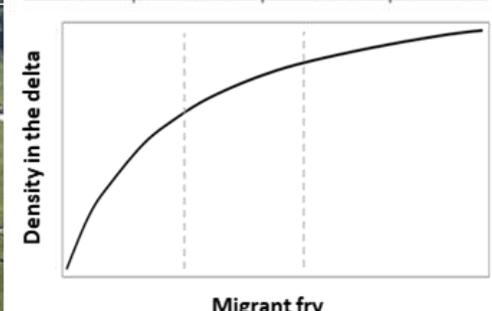
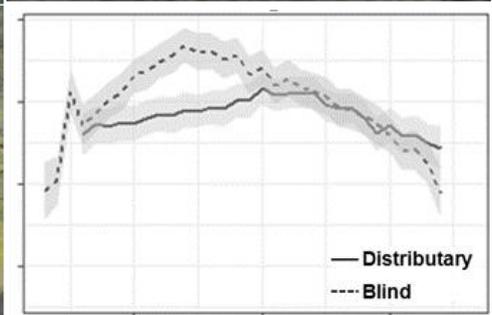


Landscape, density-dependent, and bioenergetic influences upon Chinook salmon in tidal delta habitats: Comparison of four Puget Sound estuaries



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1. Executive Summary

While it is well appreciated that juvenile Chinook salmon rely on estuaries for rearing during juvenile migration, several information gaps hamper effective science-based restoration and population recovery. To address these gaps, biologists and managers have generally proceeded in a geographically circumscribed framework, with the common refrain that “this is what Chinook do in our system.”

With the goal of developing general biological principles characterizing rearing conditions for natural-origin (NOr) juvenile Chinook that apply to a variety of estuaries, we examined fish-habitat relationships in four representative tidal river deltas of Puget Sound: the Nooksack, Skagit, Snohomish, and Nisqually (Fig. 1). The selected systems vary in landscape features and outmigrant population attributes (e.g., proportion of natural-origin vs. hatchery-origin or HOr juveniles), and thus represent the diverse characteristics we might expect in estuarine systems inhabited by juvenile Chinook across a broad geographic range within and beyond Puget Sound.

We address three issues: how does landscape structure affect juvenile Chinook salmon distribution and abundance in tidal deltas, how common are habitat limitations (i.e., density dependence), and under what conditions do fish experience growth variability and food limitation in delta wetlands? These questions underlie whether estuary habitat restoration is likely to benefit Chinook salmon populations, and thereby will facilitate recovery from listed status.

Landscape attributes (Chapter 2)

Using long-term records from beach seine and fyke trapping, we evaluated three potential landscape-based drivers of NOr and HOr juvenile Chinook abundance within estuaries: landscape connectivity, wetland habitat type, and channel type. Landscape connectivity quantifies habitat access/opportunity to a particular site by summarizing position of sites along pathways comprised of varying channel size (width), distance, and complexity. Wetland habitat types consisted of forested riverine tidal (FRT), estuarine forest transition (EFT), and estuarine emergent marsh (EEM). Channel types were either river delta distributaries or off-channel environments such as blind tidal channels or impoundments.

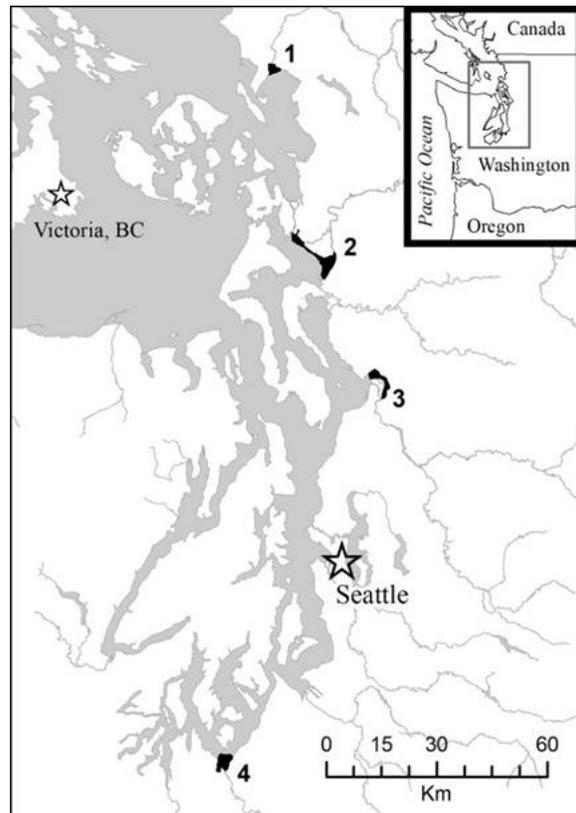


Figure 1. Locations of the Nooksack (1), Skagit (2), Snohomish (3), and Nisqually (4) deltas (numbered black polygons).

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NOr migrants. Statistical analysis revealed that NOr presence/absence depended on delta system, week, channel type, and the interaction between channel type and delta system (Fig 2.5). While NOr presence in the delta was unaffected by other landscape attributes, NOr density (when present) increased with higher connectivity, was greater in blind tidal channels than distributaries, and declined with increasing marine influence: density in FRT > EFT > EEM wetland habitats. Channel type and wetland habitat type interacted with week, reflecting movement of fish through the delta landscape during their seaward migration, from FRT to EEM habitats and from blind channel rearing to system emigration via distributaries. Overall, the significant effects explain ~62% of the model deviation, but system effects (Skagit vs. Snohomish vs. Nooksack vs. Nisqually) also interacted with the other variables, reflecting system differences in outmigration population structure and habitat availability. For example, the Nooksack is dominated by relatively large and physiologically mature parr outmigrants that spend little time rearing in tidal marshes; the Skagit and Snohomish are dominated by relatively small fry outmigrants that rear extensively in blind tidal channels and transition more slowly through the wetland habitat types. Additionally, the Nooksack Delta has relatively little blind channel habitat, requiring more rearing in distributaries. Thus, NOr fish were more common in blind tidal channels than distributaries in the Skagit and Snohomish Deltas, while the reverse was true in the Nooksack Delta. There was no channel type difference in the Nisqually Delta.

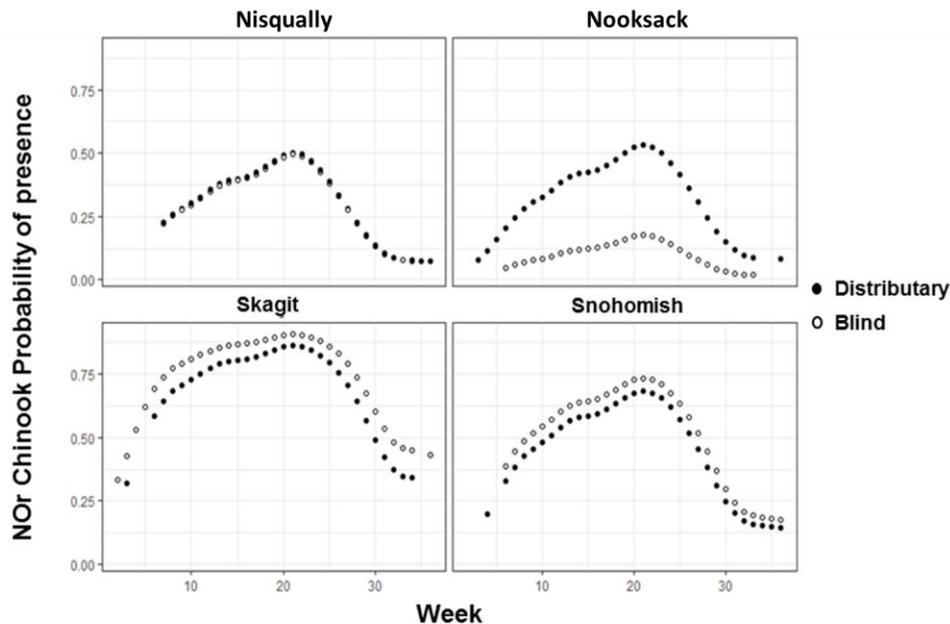


Figure 2.5. Best model fit outputs for the probability of presence of NOr juvenile Chinook by system, week, and channel type.

HOr migrants. HOr presence/absence depended on delta system, week, channel type, and the interaction between channel type and delta system (Fig. 2.6). The Skagit Delta had the lowest probability of HOr migrant presence and the Nisqually Delta the highest, in accordance with their respective hatchery releases. The Skagit, Nisqually, and Nooksack deltas had higher probability of HOr migrants in distributaries than in blind channels. Most HOr individuals resemble NOr parr in size and migration timing, so higher HOr presence in distributaries reflected their strong migratory tendency. However, Snohomish HOr juveniles were more likely

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to be present in blind channels than distributaries and may reflect out-of-system fish using blind channel habitat in the lower delta.

