	7,083	-	2,742	31	1,848	-	1,020	9	-	(0)	-	5,650
Subtotal		-	22,559	4,490	5,252	-	4,143	135	1,289	688	129	38,685
2018 Total		-	180,170	20,773	34,537	-	52,338	5,900	6,687	317,214	593	618,212

Table 6-continued

													-
													Total
2019													Consump-
Age													tion kg/mo
0.1	Nt	Chinook	Herring	Sand-lance	Other Fish	Unid. Fish	Gammarid Amphipod	Hyperiid Amphipod	Crab Larvae	Other Inverts	Unid. Food		
May	843,992	-	-	11,106	-	-	793	2,380	134,476	7,933	781	157,469	
Jun	711,257	-	-	3,180	424	-	4,027	848	131,254	1,272	2,495	143,499	
Jul	599,493	-	8,434	15,285	2,038	-	29,793	4,298	62,619	6,558	8,916	137,941	
Aug	503,836	-	39,872	1,660	221	3,945	46,539	5,333	5,312	9,749	16,187	128,818	
Sep	424,598	-	20,912	-	-	17,619	4,073	17,705	-	32,301	19,695	112,305	
Subtotal		-	69,218	31,231	2,683	21,564	85,225	30,564	333,661	57,813	48,074	680,032	
0.2													-
May	109,006	-	19,951	2,266	2,266	3,292	4,236	2,266	26,765	4,252	-	65,294	
Jun	91,862	-	12,123	3,536	3,536	3,058	6,487	3,536	23,662	3,312	-	59,250	
Jul	77,427	-	10,355	398	398	14,531	12,079	398	14,010	4,021	-	56,190	
Aug	65,073	-	47,811	13	10	1,599	1,292	13	1,378	423	-	52,541	
Sep	54,839	-	25,814	1,107	830	2,490	3,043	1,107	10,235	1,660	-	46,285	
Subtotal		-	116,055	7,319	7,039	24,970	27,137	7,319	76,051	13,668	-	279,559	

Table 6-continued

Age 0.3	Nt	Chinook	Herring	Sand- lance	Other Fish	Unid. Fish	Gammarid Amphipod	Hyperiid Amphipod	Crab Larvae	Other Inverts	Unid. Food	Total Consump- tion kg/mo
May	14,079	-	5,610	628	628	934	1,185	628	7,504	1,196	-	18,312
Jun	11,864	-	3,206	935	935	792	1,702	935	6,244	872	-	15,621
Jul	10,000	-	2,556	101	101	3,637	3,025	101	3,517	1,007	-	14,046
Aug	8,404	-	11,173	3	2	384	310	3	330	102	-	12,307
Sep	7,083	-	5,702	241	181	543	664	241	2,234	362	-	10,169
Subtotal		-	28,247	1,909	1,847	6,291	6,886	1,909	19,828	3,539	-	70,456
2019 Total		-	213,520	40,458	11,570	52,825	119,249	39,792	429,540	75,020	48,074	1,030,047

Table 7. Monthly population-level consumption estimates (kg/mo) for resident Coho by age during May-September 2018 and 2019.

												Total Consump- tion kg/mo
2018 Age 1.0	Nt	Chinook	Herring	Sand- lance	Other Fish	Unid. Fish	Gammarid Amphipod	Hyperiid Amphipod	Crab Larvae	Other Inverts	Unid. Food	
May												
Jun	918,876	-	609	-	17,504	-	3,459	7,625	114,174	9,263	-	152,634
Jul	769,228	-	3,941	-	11,449	-	12,454	23,194	91,033	6,908	-	148,979
Aug	643,951	-	3,639	-	3,430	-	49,191	23,091	26,032	33,202	721	139,304
Sep	539,077	-	454	-	302	-	52,045	40,600	3,191	21,557	4,293	122,442
Subtotal		-	8,642	-	32,686	-	117,149	94,510	234,430	70,929	5,013	563,360
Age 1.1												-
May	125,486	-	31,811	-	-	-	25,449	-	75,325	-	-	132,585
Jun	105,049	675	61,054	2,194	169	-	52,961	-	11,130	-	-	128,184
Jul	87,941	3,977	41,706	12,926	994	-	59,504	-	1,452	1,352	-	121,913
Aug	73,619	2,231	36,573	7,250	558	-	56,259	-	-	9,647	-	112,519
Sep	61,629	244	32,579	793	61	-	49,454	-	-	15,777	-	98,908
Subtotal		7,127	203,723	23,164	1,782	-	243,628	-	87,908	26,777	-	594,109
2018 Total		7,127	212,365	23,164	34,468	-	360,777	94,510	322,337	97,706	5,013	1,157,468

Table 7-Continued, Coho consumption

												Total Consump- tion kg/mo
2019 Age 1.0	Nt	Chinook	Herring	Sand- lance	Other Fish	Unid. Fish	Gammarid Amphipod	Hyperiid Amphipod	Crab Larvae	Other Inverts	Unid. Food	
May												
Jun	918,876	-	-	-	-	-	3,046	10,124	148,378	2,176	-	163,724
Jul	769,228	-	1,439	-	206	-	26,022	51,019	64,094	12,862	206	155,847
Aug	643,951	-	7,631	-	1,090	-	64,053	27,970	22,497	10,393	1,842	135,476
Sep	539,077	-	1,109	-	158	-	76,540	17,452	7,894	20,092	4,700	127,944
Subtotal		-	10,178	-	1,454	-	169,661	106,564	242,863	45,523	6,747	582,990
Age 1.1												-
May	125,486	-	-	-	-	-	33,309	-	111,771	1,543	1,417	148,040
Jun	105,049	-	-	-	-	-	74,464	-	61,338	-	2,405	138,207
Jul	87,941	-	-	-	-	-	117,813	-	7,761	162	304	126,041
Aug	73,619	-	-	-	-	-	104,320	144	-	8,045	-	112,509
Sep	61,629	-	-	-	-	-	53,508	849	-	42,584	-	96,941
Subtotal		-	-	-	-	-	383,413	993	180,871	52,334	4,127	621,739
2019 Total		-	10,178	-	1,454	-	553,075	107,558	423,734	97,857	10,874	1,204,729

Table 7-Continued, Coho consumptionAge 1.1 Alternative diet
2019

	Nt	Chinook	Herring	Sand- lance	Other Fish	Unid. Fish	Gammarid Amphipod	Hyperiid Amphipod	Crab Larvae	Other Inverts	Unid. Food	Total Consump- tion kg/mo
May	125,486	-	27,492	-	-	-	4,811	-	107,818	1,485	1,375	142,981
Jun	105,049	-	55,717	-	-	-	19,490	-	61,667	-	2,418	139,293
Jul	87,941	-	49,720	-	-	-	74,691	-	8,076	174	317	132,976
Aug	73,619	-	27,347	-	-	-	85,720	157	-	8,758	-	121,982
Sep	61,629	-	21,262	-	-	-	37,397	932	-	46,719	-	106,310
Subtotal		-	181,538	-	-	-	222,109	1,089	177,561	57,136	4,110	643,543
Alternate 2019 total		-	191,716	-	1,454	-	391,770	107,653	420,424	102,659	10,856	1,226,534

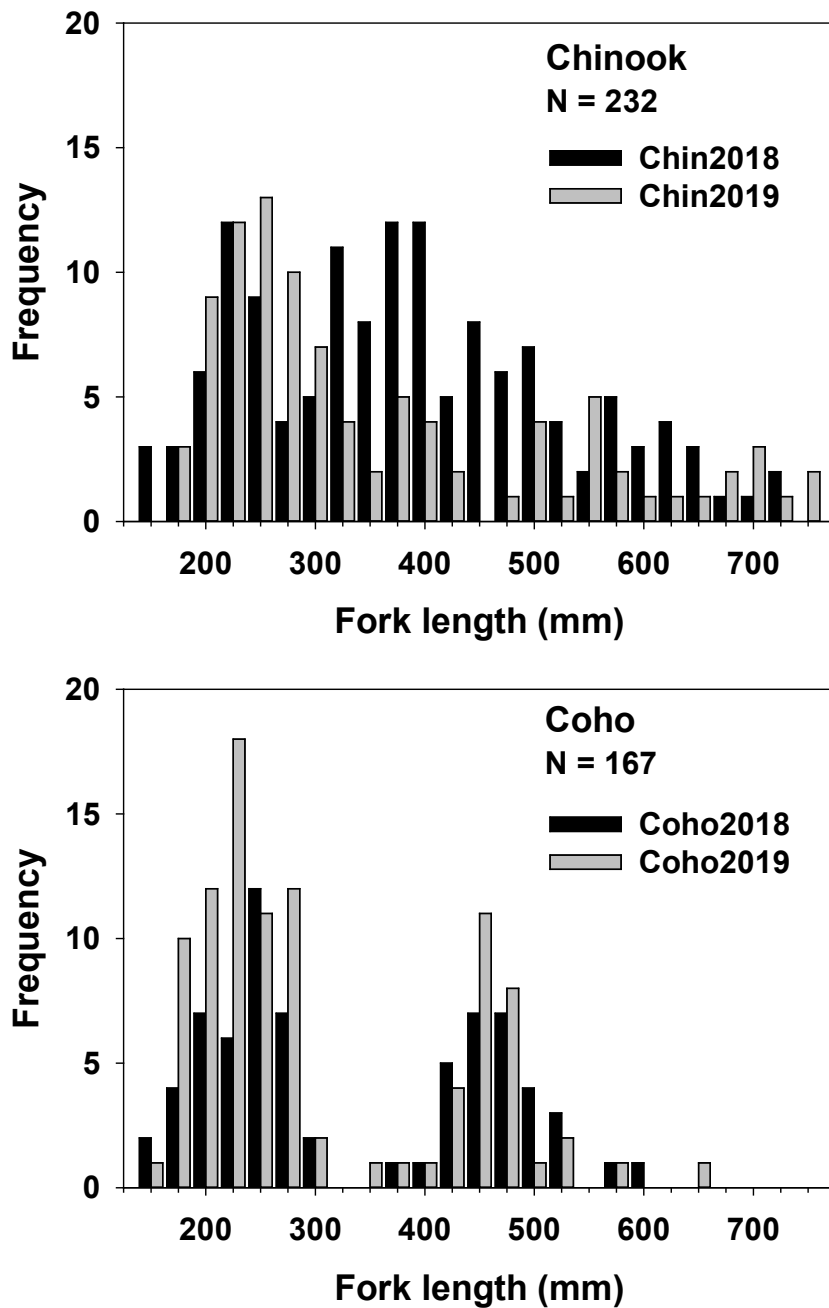


Figure 1. Fork length frequency distributions for Chinook (top panel) and Coho (bottom panel) sampled via microtrolling during May-September 2018 and 2019.

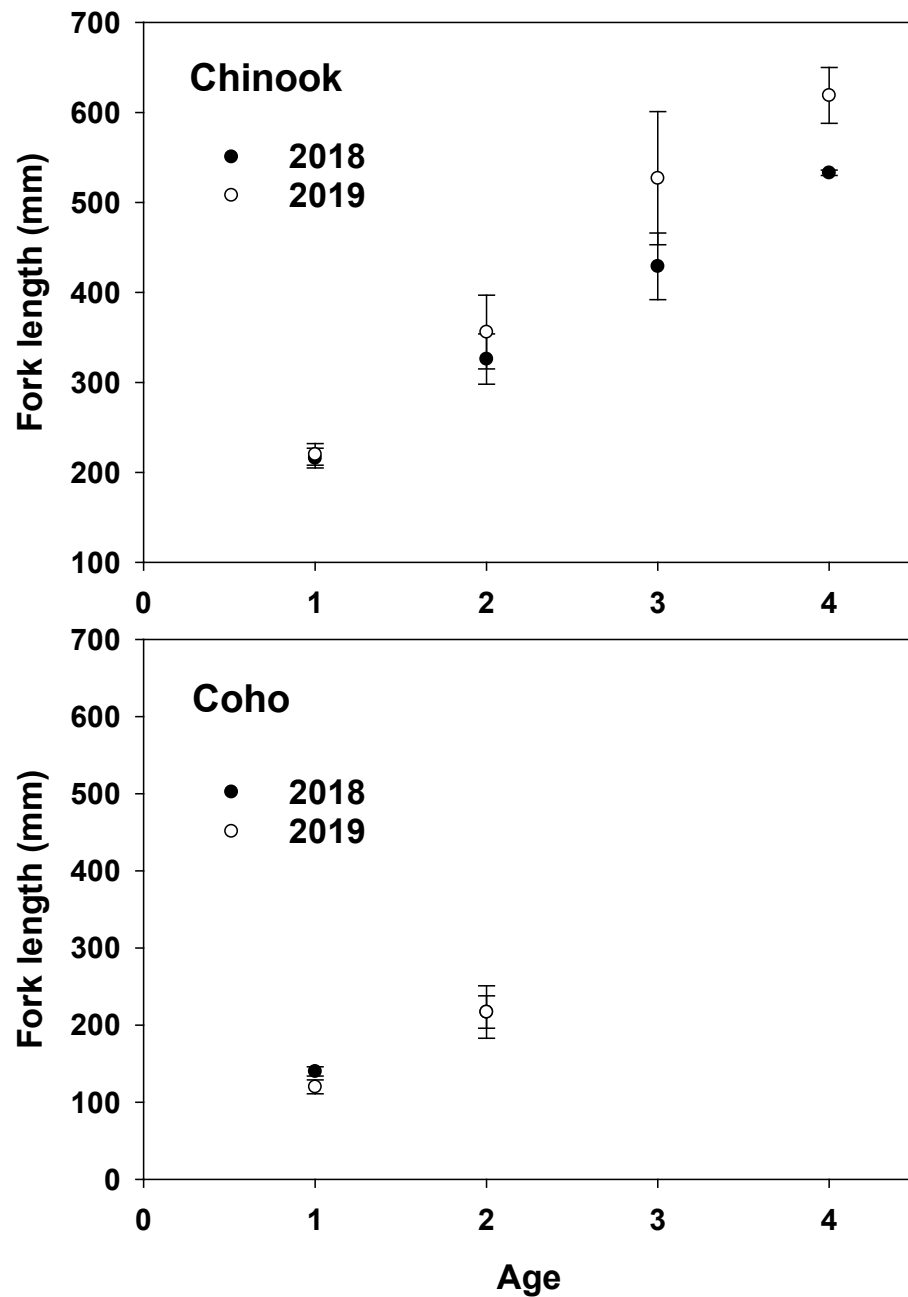


Figure 2. Mean (± 2 SE) fork length at age for sub-adult and adult Chinook salmon (top) and Coho (bottom) sampled by microtrolling in Puget Sound during 2018 and 2019. Subyearling Chinook enter epi-pelagic habitats in Puget Sound during June at approximate fork lengths of 100 mm (Gamble et al. 2018), and subsequent growth is acquired in epi-pelagic marine habitats. For Coho, the first annulus forms during freshwater rearing, but most growth between annuli 1 and 2 is acquired via feeding in epi-pelagic marine habitats.

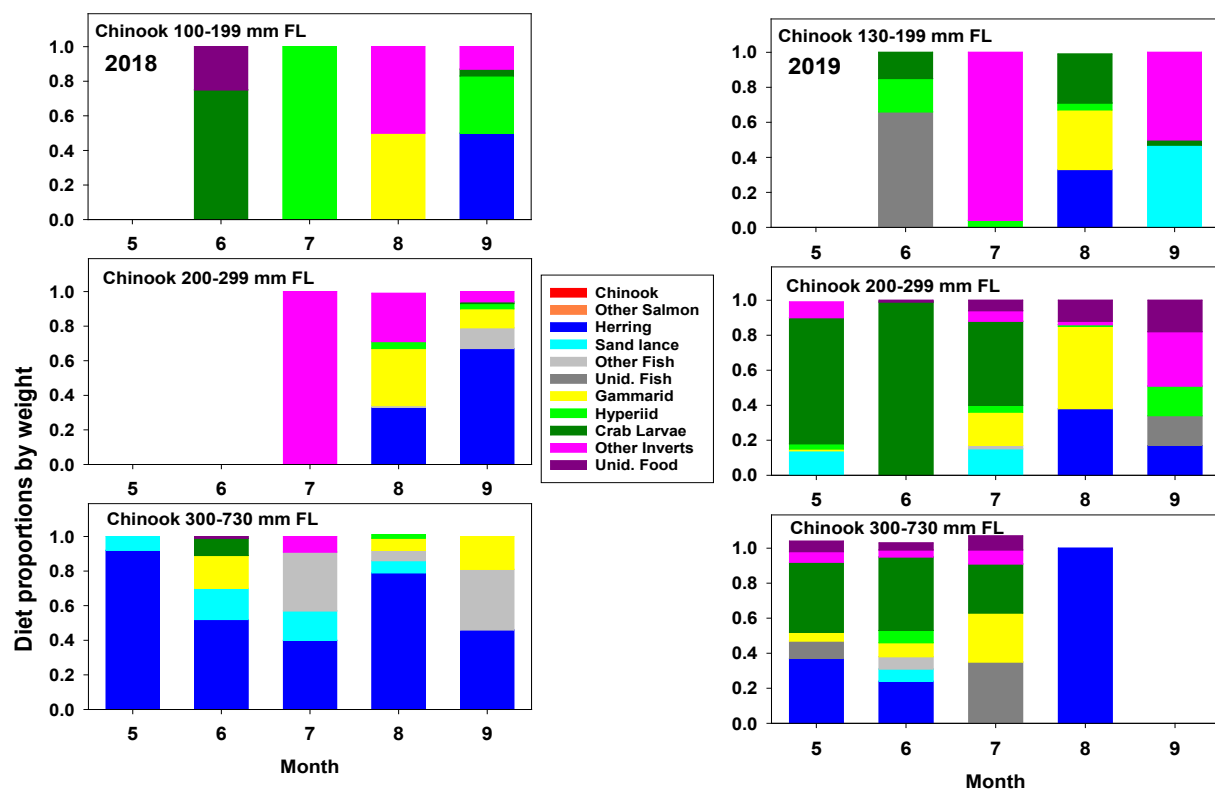


Figure 3. Monthly diet composition by different size classes of resident Chinook salmon in Puget Sound during spring-summer in 2018 and 2019.

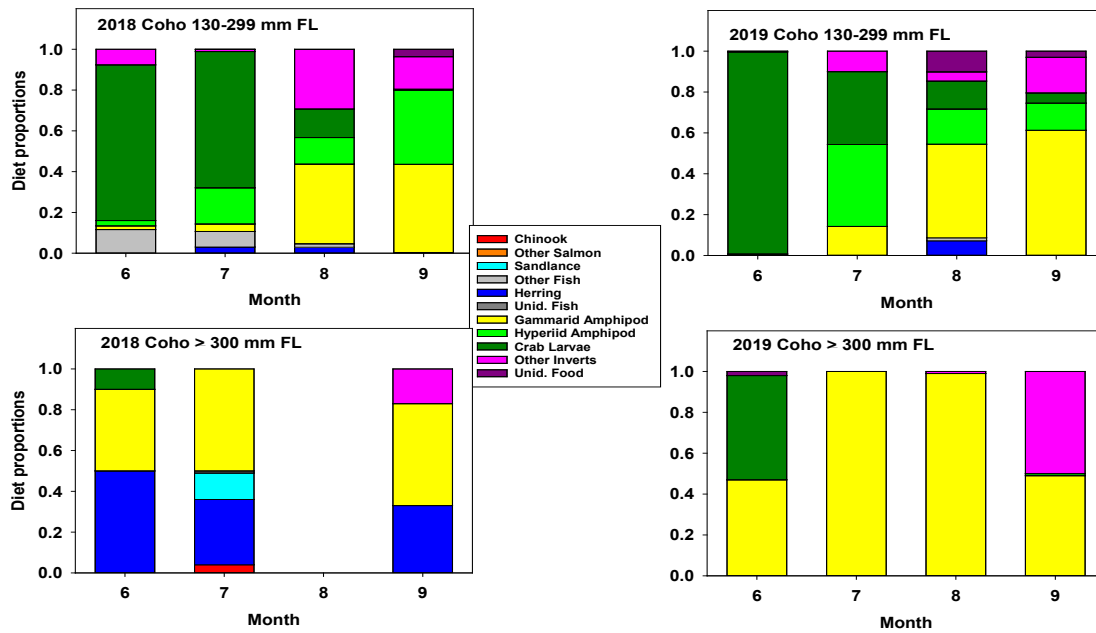


Figure 4. Monthly diet composition by different size classes of resident Coho salmon in Puget Sound during spring-summer in 2018 and 2019.