HOr density (when present) was dominated by the week*system interaction, reflecting system differences in release timing and abundance of hatchery fish. Other significant effects in decreasing order of importance were year, connectivity, week*channel type, and week*wetland type. The significant effects explained ~40% of the model's deviance. Because they migrate quickly through deltas, HOr migrants were likely less influenced by connectivity than NOR individuals.

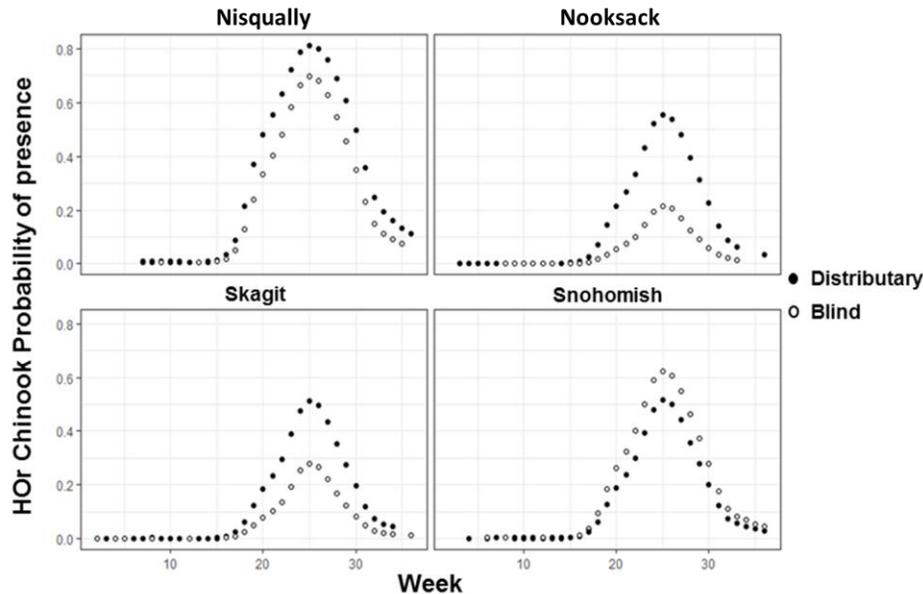


Figure 2.6. Best model fit outputs for the probability of presence of HOr juvenile Chinook by system, week, and channel type.

Density dependence (Chapter 3)

Previous analysis has shown that juvenile Chinook in the Skagit Delta experience density-dependent consequences of limited habitat availability. How general is this phenomenon in other Puget Sound river deltas that vary in outmigration size as well as tidal wetland habitat area? To compare density dependence among the Skagit and the Nooksack, Snohomish, and Nisqually deltas, we scaled NOR outmigrants by total tidal wetland channel area, i.e., distributaries plus blind tidal channels, and combined data from all four systems into a stock-recruit analysis at the level of individual sampling events. This enabled us to detect when density might exceed predicted capacity at an instantaneous level, and to use this relationship to determine seasonal and landscape patterns of density dependence.

We examined three questions: 1) How does density dependence vary across the landscape (e.g. systems and wetland types)? 2) How frequently is tidal delta carrying capacity exceeded? 3) How do landscape variables affect the frequency of extremely high densities?

Variation in presence and density. Variation in presence of NOR juveniles and density when present was largely independent of outmigration size, even at the highest outmigration sizes. Presence generally showed strong stability within systems, such that 25-90% of sampling

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attempts captured 0 Chinook salmon even during the highest outmigrations. Variation in log-transformed density also was fairly similar across the range of different outmigrations. These results imply substantial variation in local densities across the range of outmigration sizes. These results refute the notion that tidal delta habitats “completely fill” with juveniles at high outmigration sizes, suggesting a re-evaluation of the concept of habitat capacity.

We also observed substantial overlap between presence of NOR and HOR salmon during management weeks associated with hatchery releases. Within the subset of observations in which either NOR or HOR juveniles were present, the proportion of observations exhibiting co-occurrence peaked between weeks 17 and 36 in all four systems, significantly overlapping NOR residence (weeks 10-27). Furthermore, the duration and peak level of co-occurrence varied by system, with Nisqually showing the largest co-occurrence and Skagit exhibiting the least. Hence, NOR and HOR fish considerably overlapped in time and space between one quarter to over half of the typical NOR rearing period.

Delta system patterns. We evaluated system scale density dependence by combining data from all systems. A Beverton-Holt model with all systems included revealed strong evidence for density dependence compared to the density independent model, and also included a moderate effect of landscape connectivity. This model predicted habitat capacity at 252.7 fish/ha when connectivity was held constant at 0. A “leave-one-system-out” sensitivity analysis revealed that stock-recruit parameter estimates did not depend on any single delta system.

Habitat differences. At the habitat scale, we examined whether models summarizing data from particular wetland (FRT, EFT, EEM) or channel types (distributary, blind) explained the data better than a single model estimated across all systems and habitat types. All models produced strong density-dependent relationships ($p < 0.001$). Model comparison using AIC indicated the strongest support for a single stock-recruit function, and 50% less support for models with multiple curves for either wetland type or channel type. Those models were nevertheless informative, and predicted the combined FRT and EFT wetland type to have a higher capacity than EEM (480 vs 175 fish/ha, respectively) and revealed blind channel sites to have a higher capacity compared to distributaries (260 vs 249 fish/ha, respectively), respectively. Models that included separate relationships for all four wetland and channel type combinations received much less support (probability = 0.03).

Frequency of capacity exceedance. We examined the predicted probability of the four systems to approach carrying capacity by comparing individual observations in each year to the 95% level of carrying capacity estimated in the best model. We used the best Beverton-Holt function to evaluate where and when densities exceeded 95% of predicted capacity (240 fish/ha) across systems, and to what degree HOR fish increased densities above capacity. The results indicated that local densities surpassed capacity in every system in almost every year, although patterns varied substantially among systems. Tidal delta capacity exceedance ranged from < 20% of observations in the Nisqually Delta to > 60% in the Skagit Delta. Regardless of system, observations of NOR migrants exceeding 95% capacity were twice as likely during weeks 13-27 (March 24 – June 30) than at other times. The timing of highest density values varied by system, with the Skagit exhibiting high densities prior to week 20 (May) (primarily due to NOR migrant fry), while Nooksack and Snohomish peaked between weeks 20 (May) and 26 (June)(primarily

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due to NOr migrant parr). HOr fish increased the exceedance frequency between weeks 17-30 (April 21-July 21), although the effect was system-dependent; HOr migrants had a negligible effect in the Skagit delta, but tripled exceedance frequency in certain weeks in the Nisqually.

Frequency of capacity exceedance varied by wetland and channel type, although there were system differences (Fig. 3.6). In the Skagit and Snohomish deltas, FRT and EFT sites were more likely to exceed capacity than EEM sites, as were blind channels compared to distributaries. In contrast, in the Nooksack and Nisqually deltas, distributaries were more likely to exceed capacity than blind channels. Hatchery fish increased habitat-specific exceedance frequency mostly in the Snohomish and Nisqually deltas, but these increases were small compared to seasonal increases. HOr fish increased system-scale annual exceedance frequencies by 4-50% in the Snohomish, and by 0-100% in the Nisqually, depending on the year. Annual differences in total subyearling outmigrants accounted for much of the observed differences in exceedance frequency among systems. The annual exceedance frequency of 95% capacity was strongly linked to total outmigration densities among deltas and resembled a stock-recruit curve itself (Fig. 3.8).

Observed local densities often exceeded the 95% capacity predicted by the Beverton-Holt model. One explanation may be that the cost of emigrating from high-density rearing environments (greater predation risk, physiological stress) may be greater than the cost of enduring competition for food (slower growth). To evaluate variation in extreme densities, we examined the 90th and 95th quantiles of local densities in the four deltas. These values ranged from 2,040 to 4,267 fish/ha when considering just NOr juveniles, and 2,335 to 4,841 fish/ha for total density (NOr and HOr fish), which was 10-20 times higher than habitat capacity predicted by the Beverton-Holt model. Blind channel sites had approximately twice the extreme density as distributaries, and as did FRT and EFT wetland sites compared to EEM sites.

This analysis shows that reduced tidal wetland habitat in large river deltas is limiting juvenile Chinook salmon recruitment by imposing density dependence. The four deltas we examined exist on a spectrum of density dependence within and between years; local densities in the Skagit, with its large population of NOr subyearling outmigrants, regularly exceed capacity, while the Nisqually does so only occasionally each year, primarily when large numbers of HOr fish are released. These results suggests tidal wetland restoration will reduce early rearing bottlenecks for juvenile Chinook migrating into Puget Sound, and that both habitat restoration and hatchery management strategies can work in concert to improve rearing conditions.