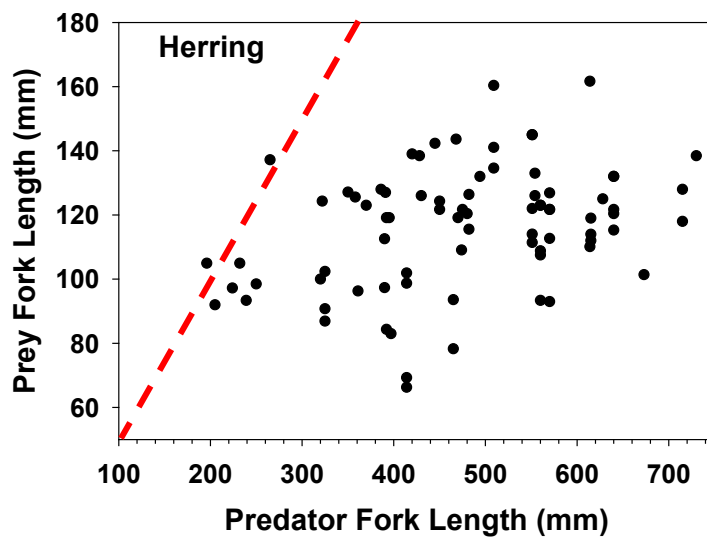
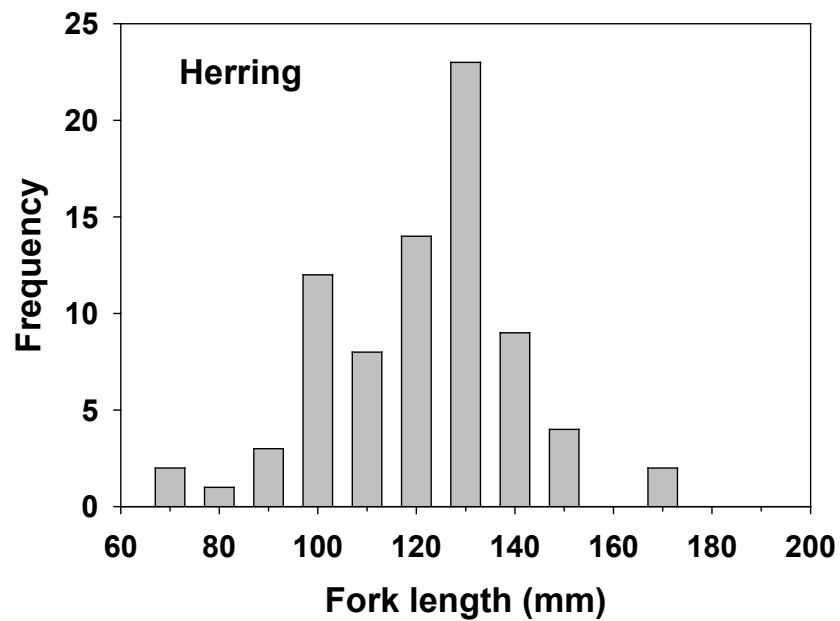


Figure 5. The length frequency distribution of Pacific Herring found in the diets of resident Chinook and Coho Salmon (top panel); and the size of Herring consumed related to the size of predator (bottom panel). The dashed line represents the FL of prey equal to 50% of the FL of the predator.

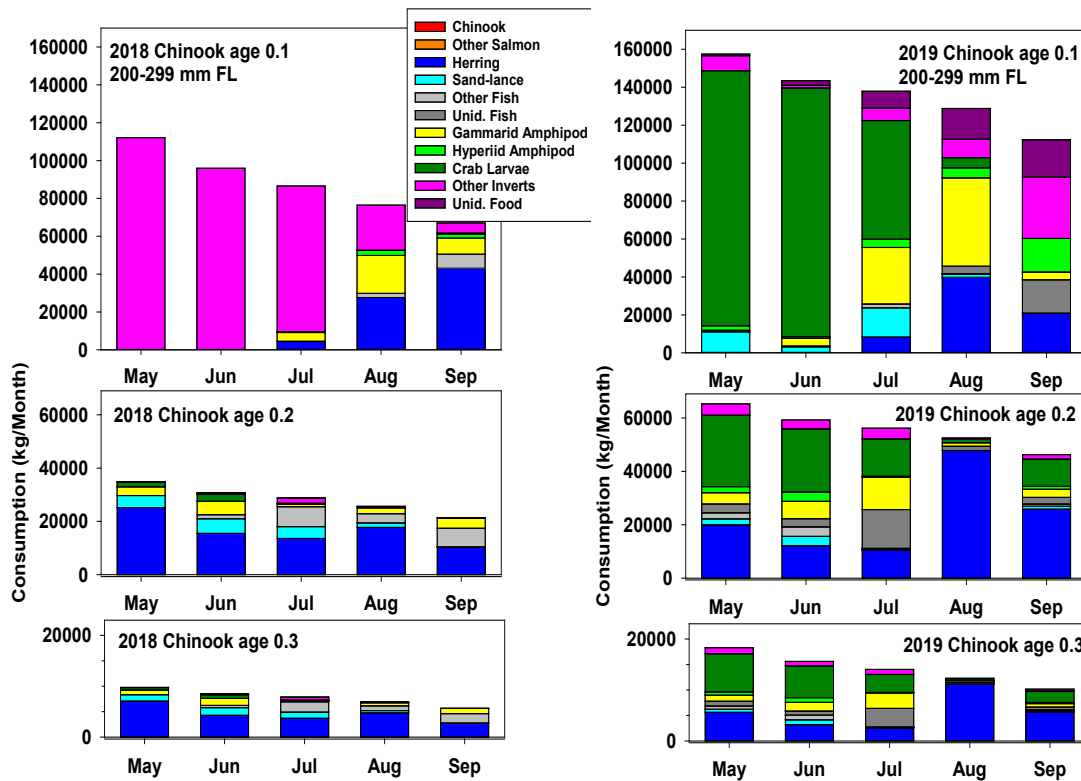


Figure 6. Monthly population-level consumption (kg/month) by 3 age classes of resident Chinook salmon in Puget Sound during spring-summer 2018 and 2019. Note: the Y-axes have been modified to improve readability while still conveying the reduction in consumption by older age classes.

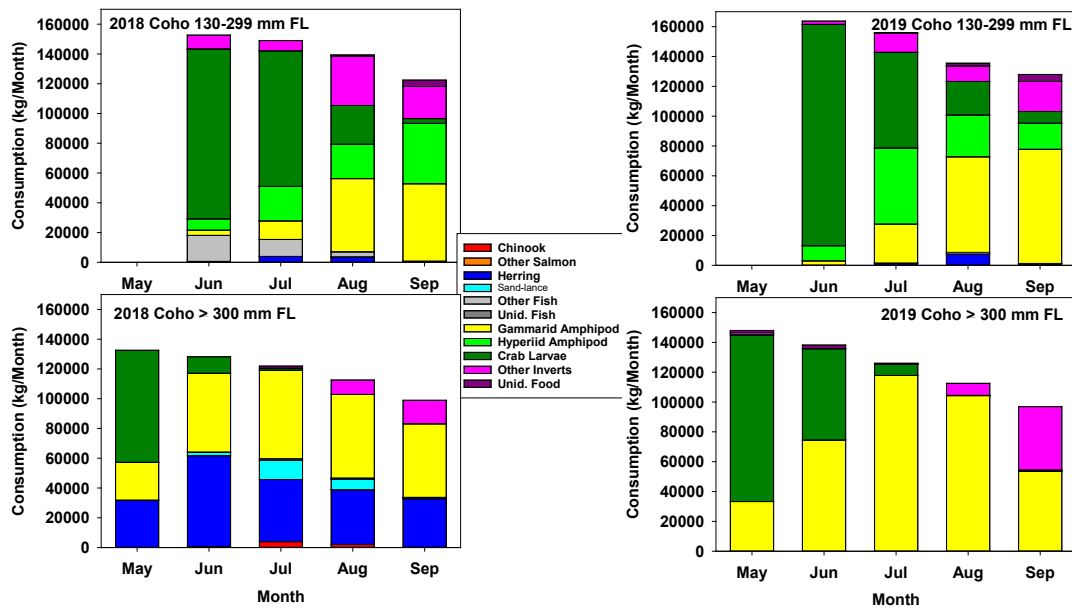
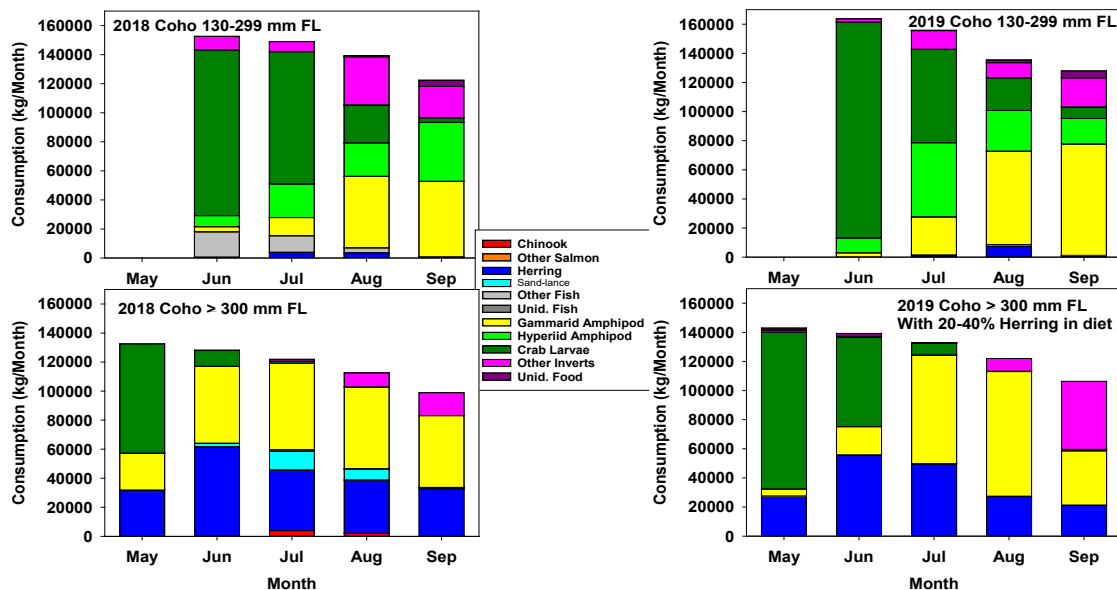


Figure 7. Monthly population-level consumption demand by age-1 and age-2 Coho during May-September 2018 and 2019. During 2019, the monthly consumption rate shown for Coho ≥ 300 mm FL represents feeding at the theoretical maximum rate ($C_{max} = 100\%$), but fish could not achieve the observed final body weight under the observed diet depicted here. See figure below for a comparison to a diet where 20-40% Herring were allowed into the diet, which enabled the older Coho to reach the observed final weight by feeding at 96% C_{max} with the substitution of Herring as a higher energy prey for some of the invertebrates.