However, due to the broad range of outmigration sizes in these four systems, we should not expect a uniform response to habitat restoration. Small outmigration population sizes, relative to extant delta channel rearing area, may show more muted responses to restoration than high outmigration populations. Conversely, systems at capacity may nonetheless exhibit strong patchiness, potentially confounding a restoration response if not systematically sampled.

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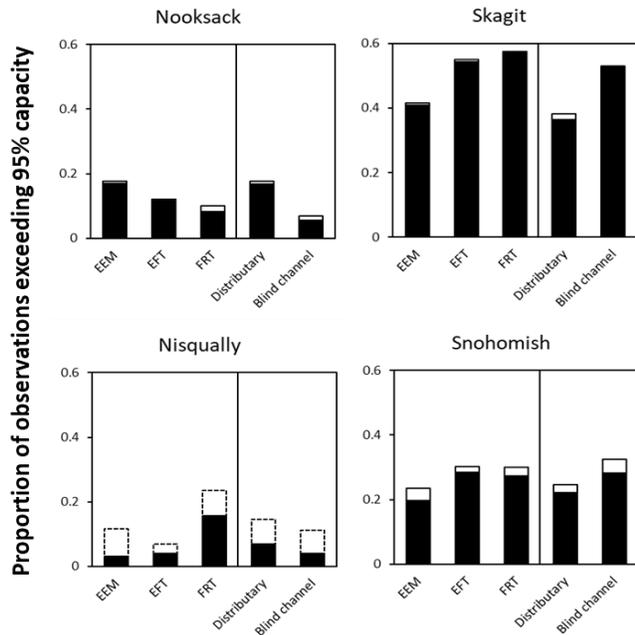


Figure 3.6. Proportion of observations exceeding 95% predicted capacity of the Beverton-Holt model in the Nooksack, Skagit, Snohomish, and Nisqually deltas, summed across either wetland type (EEM = estuarine emergent marsh, EFT = estuarine forest transition FRT = forested riverine tidal) or channel type (distributary or blind channel). Black bars represent exceedance frequency associated with NOr fish only; white bars account for increased exceedance from HOR fish.

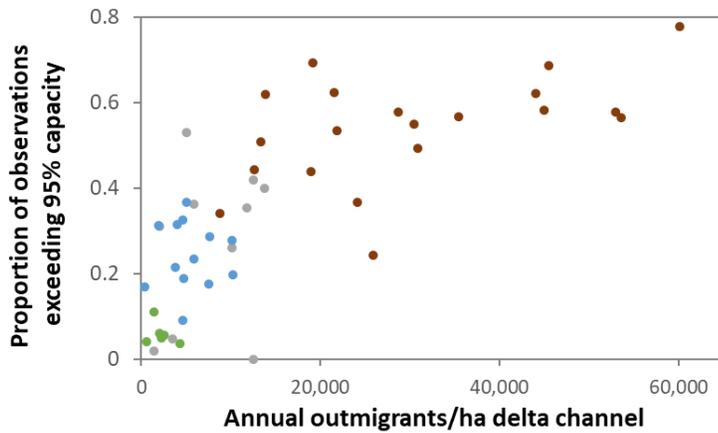


Figure 3.8. Annual proportion of observations in the four tidal deltas (orange = Skagit, blue = Snohomish, gray = Nooksack, green = Nisqually) exceeding 95% of capacity predicted by a Beverton-Holt model as a function of the annual outmigration density of NOr subyearling migrants/ha of delta channel area.

Bioenergetics of different habitat types (Chapter 4)

We used bioenergetic models to evaluate individual growth among wetland habitats and to quantify food limitations within systems (i.e. consumption demand). Inputs to the bioenergetics models included ambient temperature, weekly estimates of NOr migrant fry and parr abundance and HOR releases, fish sizes and diets. Unlike bioenergetic models that examine snapshots of the population entering at different times in the season, our modeling framework incorporated temporal dynamics of fish cohorts migrating into deltas throughout the season to reflect seasonal and life-history specific variation in size at delta entry and abundance.

Additionally, we compared predicted growth patterns with observed patterns of growth in the Skagit and Snohomish as determined from otolith microstructure analysis (Appendix 4.3). Otolith microstructure revealed that growth rates determined by the bioenergetics model were in line with actual growth rates, and that growth pattern depended upon arrival date and size as assumed in the model.

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Wetland-specific growth. Mean growth potential was highest in FRT wetlands early in the outmigration period while mean growth potential in EFT wetlands was higher later (Fig. 4.4). Individual growth opportunity was highly dynamic and varied considerably among wetland types for fish entering the estuary during different periods. Diets did not accurately reflect the prey assemblage available to juvenile fish in any wetland type or system. Among the wetland types, FRT had the least overlap between prey and diet samples (mean = 8.75%), while EFT had the most (mean = 14.35%). Salmon diets, when averaged by system or wetland type, always had higher proportion of insects than the associated prey availability samples. Insects ranged from 46.8-94.3% and 70.4-90.1% of individual diets by system and wetland type, respectively. In contrast, the percentage of insects in prey availability samples never surpassed 35% among systems or wetland types.

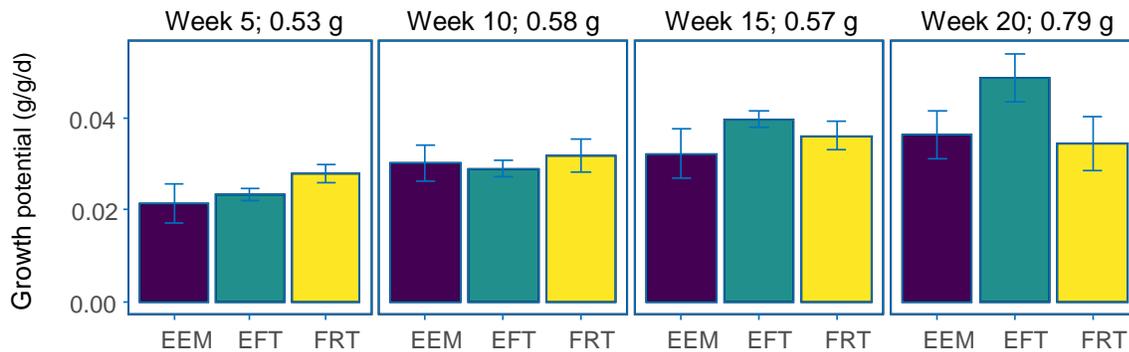


Figure 4.4. Mean growth potential (growth per unit body weight per day) estimated by the bioenergetics model by wetland types. Cohorts are labeled with the week and size at entry to the estuary.

The main finding from the bioenergetics model was that diet energy density among wetland types was variable throughout the rearing period; each wetland type offered high growth conditions at some point in time. General trends across the rearing period suggested freshwater wetlands (FRT) are more beneficial early in the season, while marine-influenced environments (EEM) afford higher estimated growth potential as the season advanced. These results indicate that wetland habitat diversity in tidal deltas is important to maximize growth opportunity for juvenile salmon across the full outmigration period.

Consumption demand. Consumption estimates from bioenergetics models were scaled to the populations and compared to prey availability to examine potential food limitations. Consumption in the Skagit tidal delta was generally 2x higher than the Snohomish and 3.5 to 10x higher than the Nooksack or Nisqually, respectively. Peak consumption in the Skagit and Snohomish deltas also occurred earlier in the season (Mid-April) than either the Nisqually or Nooksack deltas (early May). Consumption in the Skagit and Snohomish tidal deltas was largely dominated by NOr fry between weeks 5-22 (i.e. Feb- May) before switching to NOr parr and/or HOr migrant consumption throughout the remainder of the season.

The ratio between prey availability and consumption demand approached 1 (i.e., consumption and prey availability are equal) in the Skagit and Snohomish tidal deltas beginning in early April and continued through late May (Fig. 4.7). In contrast, the ratio was lowest in the Nooksack and

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Nisqually for a much shorter period, and prey availability was never less than 10x that of consumption demand. Consumption by HOr salmon accounted for 50-100% of total consumption in each system soon after they are initially encountered in the estuary. Increased hatchery production under current release strategies would increase the estimated consumption in tidal deltas where this occurred. Should increased consumption regularly surpass available energy, hatchery releases could negatively impact both NOr and HOr groups and be

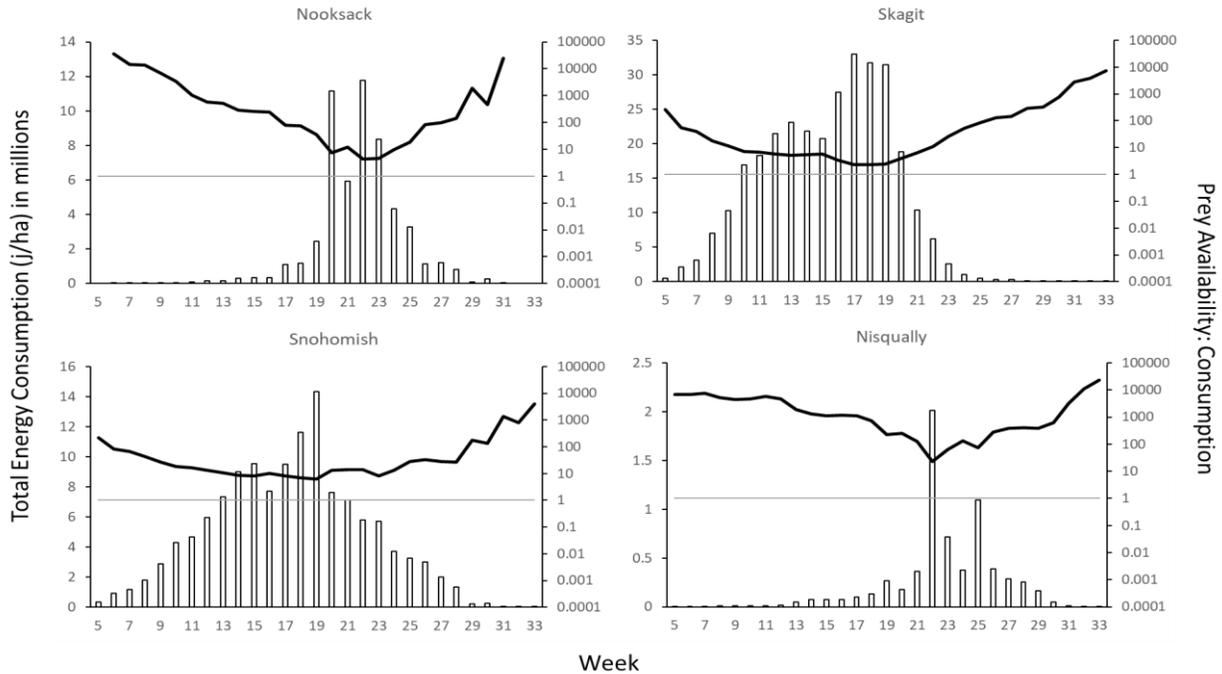


Figure 4.7. Total energy consumption (NOr fry + NOr parr + HOr) by week (bars; primary y-axis), and the ratio of consumption demand to prey energy availability (lines; secondary y-axis). Note the differences in primary y-axis scale for each delta. Grey line at value of 1 (secondary y-axis) represents equality between consumption demand and prey energy availability. Values higher than 1 indicate prey energy availability higher than consumption demand.

counterproductive to recovery of NOr populations as well as predators such as Southern resident orca whales. Evaluating release strategies that minimize prey competition between NOr and HOr juvenile Chinook salmon in large river deltas may offer solutions for maintaining productive estuarine habitats for both NOr and HOr migrants.

Although consumption demand did not outpace prey energy availability under our selected model conditions in any of the four tidal deltas, it is important to consider how changes in thermal conditions and population size may alter the results. For example, increased abundances and/or temperatures would influence consumption and metabolic processes, respectively, with potential consequences for individual growth. This conclusion is also supported by results from archived otolith microstructure illustrating that strong density-dependent patterns of growth exist in certain years (Appendix 4.3).

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Lastly, because the analysis focused on the bioenergetics of only a single species, the roles of other consumers and their prey preferences could not be considered. Many other estuarine fish, some considerably more abundant than juvenile Chinook salmon, may consume available invertebrate prey, and are not accounted for in the current model. Thus, our modeling effort provides a conservative estimate of bioenergetic constraints on growth of outmigrants in river delta marshes. A more complete evaluation would require a community ecology perspective.

Prey/Diet similarity. We calculated the degree of overlap between prey field samples and diet composition of individual Chinook salmon across systems and wetland types and evaluated how changes in local density and/or individual size (fork length) may influence prey selectivity. We assumed low similarity values between prey field samples and diets suggested a higher degree of selectivity and hypothesized that increasing local Chinook density may increase prey/diet similarity thus reducing selectivity. Although the variability in prey/diet similarity was considerable, prey/diet similarity increased with Chinook salmon density (NOr + HOr). This pattern was consistent across all four tidal deltas, and suggests that as demand for food resources increases, some individuals must reduce prey selectivity. Reduced selectivity may require individuals to feed on less desirable prey, potentially reducing the overall energetic quality of individual diets. While increased diet diversity resulting from relaxed selectivity may help to compensate for lack of preferred prey, such changes to foraging strategy likely come with increased metabolic costs that may make individuals more susceptible to changes in thermal conditions relative to growth opportunity. Further investigation of the potential implications of foraging strategy on growth are warranted.

Implications for science-based restoration and recovery planning

Our studies provide a broad array of conclusions that can improve restoration for juvenile Chinook salmon in estuaries:

- Implement restoration that increases landscape connectivity, allowing juvenile Chinook to access otherwise inaccessible tidal marsh.
- Emphasize restoration of blind channels, given their observed importance to NOr fish.
- Manage for a restoration portfolio of habitat types that provide different benefits in different years and throughout the rearing period. These benefits derive from variability not only in temperature but also inputs of terrestrial, freshwater, and marine prey. Different analytical techniques (patterns of habitat use, capacity estimates, bioenergetics model results, diet overlap, and otolith microstructure) did not point to one wetland type as “optimal”, and suggested that the contributions of different wetlands to growth and survival is dynamic. Addressing restoration from a portfolio perspective may provide improved resilience to climate impacts such as sea level rise and temperature increases.
- Re-evaluate the concept of restoring estuary habitat capacity. Habitat restoration is often gauged from the perspective of increasing capacity, an important concept when large outmigrations relative to habitat opportunity are common. While all four systems exhibited densities exceeding capacity at some times in most years, two of the four systems examined did not often see these high levels of density except in the context of large, pulsed hatchery releases. Even when outmigration levels predicted capacity exceedance, both probability of presence and density when present were highly variable (Chapter 3), indicating that the concept of capacity does not equate to “complete filling”

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of rearing opportunities within a system. Juvenile Chinook may tolerate particularly high densities despite the fact that these levels negatively affect growth (Appendix 4.3) and prey selectivity (Chapter 4), potentially pointing to the dual roles of estuary wetlands as predator refugia and hotspots for growth.

- Investigate in more detail the potential role of various aspects of hatchery releases (e.g., number released, individual size, or timing or location of releases) in affecting NOr juveniles residing in estuaries. Our analyses suggest that large hatchery releases may increase the likelihood of systems to exceed capacity (Chapter 3) and increase competition for preferred prey (Chapter 4), but better documentation of potential causes is warranted.
- Utilizing findings from this study, we provide a decision framework to help managers select appropriate estuary habitat strategies for any specific estuary system for Puget Sound Chinook Salmon (Figure 3.11). We suggest three restoration strategies are possible in light of current and desired future condition (DFC) of estuary habitat and juvenile Chinook salmon populations in a system.
 1. Strategy 1 (*maintain current habitat conditions*) makes sense for a system where (a) the current juvenile Chinook salmon outmigration is within the range of its DFC, (b) the current outmigration does not exceed the indicators for density dependence in the estuary derived from this study, and (c) the current estuary is well connected and diverse in terms of wetland and channel type complexity. Estuaries that fit this strategy would essentially be pristine areas with Chinook salmon populations (NOr and HOr) at current (or DFC) levels where density dependence pressures within the estuary does not occur.
 2. Strategy 2 (*restore habitat connectivity and diversity*) makes sense for a system where (a) the current juvenile Chinook salmon (NOr and HOr) outmigration is within the range of its DFC, (b) the current outmigration does not exceed the indicators for density dependence in the estuary derived from this study, but (c) the current estuary is not well connected and/or not diverse in terms of wetland and channel complexity. Estuaries that fit this strategy have reduced habitat extent but their Chinook salmon populations don't exhibit regular density dependence pressures within the estuary. Because the current (or DFC) population generally does not express density dependence conditions, habitat restoration within these estuaries does not need to focus on restoring vast areas (i.e., capacity) but should work toward restoring connectivity and the diversity of wetland types and channel types within the estuary which will support resilience in the face of extrinsic pressures such as climate change.
 3. Strategy 3 (*restore habitat capacity, connectivity and diversity*) makes sense for a system where the current or DFC outmigration levels exceed the indicators for density dependence in the estuary derived from this study. Estuaries that fit this strategy have reduced habitat extent and their Chinook salmon populations regularly exhibit density dependence within the estuary. Because of this, habitat restoration within these estuaries needs to focus on restoring large areas (i.e., capacity) as well as connectivity and diversity of wetland types and channel types within the estuary.