Appendix 1

The terminal tackle for microtrolling included a rubber snubber, monofilament leaders, flasher/dodgers and lures were clipped directly to a downrigger cable at 6 depths to fish simultaneously from a downrigger on each side of the boat (sampling range spanning 5-30 m).

Terminal tackle

Gear Type	Manufacturer	Model	Color Pattern	Length
Spoon	Luhr Jensen Silver Horde	Coyote spoon	black/ white (cop car)	3 1/2"
		Coho Killer	black/glow purple/ glow blue/glow green/glow	
		Kingfisher	green/glow black/glow	3", 3 3/8"
Flashers	Apex	Hot Spot	glow/green glow/black	11"
Dodgers	Luhr Jensen		Chrome	8"
Hoochies	?		green/glow blue/glow green/silver blue/silver	4"

Leaders from the snubber/clip to the flasher/dodger was ~6 ft using 50lb test

Leaders from the flasher/dodger to the spoons was ~32" using 25lb

Leaders from the snubber/clip to a spoon was ~8 ft using 25 or 30lb test

Leaders from the flasher to hoochies was 30-36" using 25lb test

Hooks were generally 2/0 Siwash for all terminal tackle. For spoons, the original stock hooks were used initially, but were replaced with 2/0 Siwash hooks.

The Coho Killer spoon was always used with a dodger

SECTION 2

Influence of Artificial Light at Night (ALAN) on Predation Risk for Juvenile Salmon and Forage Fishes in Puget Sound

Interim Report to Long Live the Kings, Salish Sea Marine Survival Project

February 2020

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SECTION 2

EVALUATING THE INFLUENCE OF ARTIFICIAL LIGHT AT NIGHT (ALAN) ON PREDATION RISK FOR JUVENILE SALMON AND FORAGE FISHES IN PUGET SOUND

Abstract— Major predators on juvenile salmon rely primarily on vision to hunt for their prey. Artificial light at night (ALAN) has increased considerably over recent decades and has potentially altered the ability of visual predators to feed at night and thus increase predation risk and mortality for juvenile salmon and forage fishes. Empirical measures of nocturnal light and turbidity data were sampled and combined with a visual foraging model for Coastal Cutthroat Trout and Chinook Salmon, common marine piscivores in the Salish Sea, to examine contemporary spatial-temporal variability in the nocturnal predation risk for juvenile salmon and forage fishes in nearshore and offshore habitats of urbanized and non-urbanized regions of Puget Sound. Contemporary nocturnal light patterns indicate that ALAN has significantly increased predation risk for juvenile salmonids and forage fishes in the Puget Sound region. Light-dependent visual predation risk was 6X higher in urbanized nearshore habitat than in non-urbanized nearshore habitats. In offshore habitats, increased skyglow extended at least 6 km from urbanized shorelines and imposed nearly 2-fold higher risk than offshore habitats in non-urbanized regions. Understanding how the visual environment varies through time and space, and how these variations affect visually-based predation risk on juvenile salmon can provide insights into marine survival trends through time and inform future restoration priorities.

INTRODUCTION

Predation is considered a major source of mortality for salmon during early marine life stages. Predation mortality can increase if search or capture efficiency of predators improves due to increased detection capability by predators or longer

exposure to prey under enhanced foraging conditions. Most aquatic vertebrates and some invertebrates rely on vision as the primary sensory mechanism for movement, feeding, and avoiding predation, especially in pelagic environments. All major predators on juvenile salmon rely primarily on vision to search for and consume their prey. Therefore, understanding how the visual environment varies through time and space, and how these variations affect visually-based predation risk on juvenile salmon can provide considerable insight into marine survival trends through time and inform future restoration priorities.

Most aquatic vertebrates and some invertebrates rely on vision as the primary sensory mechanism for movement, feeding, and avoiding predation, especially in pelagic environments. All major predators on juvenile salmon rely primarily on vision to search for and consume their prey. Therefore, understanding how the visual environment varies through time and space, and how these variations affect visually-based predation risk on juvenile salmon can provide considerable insight into marine survival trends through time and inform future restoration priorities.

Visual conditions underwater vary dramatically among water bodies and across day-twilight-night periods, seasons and among years within the same waters. Human activities have significantly altered the underwater visual environment, but the implications of these changes for survival and growth of aquatic species and function of aquatic food webs have been largely ignored until recently. The ecological impacts of Artificial Light at Night (ALAN) to terrestrial and aquatic life is an emerging global concern due to disruptions in orientation, timing and maladaptive behaviors which affect reproduction, growth, distribution, movement and survival (Longcore and Rich 2004; Perkin et al. 2011). ALAN has increased worldwide in recent decades due to changes in land use and lighting technology (Falchi et al. 2016), and impacts can be particularly important in urbanized environments.

We hypothesize that the efficacy of piscivorous mammals, birds, and fish have increased considerably since the 1980s as a result of rapid increases in artificial light pollution associated with accelerating urbanization. We propose to measure the spatial-

temporal variability in the nocturnal underwater light environment among regions and habitats in Puget Sound during critical spring-summer marine rearing periods for juvenile salmon, translate these measurements into spatial-temporal patterns of light-dependent predation risk, and determine how much light reduction would be required to significantly reduce predation risk.

The objectives of this study were to: 1) Quantify the surface and underwater nocturnal light environment at representative offshore marine waters in Puget Sound during the spring-summer juvenile salmon outmigration and first marine growing season; 2) Incorporate variability in ambient underwater turbidity at key locations within each of the marine regions during ecologically significant periods such as: algal blooms, sediment plumes, and early summer conditions to record the temporal range and geographic variability in turbidity associated with routine natural events and human perturbations; and 3) Combine the nocturnal light and turbidity data with visual foraging models (VFM) for piscivorous salmonids (i.e., demonstrated predators on juvenile salmon) to estimate the contemporary nocturnal threat environment and evaluate the spatial-temporal variability in predation risk corresponding to critical early marine life stages of anadromous salmonids. This evaluation can help identify locations and times associated with particularly high predation risk and provide recommendations for minimizing these risks within the operating constraints of those locations.

METHODS

We measured spatial variability in the surface and underwater nocturnal light environment, as mediated by ambient levels of turbidity, then used visual foraging models for piscivorous salmonids (demonstrated major predators on juvenile salmon) to estimate how the nocturnal predation-threat environment changes through time and space, based on observed variability in nocturnal light and turbidity. Surveys of nocturnal light levels were conducted within representative marine shoreline and

pelagic habitats in urbanized and non-urbanized regions of Puget Sound during June-July 2018 to correspond with the early marine rearing period for juvenile Chinook salmon.

Light Measurements

We measured light levels with Wildlife Computers TDR-MK9 light sensing tags. Light intensity data were converted to lux by calibrating with a lux meter individually to each light sensor. These sensors were particularly useful for this application, because their spectral sensitivity is constant across the visual range of wavelengths, and light intensities could be measured well below 0.0001 lux which was approximately one order of magnitude below the expected ecologically-relevant range of light we anticipated to measure for the purposes of evaluating effects on predation risk.

Transect Surveys

Spatial and temporal variability in the nocturnal light environment was measured using light sensors with mobile surveys. Nearshore and offshore transects were conducted in urban and non-urban areas in the Central Basin near Seattle and Whidbey Basin near Everett (**Figure 1**). The mobile surveys measured light above the surface and at shallow and deeper depths below the water surface. Surface and sub-surface light levels were measured continuously along longitudinal transects. The surveys were conducted after astronomical twilight on the evenings of June 29th and July 10th, 2018. Light levels were measured continuously above the water surface (on deck) and subsurface at 1-m and generally 10-m (where deep enough to safely reach this depth) with depth-sensing light sensors (TDR-MK9) mounted to a horizontal plastic towing fin that clipped with commercial trolling clips at the prescribed depths onto a downrigger line (**Figure 2**). The on-deck surface tag was shielded from onboard lights emanating from the wheelhouse. Navigation lights were turned off while measurements were recorded. For nearshore transects, light sensors were towed parallel to shore for 5 minutes. Due to safety concerns for the submerged light sensors and the vessel, transects were generally run just shoreward of the 30-m isobath.

Monthly depth profiles of water quality data collected by Washington Department of Ecology from 2009 to 2017 provided a temporal-spatial range of turbidity readings. Monthly mean (and SD) turbidity (NTU) levels were computed over the 0-30 m depth intervals corresponding to the modal depths occupied by juvenile salmon. These depth-integrated means were computed both annually and pooled across years; however, neither the annual or pooled estimates exceeded the threshold beyond which turbidity needed to be included explicitly, so only the averages and SD pooled across years were reported (see Visual Foraging Model section below).

Estimating Visual Predation Risk

The spatial-temporal data for light and turbidity were combined with visual foraging models (VFM) for piscivorous salmonids to map the nocturnal predation threat environment for juvenile salmonids and forage fishes in nearshore and offshore marine habitats within Puget Sound. The VFM computes the effective search volume in response to ambient light and turbidity at any time, depth, and location, based on the visual capabilities of the predator (**Figure 3**).