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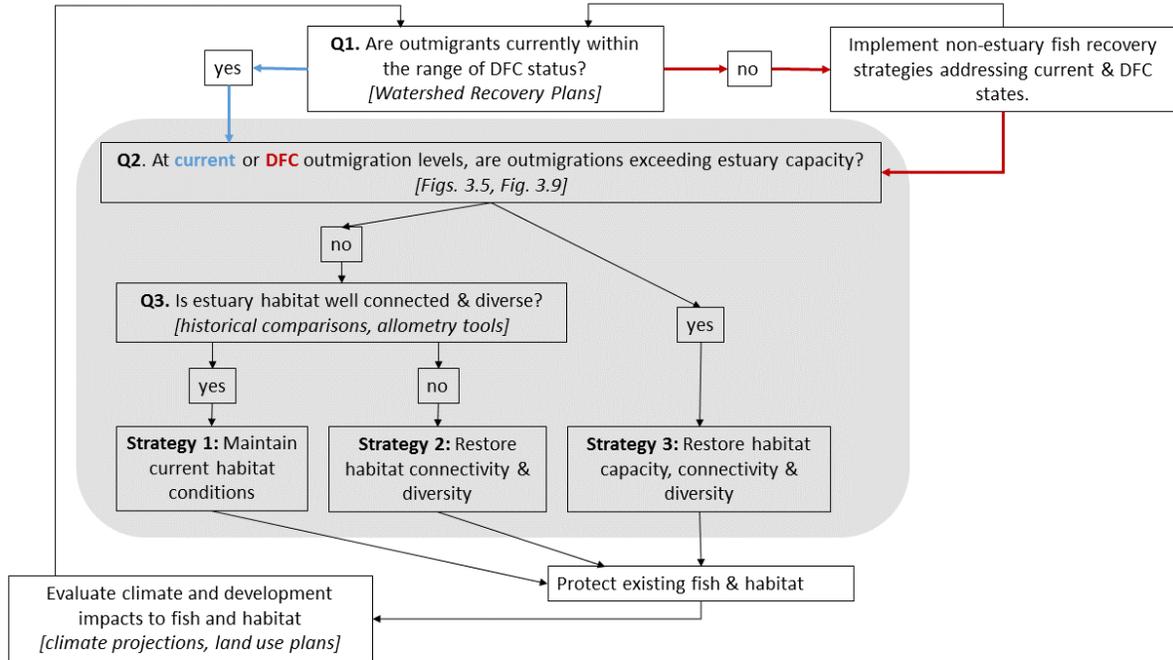


Figure 3.11. Decision diagram to evaluate what restoration strategy is appropriate for a specific estuary system for Puget Sound Chinook Salmon when populations are at current (blue arrows) or desired future conditions (DFC, red arrows), which can be addressed in parallel. The gray shaded area represents content developed within the scope of this study, and example diagnostic tools to answer questions are shown within brackets in italic. See Chapter 3 for more details.

2. Landscape determinants of estuarine river delta habitat use by juvenile wild and hatchery origin Chinook salmon (*Oncorhynchus tshawytscha*)

Eric Beamer^{1*}, Correigh Greene², Joshua Chamberlin³, W. Gregory Hood¹, Chris Ellings⁴, Sayre Hodgson⁴, and Todd Zackey⁵

*To whom correspondence should be addressed

¹ Skagit River System Cooperative, PO Box 368, LaConner WA, 98257, ebeamer@skagitcoop.org

² Fish Ecology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd E, Seattle WA, 98112, USA

³ Fish Ecology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, NOAA, Mukilteo Station, Mukilteo, WA, 98275, USA

⁴ Nisqually Indian Tribe, Department of Natural Resources, 12501 Yelm Highway Southeast, Olympia, WA 98513, USA

⁵ Tulalip Tribes, 7515 Totem Beach Road, Tulalip WA, 98271, USA

Keywords

Chinook salmon, landscape connectivity, river deltas

Abstract

To improve habitat restoration planning and design for threatened species, science from monitoring efforts can help inform what habitat features are important to populations. We examined how landscape structure influences habitat use by juvenile natural origin (NOr) and hatchery origin (HOr) Chinook salmon in four river deltas. Using long-term records from beach seine and fyke trapping, we modelled how landscape characteristics (distributary vs. blind channel types, three wetland vegetation communities, and a channel network connectivity index) influenced juvenile salmon densities. We used two-stage general additive models for zero-inflated data; the first stage estimated probability of a non-zero response, while the second stage used positive (fish present) density values to model biweekly local density. All candidate models included the terms, “Week”, “System” and “Year” to account for seasonal trends, differences between deltas, and inter-annual variation.

We found substantial evidence that landscape features structured habitat use by juvenile Chinook salmon. Models detected strong effects of estuary system, landscape connectivity, and channel type on either presence/absence or density or both responses, although the directionality and relative importance of these features differed among NOr and HOr fish. For NOr fish, system and landscape connectivity were the strongest and second strongest predictors of density,

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respectively, and channel type was a strong predictor of presence/absence. Wetland type exhibited the least predicted power. The rank order of landscape predictors was similar for HOr fish, but some strong differences existed. Notably, while NOr fish presence was positively associated with blind channels, HOr fish presence was positively associated with distributaries. In addition, while interannual differences were stronger for NOr juveniles, seasonal pattern was much stronger for HOr fish and was in fact the strongest predictor of density. For both types of fish, interactions of habitat factors existed with seasonal pattern, indicating habitat utilization changed dynamically from the beginning to the end of the rearing period. FRT and EFT habitats had higher NOr densities earlier in the year whereas EEM habitats had higher densities late in the season. The pattern was less discernible for HOr juvenile and suggested EEM habitat had higher densities from the beginning of the outmigration through the peak prior to decreasing in all wetland types.

These findings have important implications for habitat restoration. Landscape connectivity was the most significant landscape influence. Recognizing that low connectivity sites have fewer fish than high connectivity sites, we should prioritize high connectivity sites for habitat restoration and use connectivity as a covariate to compare restoration sites to reference sites. Connectivity restoration itself (e.g., reconnecting historical distributaries) can improve fish productivity by allowing access to previously isolated productive marsh, including blind channels, which emerged as important sites for residence by NOr juveniles.

Introduction

Ecologists studying habitat relationships for fish and other aquatic species have long recognized the importance of large-scale geology and geomorphology in creating suitable habitat at smaller spatial scales. River-resident fish respond to many hydrogeographic elements in their aquatic realm, including but not limited to temperature, velocity, depth, and substrate at small spatial and temporal scales (e.g., Freeman et al. 2001, Beechie et al 2005), and channel structure, connectivity, and geomorphology at large spatial and temporal scales (Angermeier and Winston 1999, Fausch et al. 2002).

Estuarine fish presumably also respond to local and landscape-scale influences on their movements. However, most estuarine studies have focused on local-scale influences, e.g., how local abiotic and biotic features such as depth, temperature, salinity, dissolved oxygen, vegetation, or prey availability influence abundance and diversity of estuarine fish species (Beck et al. 2001, Craig and Crowder 2002, Akin et al. 2005, Granados-Dieseldorff and Baltz 2008). Fewer studies have documented how landscape factors influence estuarine fish distributions, despite evidence that landscape processes such as tidal and fluvial dynamics, structural habitat features such as wetland vegetation (Ewing 1986, Sanderson et al. 2000, Marani et al. 2004, Rinaldo et al. 2004, Pennings et al. 2005) and channel morphology (Syvitski et al. 2005, Jerolmack and Swenson 2007, Fagherazzi 2008, Hood 2010) affect distributions of fish. Differences in vegetation types have received the most attention, with evidence that some vegetation types promote estuarine fish recruitment and species diversity more than others (Beck et al. 2001, Pihl et al. 2002).

The lack of general understanding of how landscape structure influences the distribution and abundance of estuarine fish is unfortunate given the large scale of habitat loss in estuaries. Many

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river deltas have suffered from conversion of estuarine wetlands to agriculture and urbanization on the landward side and dredging on the seaward side. These impacts are exacerbated by climate change impacts to riverine hydrographs and sea level rise. Wetland habitat restoration for sensitive or declining estuarine species would benefit from a sound understanding of how landscape elements influence fish distributions; this would allow better prioritization of land acquisitions and improved restoration design (Simenstad et al. 2002).

We examined landscape patterns of habitat use in juvenile Chinook salmon, whose threatened and endangered status on the Pacific Coast has advanced large-scale estuarine wetland restoration. These anadromous fish are well known for rearing in estuarine habitats during outmigration (Reimers 1973, Healey 1982, Beamer et al. 2005, Ellings et al. 2016, Levings 2016). Several studies have linked population responses to availability of estuarine habitats (Levings et al. 1989, Magnusson and Hilborn 2003, Flitcroft et al. 2016), and support the hypothesis that estuarine habitats are vital rearing areas for juvenile Chinook salmon. Studies have also related environmental factors to estuarine fish presence or abundance (see Levings 2016 for review), but few studies have developed a landscape context describing large-scale patterns of habitat use and residence.

We examine estuarine landscape features associated with varying habitat use by NOR and HOR juvenile Chinook salmon in four Puget Sound river deltas. These four systems provide a broad range of habitat variation and contrasting stock status. Populations from all four watersheds are listed as threatened, though some have larger NOR outmigrations than others. The watersheds also vary in their reliance on hatcheries to supplement NOR populations. Hatchery-reared fish migrate downstream at larger sizes than NOR fish, and so might be expected to use estuarine habitats differently as they move through the river deltas. We focus on several landscape attributes subject to natural variation, anthropogenic stressors, and improvements through restoration. These include wetland vegetation type, channel type, and landscape connectivity, in the context of systemic differences among the river deltas.

Methods

We took advantage of sampling in four Puget Sound river deltas – the Nooksack, Skagit, Snohomish, and Nisqually – to evaluate how various landscape attributes influence delta rearing by juvenile Chinook salmon. Specifically, we used data collected from 55 sampling sites within the four systems that were repeatedly sampled during later winter through mid-summer for juvenile Chinook salmon by beach seines and fyke traps for up to 20 years, depending the system. We associated each site with landscape characteristics, including delta system, wetland vegetated type, and channel types. The landscape characteristics are described below in their own sections.

Our overall analysis approach is a cross-system comparison. Cross-system comparisons are valuable, because variation in biotic and abiotic attributes can have limited range within one system. For our purpose, a comparison across systems can provide broader distributions of the attributes that may affect juvenile Chinook rearing conditions in deltas. Additionally, anthropogenic activities can differ across systems, so cross-system comparisons can offer insight

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into potential management effects on juvenile Chinook rearing habitat. Thus, cross-system comparisons provide improved opportunity to generalize juvenile Chinook population responses to estuarine habitat variation.

Four river delta systems

Historically, the Nooksack, Skagit, and Nisqually have been prograding tidal deltas, while the Snohomish is a drowned river valley. All have undergone extensive wetland habitat loss, primarily from diking and draining for agriculture, but extant channel area varies five-fold across systems (Table 2.1). Despite habitat loss and current land use, the Nooksack and Skagit have classic prograding delta fans, while the Nisqually is intermediate between the Nooksack/Skagit and Snohomish. However, the progradation rate in the Skagit delta has been slowing for decades and has recently become negative in some parts of the delta (Hood et al. 2016). Anthropogenic changes to sediment routing are sheltering areas from sediment supply, but not from sea level rise or wave attack, thereby facilitating marsh erosion (Hood et al. 2016).

Table 2.1. Characteristics of four estuarine river delta systems examined in this report. Wetland habitat loss data is from Simenstad et al. 2011 summarized for vegetated areas. Wetland channel area is based on GIS analysis completed for this report (see Appendix 2.1). Total young of year outmigrants and riverine fry outmigrants come from trapping programs by WDFW, Tulalip, and Lummi Tribes. Hatchery releases (millions) are based on Regional Mark Information System (RMIS) reports (www.rmmpc.org). Tidal ranges are from Mofjeld et al. 2002. River discharge and sediment loads from Czuba et al. 2011.

	Nooksack	Skagit	Snohomish	Nisqually
Juvenile Chinook populations:				
Years analyzed	2005 - 2015	1994 - 2015	2001 - 2015	2010 - 2015
Total outmigrants (1000s)	33.1 - 325.3	1,000.2 - 7,712.3	33.6 - 1,024.3	34.7 - 245.7
Fry outmigrants (1000s)	0.3 - 43.4	444.4 - 6,553.0	26.2 - 432.9	3.5 - 93.8
Hatchery releases (M)	0.61 - 1.94	0.15 - 0.89	1.82 - 4.30	3.35 - 4.26
Landscape characteristics:				
Habitat loss (%)**	71.2	74.1	89.3	76.6
Estuarine channel area (ha)	43.95*	293.96	136.60	248.82***
Tidal range (m)	2.59	3.37	3.38	4.12
River discharge				
Mean annual discharge (cfs)	3,200	18,000	10,000	2,100
Standardized by channel area (cfs/ha)	73	61	73	8
Sediment load				
Annual sediment load (tons/yr)	1,400,000	2,800,000	490,000	120,000
Standardized by discharge (tons/yr/cfs)	437.5	155.6	49	57.1
Standardized by channel area (tons/yr/ha)	31,854	9,525	3,587	482

*Does not include Lummi River/Red River channels.

**Based on Simenstad et al. 2011, which did not include several large scale restoration projects in each delta. The largest of these is the Nisqually delta, which underwent a 364 ha increase in tidal footprint (David et al. 2014).

*** Value includes channel habitat created by restoration of 364 ha tidal footprint in the Nisqually delta.

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All four systems have naturally spawning Chinook salmon populations, though the juvenile outmigrant population sizes vary from thousands in the Nooksack to millions in the Skagit. Chinook salmon have several juvenile life history types, including yearlings and subyearling parr migrants, with extended rearing in freshwater but not in estuaries. Fry outmigrants are the principal life history type rearing in estuaries (Healey 1982, Beamer et al. 2000, Beamer et al. 2005), and they exhibit more variation across systems than total outmigrants. In addition to wild outmigrants, all systems have hatchery programs that release thousands to millions of subyearling outmigrants each year within their natal river; these fish may also briefly inhabit estuarine habitat after release. Thus, these four systems allow comparisons based on variation in habitat extent, fish population sizes, and hatchery practices which seasonally increase local densities of fish migrating through the river deltas. These factors could be expected to influence the relative importance of estuarine habitats for threatened populations of Chinook salmon in Puget Sound.

Wetland vegetation type

The vegetated tidal delta is exposed to tidal and riverine processes and dominated by three tidal wetland types or zones: forested riverine tidal (FRT), estuarine forest transition (EFT), and estuarine emergent marsh (EEM) (after Cowardin et al. 1979). Because these wetland types are determined by their location relative to fluvial and tidal inundation, they have different abiotic and biotic characteristics. FRT areas are tidal freshwater habitats; EEM areas have greater tidal inundation and highly variable salinity while EFT areas are intermediate between the two. Wetland types may also vary in temperature due to vegetation differences (e.g., shrubs and trees vs. sedges and cattails). These varying conditions likely affect invertebrate communities and feeding opportunities for fish in these zones.

We investigated tidal wetland type effects because: 1) juvenile Chinook salmon estuarine rearing success may vary due to abiotic (salinity, temperature) and biotic (prey availability and energy content of food) differences among tidal wetland types; 2) not all tidal wetland types respond similarly to stresses, such as predicted sea level rise or nutrient pollution; and 3) some Puget Sound salmon recovery plans have goals related to specific tidal wetland vegetation types within their river deltas, so comparative analyses could inform management.

Tidal wetland types were identified by indicator habitat types. Indicator habitat types had to predominate for the area to be identified as a particular wetland vegetation type. Indicator habitat types were primarily vegetation communities that arose from distinctive combinations of hydrology and elevation. The zones were not, however, exclusively composed of their indicator habitat types; non-indicator habitats could persist in small patches within zones, due to local disturbances.

Indicator habitats for estuarine emergent marsh (EEM) were low and high saltmarsh. Other habitat types commonly co-occurring in small patches included: channels (various types), mudflat, estuarine open water, estuarine scrub shrub, and freshwater emergent marsh. Dominant emergent species in EEM included: *Carex lyngbyei*, *Distichlis spicata*, *Phalaris arundinacea*, *Sarcocornia pacifica*, *Schoenoplectus tabernaemontani*, *Schoenoplectus pungens*, and *Typha angustifolia*.

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The emergent forested transition (EFT) was a mosaic of tidally influenced emergent marsh and scrub-shrub habitats and encompassed the gradient in vegetation from forest-dominated wetlands and uplands to EEM. Other habitat types co-occurring in small patches included: channels (various types), wetland forest, upland forest (gallery forests), palustrine open water, and mudflat. Dominant shrub species in EFT include: *Myrica gale* and *Salix* spp.

Indicator habitats for the forested riverine/tidal (FRT) wetland type were palustrine and riverine forests. Other habitat types co-occurring in small patches included: channels (various types), mudflat, upland habitats, tidally influenced emergent marsh, and scrub-shrub habitats. Dominant forest species in FRT include: *Alnus rubra*, *Populus balsamifera*, and *Picea sitchensis*.