Measured light levels (lux; this study) and average turbidity levels (NTU; WA Dept of Ecology) were input into a VFM (Beauchamp et al. 1999) to calculate the reaction distances (RD, cm) and search volumes (SV, m³/h) at various depths and locations. We used VFMs parameterized for piscivorous Chinook salmon *Oncorhynchus tshawytscha* and Coastal Cutthroat Trout *O. clarki clarki* (Hansen et al. 2013) as our model predators in this application, because both species have been identified as predators of juvenile salmonids and other prey fishes in nearshore and pelagic habitats of Puget Sound (Duffy and Beauchamp 2008; Beauchamp and Duffy 2011).

Visual Foraging Model

Visual foraging rate models (VFM) or component functions have been developed for piscivorous fishes including Largemouth Bass (Howick and O'Brien 1983, Miner and Stein 1993) and various salmonids. VFMs have been developed and successfully applied to

piscivorous salmon, trout, and char feeding on juvenile salmonids and other forage fishes as functions of light, turbidity, prey size, depth, season, and diel period in freshwater and marine systems (Beauchamp et al. 1999; Vogel and Beauchamp 1999; Mazur and Beauchamp 2003 and 2006; Schoen et al. 2012; Hansen et al. 2013a,b; Hansen and Beauchamp 2014, 2015). These models estimate the search volumes (SV, m³/h) for piscivores foraging for prey fish during specified periods under various visual conditions.

The search volume is approximated by a cylinder with the radius of the circular cross-section defined by the reaction distance (RD, cm) of the predator to its prey and the length of the cylinder equivalent to the light-dependent swimming speed (SS, cm/s) of the predator over the duration (D, h) of a foraging bout.

$$SV = \pi * RD^2 * SS * D$$

All light levels encountered during the surveys fell into the range associated with nocturnal swimming by Cutthroat Trout measured in both in situ telemetry studies (Baldwin et al. 2002; Nowak and Quinn 2002) and low-light visual foraging experiments (Beauchamp et al. 1999; Mazur and Beauchamp 2003). Thus, we assigned the average nocturnal value of SS = 14 cm/s (SE = 6 cm/s) reported from these studies. Search volumes were calculated for an hour-long foraging bout, so the length of the cylindrical search volume was SS*D = 0.14 m/s * 3600 s/h = 504 m/h.

The radius, RD, of the cylinder varies as a function of light intensity I (lux) and turbidity T (NTU); however, turbidity does not impose a measurable effect on RD until it exceeds a threshold of 1.5 NTU (Mazur and Beauchamp 2003; Hansen et al. 2013). Average turbidity levels for the Nisqually Reach (NSQ002) and south Admiralty Inlet (ADM003, Washington Department of Ecology, Marine Waters Program) were below well this threshold. From 2009 to 2017, the mean monthly turbidities in the Nisqually Reach ranged T = 0.4-0.7 NTU (SD = 0.1-0.3 NTU) in the Nisqually Reach, and T = 0.3-0.6 NTU (SD = 0.1-0.4 NTU) in South Admiralty Inlet. Since both T and T+SD < 1.5 NTU, the direct effects of turbidity on RD were omitted from the visual foraging model

applications. Turbidity still affected light extinction with increasing depth, but this process was measured directly by the depth-specific light sensor readings.

In the absence of a direct turbidity effect, RD (cm) was modeled exclusively as a function of depth-specific light intensity I_z (lux) for piscivorous Chinook Salmon:

$$RD = 69.426 * I_z^{0.130} \quad \text{for } I_z \leq 67.89 \text{ lux and } T < 1.5 \text{ NTU}$$

$$RD = 120.295 \text{ cm} \quad \text{for } I_z > 67.89 \text{ lux and } T < 1.5 \text{ NTU},$$

and for piscivorous Cutthroat Trout:

$$RD = 109.994 * I_z^{0.148} \quad \text{for } I_z \leq 40.77 \text{ lux and } T < 1.5 \text{ NTU}$$

$$RD = 190.7 \text{ cm} \quad \text{for } I_z > 40.77 \text{ lux and } T < 1.5 \text{ NTU}.$$

These equations were applied to the empirical measures of light levels at the surface, shallow and deep depths in both nearshore and offshore habitats in urbanized and non-urbanized regions to estimate the resulting reaction distances and search volumes associated with these conditions for predatory Chinook Salmon and Cutthroat Trout. Predation by sea-run Cutthroat Trout was likely confined to nearshore habitats, whereas Chinook predation predominantly occurs offshore with some possibility of incursions into nearshore habitats.

RESULTS

The spatial distribution of nocturnal light levels indicated the expected tendency toward higher surface light levels in urbanized and nearshore zones (**Figure 4**). The effect of urbanization on light levels was stronger than between nearshore and offshore habitats. Light levels were significantly higher in urbanized than non-urbanized regions for all depths, whereas light levels were only significantly higher in nearshore than offshore habitats at shallow depths, marginally non-significant at the surface and non-significant at deeper depths; interactions between urbanization and nearshore-offshore effects were not significant (**Table 1; Figure 5**). The urbanized nearshore habitats were associated with the highest light levels on average overall, but also included a notable lighted hotspot along the waterfront that was separated from the other nearshore data for analysis (**Figure 6**). Comparable data were included from a 400-m transect in the

Lake Washington Ship Canal (LWSC) to demonstrate that salmonid smolts transiting urbanized outmigration corridors experience similar depth-specific light levels as along the urbanized marine nearshore zones.

The nocturnal light-dependent search volumes varied between species of predator, degree of urbanization, and between nearshore and offshore habitats (**Figure 7**). The estimated search volumes were higher for sea-run Cutthroat Trout than Chinook Salmon under all conditions. This difference was especially apparent in nearshore habitats where Cutthroat Trout feed, with search volumes ranging from 80 m³/h in nonurban to 662 m³/h in average urban nearshore zones compared to 848 m³/h around the waterfront hotspot and 544 m³/h in the LWSC.

The search volumes for predatory Chinook Salmon followed the same relative patterns as Cutthroat Trout, but at lower levels across all conditions (**Figure 7**). A closer comparison of search volumes for Chinook among habitats provides insights regarding the relative ecological impacts of localized light sources and direct illumination in the nearshore compared to skyglow in offshore zones (**Table 2**). At the shallow (1-m) depth, nearshore search volumes for Chinook were 6-fold higher in urbanized than non-urbanized regions (i.e., interpreted as the effects of localized and direct illumination in urban versus non-urban regions) and 1.8-fold higher in urbanized than non-urbanized offshore zones (i.e., the relative effects of skyglow in urbanized versus non-urbanized regions). In urbanized regions, search volumes were 3-fold higher in nearshore than offshore zones 1-6 km from shore (i.e., the relative magnitude of localized and direct illumination versus skyglow in urbanized regions), whereas in non-urbanized regions the search volumes were very similar with nearshore search volumes averaging 0.9-fold of the offshore zone.

DISCUSSION

Contemporary nocturnal light patterns indicate that ALAN has significantly increased predation risk for juvenile salmonids and forage fishes in the Puget Sound region. Risk is highest in urbanized nearshore habitats, 6X higher than in non-urbanized nearshore

habitats, but increased skyglow in offshore extending at least 6 km from urbanized shorelines have nearly 2-fold higher risk than offshore habitats in non-urbanized regions.

The ecological impacts of ALAN will vary among species and depend on the magnitude of risk and duration of exposure within various habitats. The higher risk associated with urbanized nearshore habitats is concentrated along a relatively narrow band of shorezone utilized by juvenile salmon for days to weeks (Coho, Steelhead, yearling Chinook and subyearling hatchery Chinook), or weeks to months (Pink, Chum, and wild subyearling Chinook) months (Duffy et al. 2005; Moore et al. 2015). In contrast, the relatively lower but still significantly elevated predation risk in offshore regions due to skyglow combine with the much larger area/volume affected and prolonged use (2-4 months) of the offshore epi-pelagic habitat to create a chronic level of increased predation risk. Despite the exponential attenuation of light with depth, the elevated predation risk due to skyglow extended through ecologically relevant depths for juvenile salmon (e.g., measurable through at least 1-10 m), especially through at least July when the modal depths occupied by juvenile salmon are within 0-15 m (Beamish et al. 1998; Duffy et al. 2010). This elevated chronic offshore risk corresponds with the critical early marine growth period when feeding and growth of subyearling Chinook Salmon strongly influence overall marine survival (Beauchamp and Duffy 2011; Duffy and Beauchamp 2011).

This was the first survey of ambient visual conditions at night at the water surface and through relevant depths occupied by juvenile salmonids and forage fishes in marine waters. By converting the empirical light readings into the visual capabilities of predatory fish, we evaluated the relative predation risk associated with effects of variability in lighting in urbanized and non-urbanized nearshore and offshore habitats that were relevant for rearing juvenile salmon and forage fishes during the summer growing season. This approach can estimate how predation risk would respond to incremental changes in ALAN and turbidity to identify potential mortality bottlenecks and inform recovery and restoration efforts to improve survival by improving habitat

function. By mapping the nocturnal threat environment and identifying “hotspots” of predation risk, site-specific recommendations can be developed to reduce or remove localized acute lighting impacts by moving, shielding, or altering the intensity or spectral characteristics of the light sources, and begin to address this issue on a broader regional level regarding long-range sky-glow effects.

Because the same visual constraints apply to mammals and birds, the VFM can also evaluate the relative change in predation threats from harbor seals and diving piscivorous birds in response to the current or changing visual environment as well. Estimates of the threat environment can also account for variability in light and turbidity in response to lunar and tidal cycles, seasonal variability in river discharge, and plankton blooms. Dams create effective sediment traps which have altered the seasonal cycle of river flow and turbidity which both affect predation risk during downstream migrations and the magnitude and timing of sediment plumes and wider spatial contributions to turbidity in marine waters during early marine rearing by juvenile salmonids as the plumes disperse. Similarly, changes in land and water use affect erosion and nutrient input cycles that influence the timing, magnitude and composition of turbidity patterns caused by plankton.

This assessment provides a baseline condition for comparing how nocturnal conditions change through time in response to continued land development and any policies related to regulating artificial light at night (ALAN). Global trends in ALAN have shown an average increase of 6% per year. Consequently, there is considerable opportunity to both minimize potential future increases while strategically implementing measures to ameliorate regional and localized sources of ALAN via incentives and common-sense measures for providing sufficient light for safety and security while minimizing the impacts (e.g., consult materials offered by the International Dark Sky Association, www.darksky.org).