Each site in the four delta systems was classified into one of the three tidal wetland types based on landscape position relative to tidal vs. freshwater influence and dominant vegetation type (Fig. 2.1). We used aerial photographs to determine dominant vegetation type, following classifications of Cowardin et al. (1979). Sites were also evaluated in the field to verify aerial photograph interpretations. Note that we evaluated current tidal wetland type, which may have been different from historical tidal wetland type due to subsidence, vegetation removal or other processes.

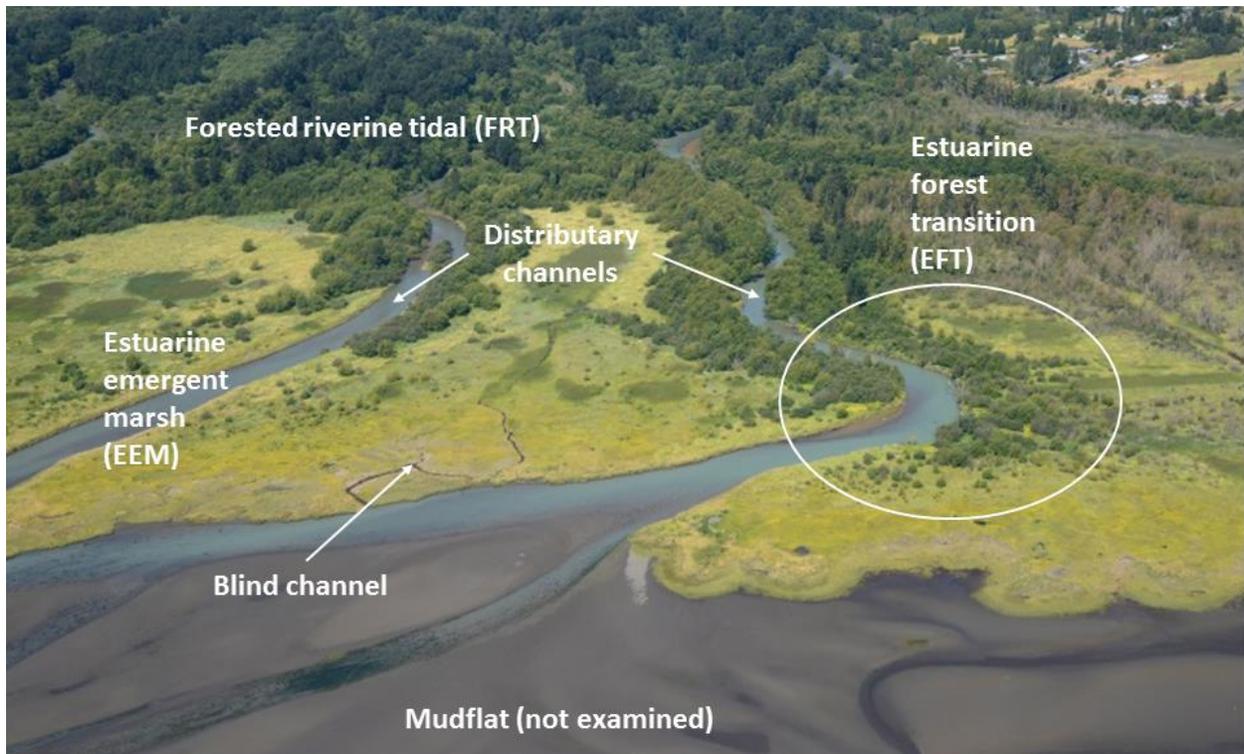


Figure 2.1. Aerial photo illustrating distinctions among tidal wetland and channel types.

Channel types

There are two general classes of channels in estuarine deltas. Distributaries connect rivers to the marine waters. While tidally influenced, they are maintained primarily by the constant flow of river water. Blind tidal channels have only one connection to another water body (a distributary or marine embayment) and are flushed only by tidal exchange (Ashley and Zeff 1988, Hood

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2006). Both channel types are likely important to resident anadromous fish for different reasons. Distributaries are almost always wetted (although the depth can change depending upon tide and river flow), while blind channel sites may often dry out or become disconnected during low tides. Distributaries serve as the main pathways by which fish move from river to sea, while blind channels are relatively shallow, low energy environments that provide rearing opportunity and predator refuges to juvenile fish (Thorpe 1994). Each site in the four delta systems was attributed as blind or distributary channel.

Landscape connectivity

Fluvial systems are defined by the pathways in which water moves, and these pathways affect the evolution and ecology of fish. These pathways, which we term landscape connectivity, are central to explaining habitat use by anadromous fish (Fausch et al. 2002). Landscape connectivity in freshwater affects habitat quality parameters such as temperature, and the ability of anadromous fish to access habitat (Fullerton et al. 2010). Restoring connectivity by removing barriers and channel modifications is a central focus of habitat restoration in freshwater (Bisson et al. 2009, Beechie et al. 2013).

In estuarine systems, connectivity is complicated by opposing river and tidal flows, and channel networks become correspondingly complex (Davis et al. 2012). Beamer et al. (2005) detected strong connectivity-based gradients in temperature and salinity in the Skagit River delta, as well as strong positive correlations of connectivity with salmon abundance. Ellings et al. (2016) related measurements of channel sinuosity and tortuosity to juvenile Chinook salmon abundance in the Nisqually River delta. Restoring lost connectivity by reconnecting channel systems has been a central focus of habitat restoration work in both deltas. Within the tidal delta and nearshore ecosystems of the Skagit River, Beamer et al. (2005) used a metric of landscape connectivity to predict juvenile Chinook use of specific habitats for restoration planning.

While various conceptualizations and measures of connectivity exist in the literature (e.g., Pascual-Hortal and Saura 2006), we developed a metric focused on potential pathways juvenile salmon might encounter while migrating from freshwater to estuarine sites in a bifurcating tidal delta network. Landscape connectivity was defined as a function of both the length, width, and complexity of the pathway that out-migrating juvenile Chinook salmon must follow to access particular estuarine locations. Habitat connectivity decreases as the complexity and distance of the migratory path increases.

We created GIS layers of point data representing all sites used in this study. For each point, we calculated a landscape connectivity value according to the methods described in Beamer and Wolf (2011), utilizing a fish pathway arc layer. The GIS arc layer uses width measurements of distributary channels to calculate landscape connectivity for each site in this study. It reflects the pathways juvenile Chinook salmon are expected to move through the delta channel network and along the nearshore to find and colonize habitat represented by the fish sampling sites. Per methods described in Appendix D.V, page 79 of Beamer et al. (2005), values for channel bifurcation order were assigned to each channel polygon.

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Landscape connectivity (LC) for each site was calculated as,

$$\text{Eq. 2.1} \quad LC = \frac{1}{1 + \sum_{j=1}^{j_{\text{end}}} (O_j * D_j)}$$

where O_j = bifurcation order for distributary channel or nearshore segment j , D_j = distance along segment j of order O_j , j = count (1... j_{end}) of distributary channel or nearshore segments, and j_{end} = total number of distributary channel or nearshore segments at destination or sample point.

Channel width was measured at each bifurcating channel and used to determine channel order per Table D.V.1. in Beamer et al. (2005). See Appendix 2.2 (c.f. Beamer et al. 2016) for rules for determining bifurcation order and subsequent channel-specific values of $O_j * D_j$.

In a bifurcating tidal distributary network, multiple possible pathways exist to reach the same location. We focused on the maximum connectivity value of a site to the freshwater mainstem. Possible landscape connectivity values ranged 0 (completely isolated) to 1 (mainstem river at the head of tide). Higher values of landscape connectivity have a shorter and/or less complex pathway to the river mainstem, the source of fish.

However, the four delta systems vary in size and distributary channel complexity so the calculated landscape connectivity values across delta systems are not uniform (Nooksack site landscape connectivity values range from 0.042 to 0.084; Skagit from 0.015 to 0.081; Snohomish from 0.012 to 0.351; Nisqually from 0.059 to 0.290). In order to compare landscape connectivity across the four delta systems uniformly, we scaled connectivity values to the highest landscape connectivity value within each delta, thus forcing each system to fit more uniformly with each other. We called the standardized version of landscape connectivity ‘Maximum Standardized Landscape Connectivity’ (Max.Std.Conn., Table 2.2)).