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REFERENCES

- Beamish, R.J., M. Folkes, R. Sweeting, and C. Mahnken. 1998. Intra-annual changes in the abundance of Coho, Chinook, and Chum Salmon in Puget Sound in 1997. *Puget Sound Research* 1998. 531-541.
- Beauchamp D.A., Vecht S.A., and Thomas G.L. 1992. Temporal, spatial, and size-related foraging of wild cutthroat trout in Lake Washington. *Northwest Science*, 66:149–159.
- Beauchamp, D.A., C.M. Baldwin, J.L. Vogel, and C.P. Gubala. 1999. Estimating diel, depth-specific foraging with a visual encounter rate model for pelagic piscivores. *Canadian Journal of Fisheries and Aquatic Sciences* 56(Supplement 1):128-139.
- Falchi, F. and 8 co-authors. 2016. The new world atlas of artificial night sky brightness. *Science Advances* 2:e1600377
- Hansen, A.G., and D.A. Beauchamp. 2015. Latitudinal and photic effects on diel foraging and predation risk in freshwater pelagic ecosystems. *Journal of Animal Ecology* 84:532-544. doi: 10.1111/1365-2656.12295
- Hansen, A.G., and D.A. Beauchamp. 2014. Effects of prey abundance, distribution, pigmentation, and morphology on apparent selection by a pelagic piscivore. *Freshwater Biology* 59:2328-2341. doi:10.1111/fwb.12436
- Hansen, A.G., D.A. Beauchamp, and E.R. Schoen. 2013. Effects of light and turbidity on the reaction distance of anadromous salmonids to prey of different sizes. *Transactions of the American Fisheries Society* 142:854-867.
- Hansen, A.G., D.A. Beauchamp, and C.M. Baldwin. 2013. Environmental stress mediates the foraging success of apex predators in a pelagic system. *Transactions of the American Fisheries Society* 142:300-316.
- Howick, G.L., and O'Brien, W.J. 1983. Piscivorous feeding behavior of largemouth bass: an experimental analysis. *Transactions of the American Fisheries Society* **112**: 508–516.
- Kitano, J., D.I. Bolnick, D.A. Beauchamp, M.M. Mazur, S. Mori, T. Nakano, C.L. Peichel. 2008. Reverse evolution of armor plates in threespine stickleback. *Current Biology* 18:769-774.
- Longcore, T., and C. Rich. 2004. Ecological light pollution. *Frontiers in Ecology and the Environment* 2(4):191-198.
- Moore, M.E., B.A. Berejikian, F.A. Goetz, A.G. Berger, S.S. Hodgson, E.J. Connor, and T.P. Quinn. 2015. Multi-population analysis of Puget Sound steelhead survival and migration behavior. *Marine Ecology Progress Series* 537:217-232.
- Mazur, M.M., and D.A. Beauchamp. 2006. Linking piscivory to spatial-temporal distributions of pelagic prey fish with a visual foraging model. *Journal of Fish Biology* 69:151-175.
- Mazur, M.M., and D.A. Beauchamp. 2003. A comparison of visual prey detection among species of piscivorous salmonids: effects of light and low turbidities. *Environmental Biology of Fishes* 67:397-405.

- Miner, J.G., and Stein, R.A. 1996. Detection of predators and habitat choice by small bluegills: effect of turbidity and alternative prey. *Transactions of the American Fisheries Society* **125**: 97–103.
- Nowak G.M., Tabor R.A., Warner E.J., Fresh K.L. and Quinn T.P. 2004. Ontogenetic shifts in habitat and diet of cutthroat trout in Lake Washington, Washington. *North American Journal of Fisheries Management*, 24, 624–635.
- Perkin, E.K., F. Holker, J.S. Richardson, J.P. Sadler, C. Wolter, and K. Tockner. 2011. The influence of artificial light on stream and riparian ecosystems: questions, challenges, and perspectives. *Ecosphere* 2(11):122. doi:10.1890/ES11-00241.1
- Schoen, E.R., D.A. Beauchamp, and A.G. Hansen. 2012. Effects of turbidity on the foraging behavior and capture success of piscivorous juvenile Chinook salmon. Interim Report to USGS Cooperative Research Units Program. WACFWRU Report #2012-1. 17 pages.
- Vogel, J.L., and D.A. Beauchamp. 1999. Effects of light, prey size, and turbidity on reaction distances of lake trout (*Salvelinus namaycush*) to salmonid prey. *Canadian Journal of Fisheries and Aquatic Sciences* 56:1293-1297.

Table 1. The p-values (significant comparisons in bold type) for the main effects and interaction two-way ANOVA comparisons of light levels between nearshore v offshore and urban v non-urban regions within Puget Sound. Tests were conducted separately for surface, shallow and deep depths.

Variables	Surface	Shallow	Deep
Nearshore/Offshore	0.05920	0.00265	0.19476
Urbanization	0.00802	1.84e-05	0.00375
Interaction	0.61162	0.08577	0.20252

Table 2. Mean nocturnal search volumes (m³/h) and ratio comparisons for predatory Chinook for shallow (1-m) and deep (10-m) depths.

Chinook Search Volumes & ratio comparisons

	Shallow depth			Deep depth		
	Nearshore	Offshore	Near/Off=	Nearshore	Offshore	Near/Off
Urban	291.8	94.3	3.1	75.7	44.6	1.7
Non-Urban	46.3	51.3	0.9	30.3	34.1	0.9
Urban/Non=	6.3	1.8		2.5	1.3	

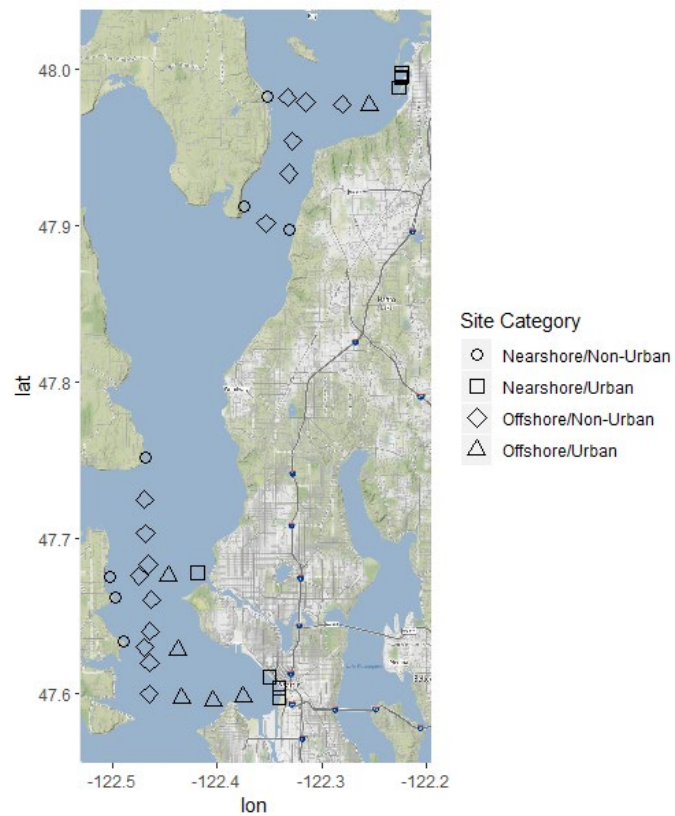


Figure 1. Nocturnal light survey locations in the Whidbey and Central Basins of Puget Sound. The shapes of the symbols represent habitat categories including nearshore (~30-m isobath) or offshore locations in Urban or Non-Urban regions.

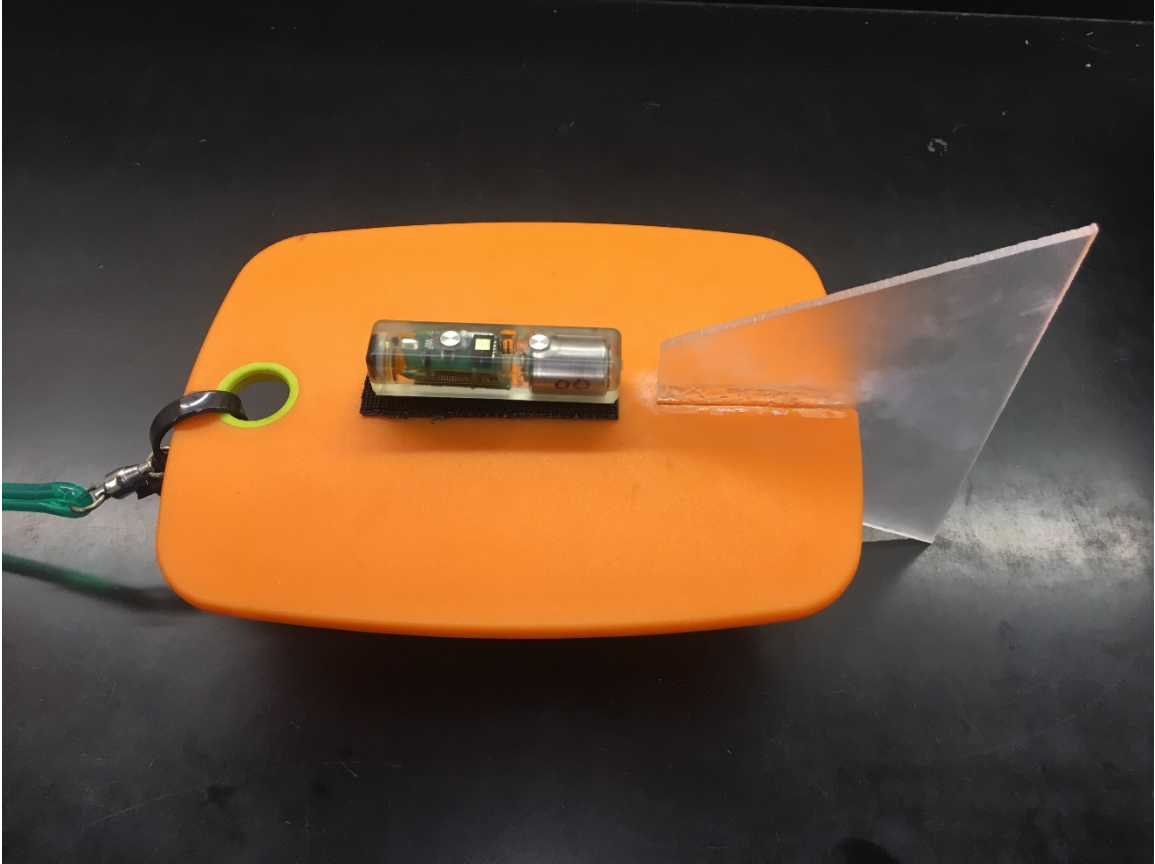


Figure 2. Tow fin with light sensing tag attached. The harness to the left is attached to a downrigger cable with a commercial trolling clip.

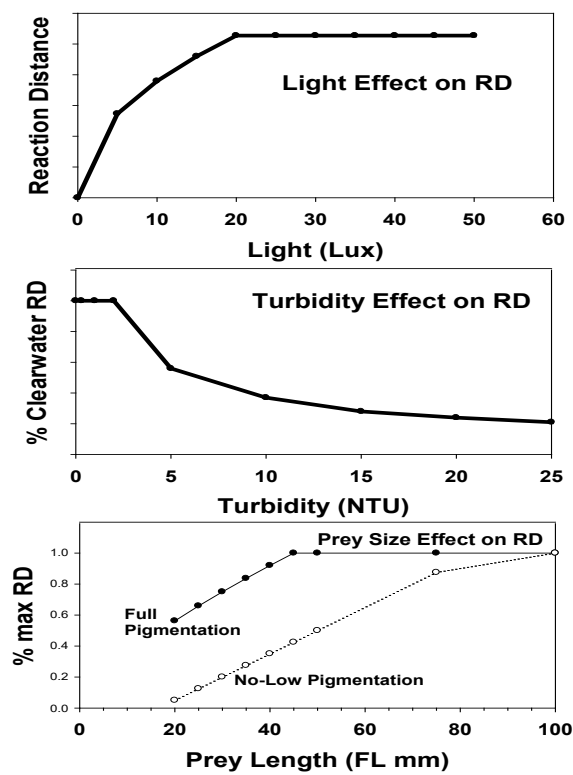
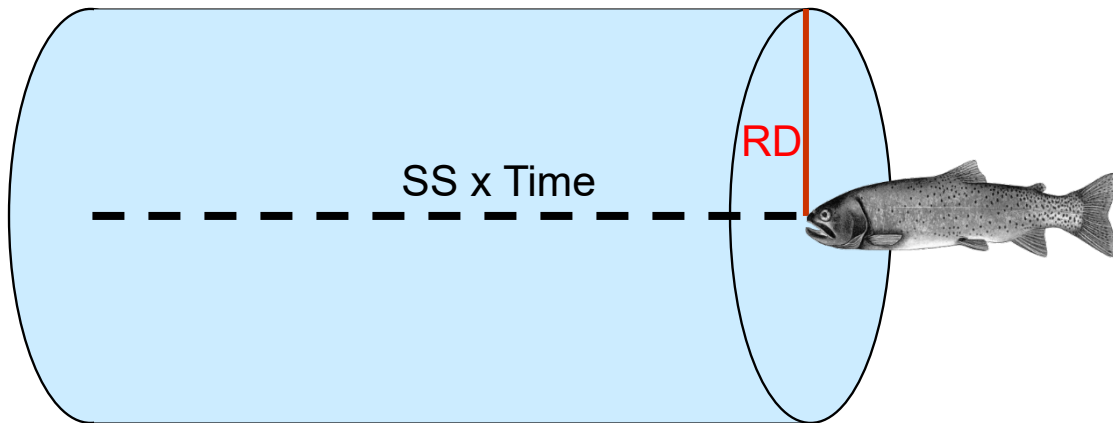


Figure 3. Schematic view of the estimated search volume ($SV \text{ m}^3/\text{h}$) of a piscivorous salmonid, wherein the radius of the cylindrical search volume RD is a squared reaction distance term which varies as functions of light level, turbidity, and prey size and pigmentation. Given the prevailing turbidity conditions and sizes of juvenile salmon in Puget Sound, the effect of light was the only relevant factor considered explicitly in this study.

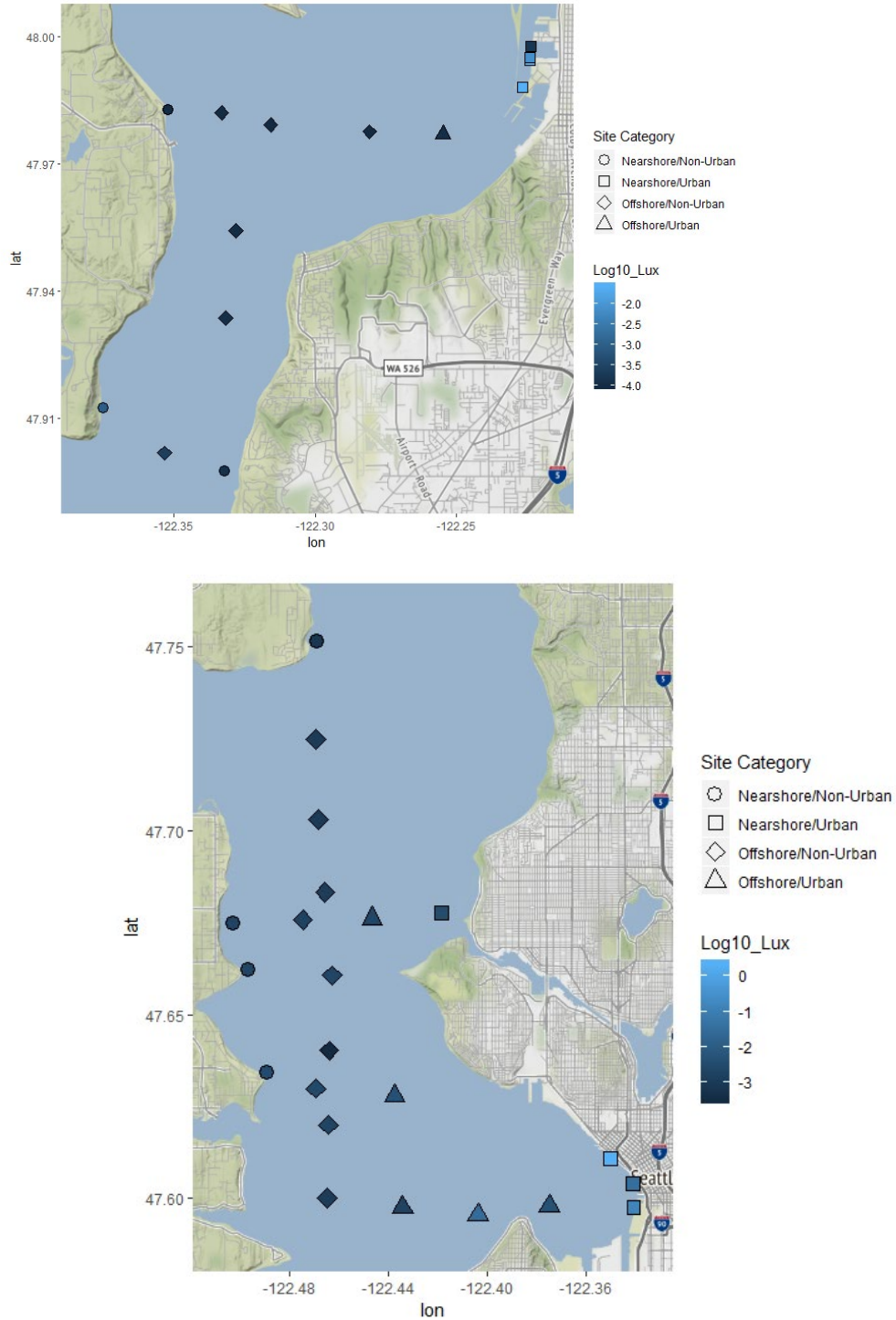


Figure 4. Light survey locations of nearshore and offshore light readings in urban and non-urban regions of (upper panel) the Whidbey Basin including Everett Harbor, and (lower panel) Central Puget Sound including Elliott bay and the Seattle Waterfront.

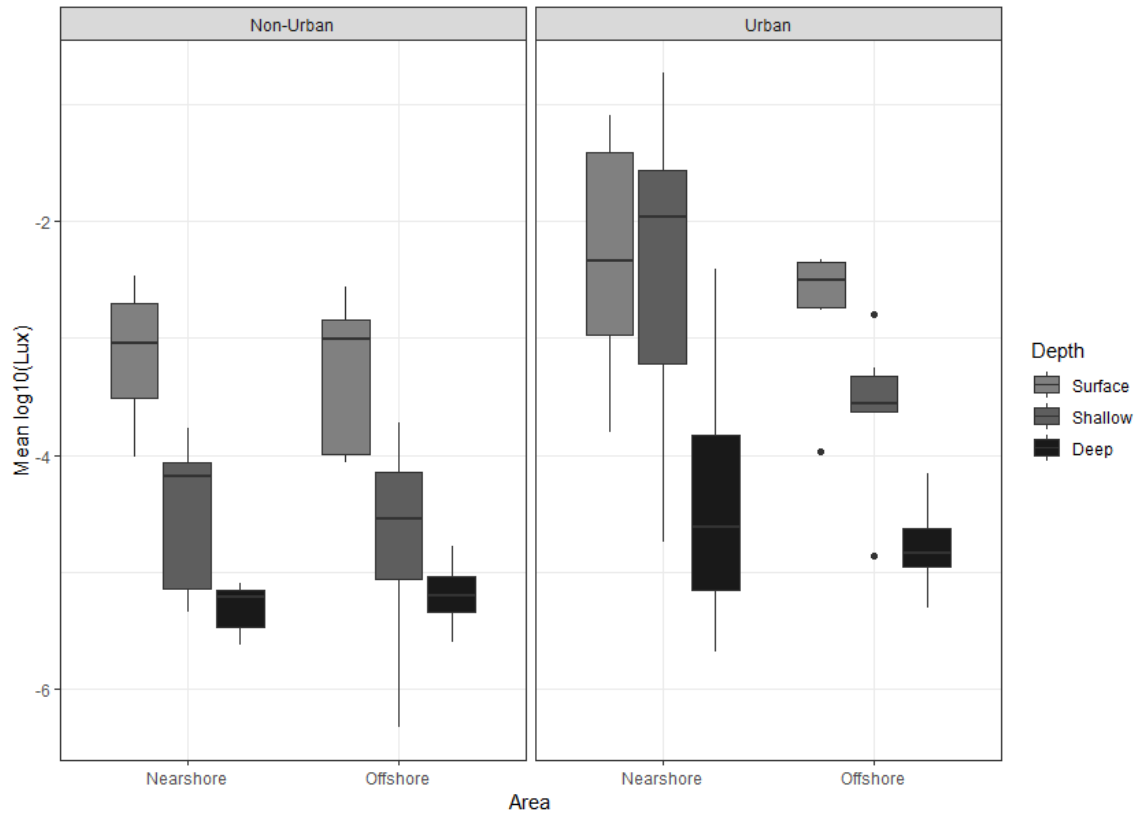


Figure 5. Depth-specific mean light log10(lux) for nearshore and offshore habitats in non-urban and urban regions.

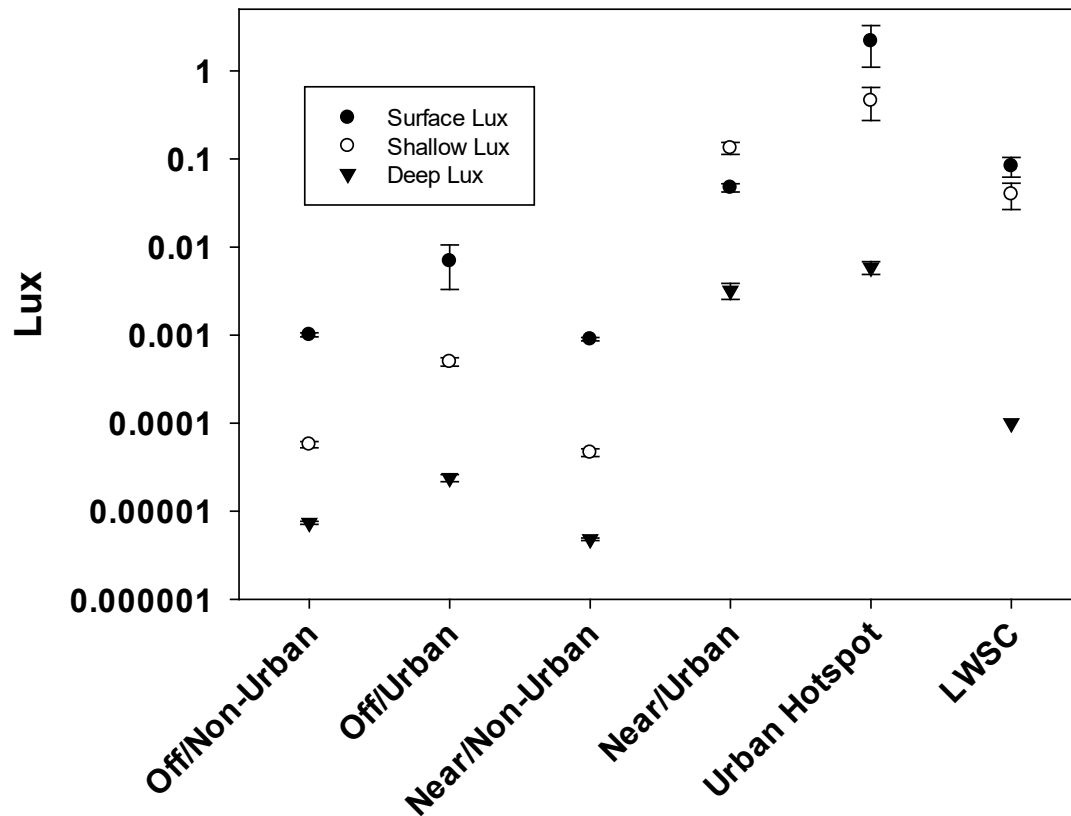


Figure 6. Depth-specific mean ($\pm 2SE$) nocturnal light levels in offshore and nearshore urbanized and non-urbanized habitats with the higher measurements associated with an urbanized waterfront hotspot separated from the other urbanized nearshore samples. Comparable measurements from a 400-m transect through the Lake Washington Ship Canal (LWSC) is included to represent light levels encountered through urbanized migration corridors for salmonid smolts.

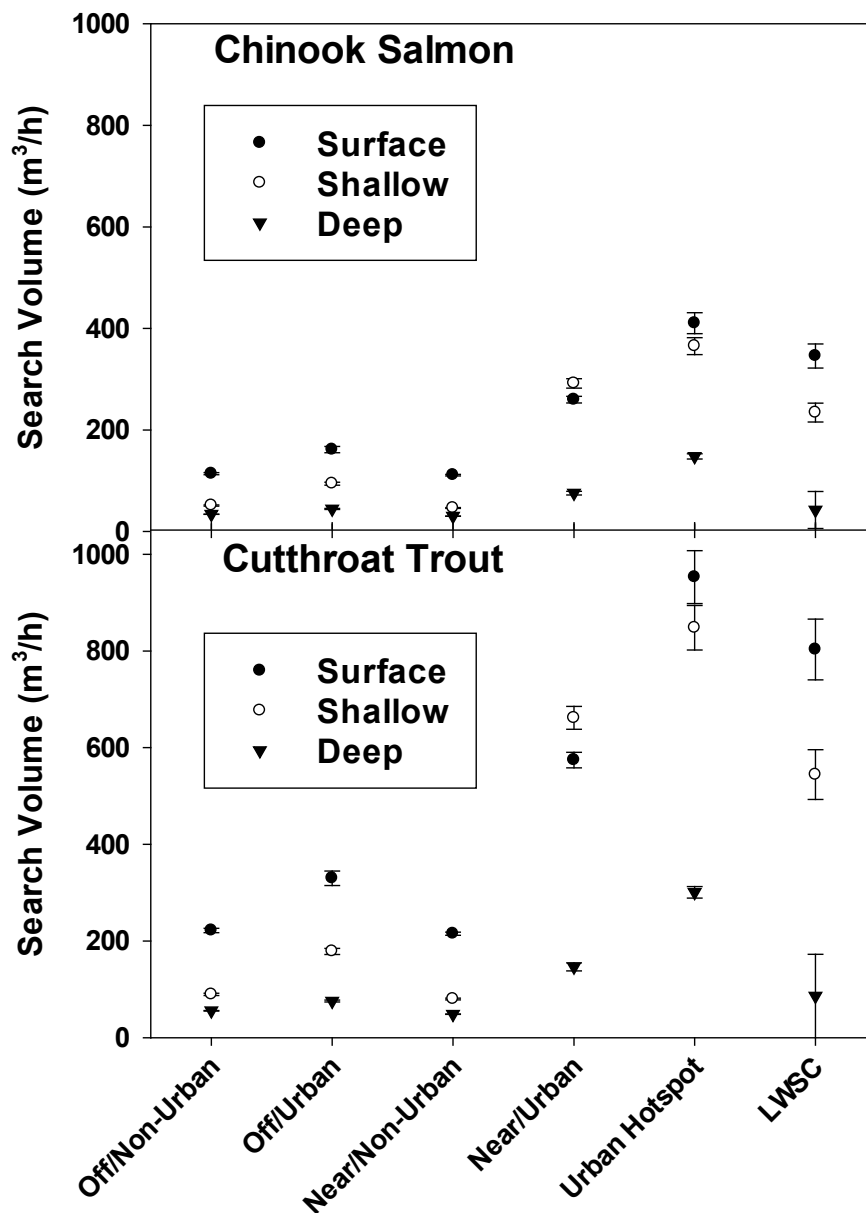
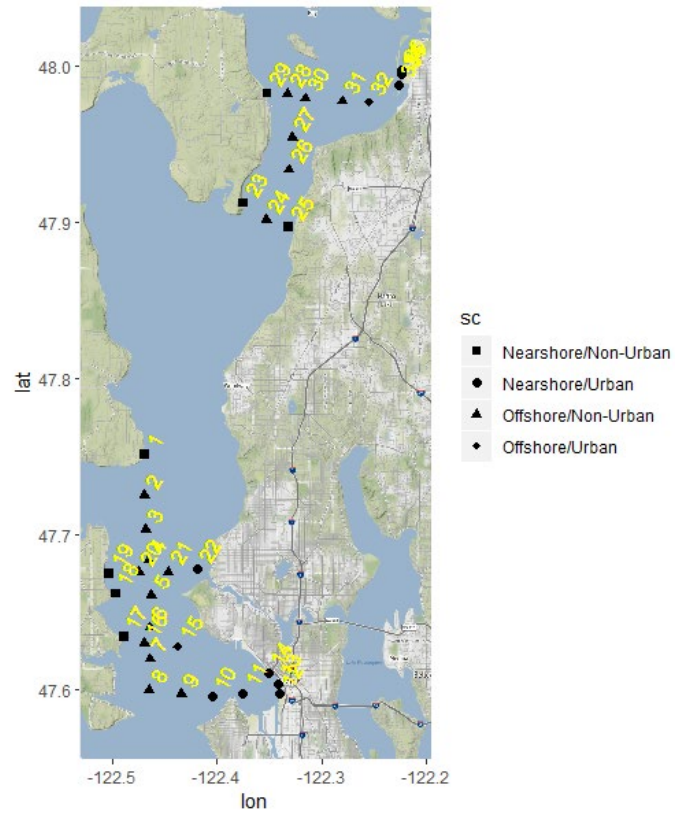


Figure 7. Estimated search volumes for piscivorous Chinook Salmon and Sea-run Cutthroat trout in urbanized and non-urbanized nearshore and offshore habitats, based on prevailing turbidities and nocturnal light levels. Depth-specific search volumes were computed separately for the general nearshore urban regions versus the waterfront associated with an urban waterfront hotspot. Comparable measurements from a 400-m transect through the Lake Washington Ship Canal (LWSC) is included to represent light levels encountered through urbanized migration corridors for salmonid smolts.

Appendix



Appendix Figure A1. Map of Puget Sound showing numbered sample sites measured in the Central Basin near Seattle (sites 1-22) and the Whidbey Basin near Everett (sites 23-36).