Fish sampling

Calculating fish density

We compiled records of juvenile Chinook salmon abundance from beach seine and fyke trapping in all four river deltas (Fig. 2.2, Table 2.2), and converted counts to local density (fish/ha) by estimating set or channel area and recovery efficiency (proportion recaptured). Hence, density = count/recovery efficiency/area. Set areas and recovery efficiency are gear-specific (see Appendix 2.3). Density data were transformed ($\ln[x+1]$) to correct for lognormal variation. This procedure was done separately for NOr and HOr catches, resulting in separate density estimates for NOr and HOr Chinook. While recent monitoring across all systems is biweekly or monthly from February to August, earlier years (particularly in Nooksack and Snohomish systems) sometimes included fewer annual observations.

Beach seine

Small net beach seine methods were used for sampling shallow distributary channel or larger blind channel habitat in the Skagit and Nooksack tidal delta (see Appendix 2.3 for dimensions of different nets). The areas seined were typically shallow (<1.5 m) and had relatively homogeneous habitat features such as water depth, velocity, substrate, and vegetation. The 24.4m (l) by 1.8m (d) net was set by fixing one end of the net on the beach while deploying the

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other end of the net ‘upstream’ against the water current using a floating tote, and then returning to the shoreline in a half-circle. If the water was too deep to wade, the tote was towed by boat. Both ends of the net were then retrieved, yielding a catch. A ‘smaller’ net (“LNRD BS 9x2” in Appendix 2.3) was used for sites at which access required hiking overland into the site, usually blind channel habitat. This net was deployed using a drag and haul method, where both ends of the net were pulled down the beach for a given distance and then pursed up, yielding a catch.

A large net beach seine method was used for sampling larger and deeper distributaries in the Skagit delta. One end of the 36.6m (l) by 3.7m (d) net was fixed on the beach while the other end was set by boat across the current at an approximate distance of 65% of the net’s length, and then the boat end was brought to the shoreline edge and pulled in by hand.

In the Snohomish and Nisqually deltas, monitoring crews used the Puget Sound Protocol seine method to deploy a 36m (l) x 1.8-3.0m (d) tapered net. The seine was set in a semi-circle from upstream to downstream (or in the direction of the current) with one end held on shore and the other set from the boat. Once the net was set, both sides were pulled in together until the entire catch was consolidated in the bag (i.e. center of the net) at which time processing begins immediately.

The standard set area values are shown by net type and method of deployment in Appendix 1. Beach seine set area is the area swept by the net during a set. We typically calculated a standard set area for each net/method combination and then recorded in the field how much we deviated from the normal set area to calculate a unique set area value for each beach seine set. For example, the standard set area for the small net method when set in a half circle is 96 m². This was recorded as 100% set area. If the net was set so that the beach end of the net did not come to the shoreline edge, or not all of the net was deployed out of the tub, the area covered by the net was estimated and recorded as a percent of the standard set area. When using the drag and haul net method, the length and width of the area covered during the set were recorded and multiplied to estimate set area. Standard set area for the large net method is 235 m². Standard set area for PS protocol methods in the Snohomish and Nisqually is 206 m². We applied an average recovery efficiency of 75% for all beach seine sets based on previous estimates using mark-recapture trials on 39 large and small net sets (E. Beamer, unpublished data).

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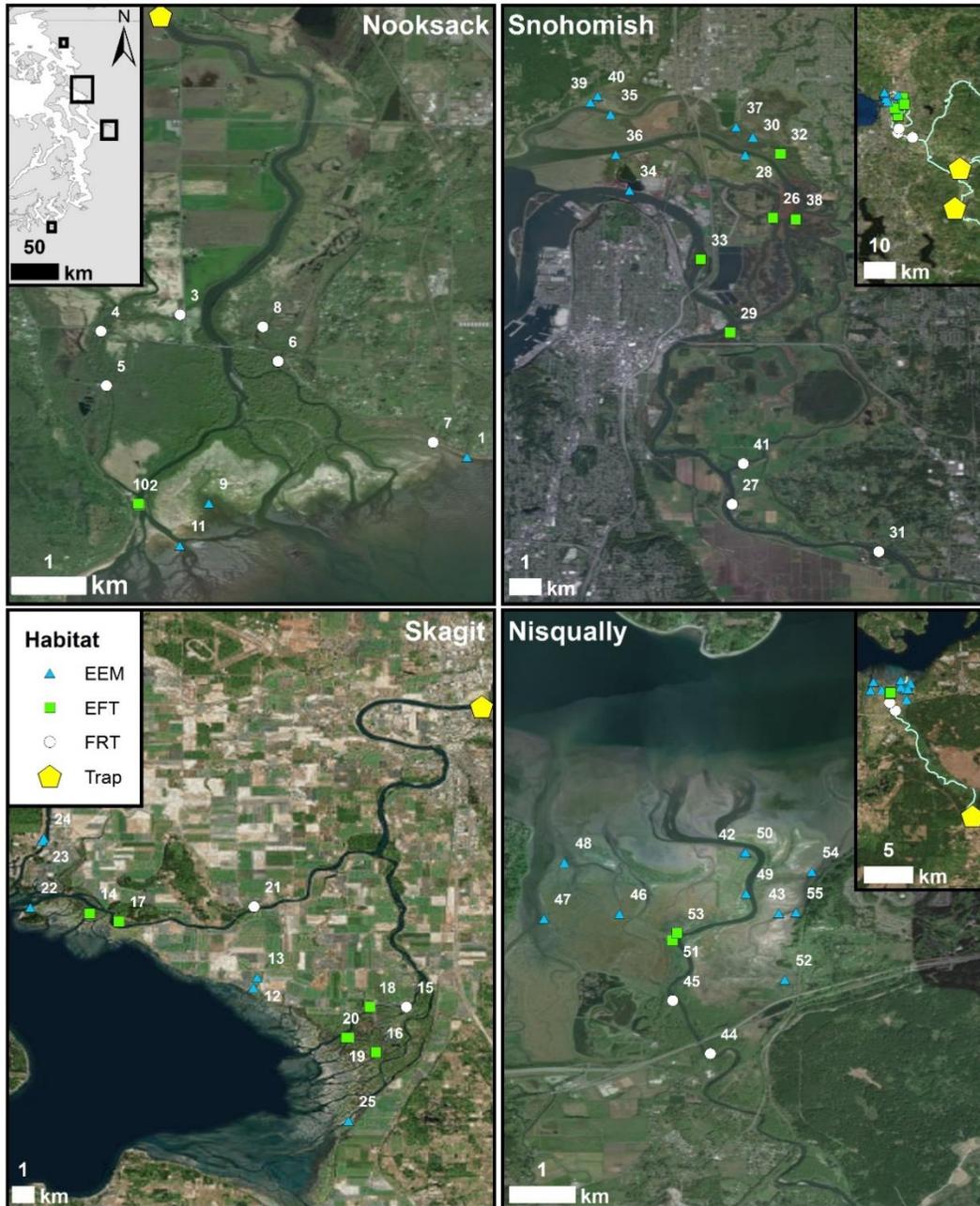


Figure 2.2. Four Puget Sound river delta systems examined in this report. Symbols represent smolt traps (yellow pentagons) and delta sampling sites, with numbers corresponding to the site list in Table 2.2. White circles, green squares, and blue triangles indicate forest-riverine tidal (FRT), estuarine-forest transition (EFT), and estuarine-emergent marsh (EEM) sites, respectively.

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Table 2.2. Sites used to calculate densities of juvenile Chinook salmon in the Nooksack, Skagit, Snohomish, and Nisqually delta systems, along with landscape characteristics of each site, and gear used for sampling.

System	#	Site	Landscape Connectivity	Max Std Conn	Tidal wetland	Channel type	Gear used
Nooksack	1	Airport Cr	0.063	0.750	EEM	Distributary	Seine
	2	Fish Pt	0.061	0.726	EFT	Distributary	Seine
	3	Kwina SI 1	0.065	0.774	FRT	Distributary	Seine
	4	Kwina SI 2	0.065	0.774	FRT	Distributary	Seine
	5	Kwina SI.Smokehouse	0.05	0.595	FRT	Distributary	Seine
	6	Silver Cr 1	0.084	1.000	FRT	Blind	Seine
	7	Silver Cr 3	0.068	0.810	FRT	Blind	Seine
	8	Silver Cr Upper	0.064	0.762	FRT	Blind	Seine
	9	Tidal Delta 2	0.042	0.500	EEM	Blind	Seine
	10	W Chan Forested	0.066	0.786	EFT	Distributary	Seine
	11	W Chan Saltmarsh	0.052	0.619	EEM	Distributary	Seine
Skagit	12	Browns SI Barrow Ch	0.015	0.185	EEM	Blind	Fyke
	13	Browns SI Diked Side	0.015	0.185	EEM	Blind	Fyke
	14	Cattail Saltmarsh	0.039	0.481	EFT	Blind	Fyke
	15	DW Old Site	0.052	0.642	FRT	Blind	Fyke
	16	DW Ref E Blind	0.029	0.358	EFT	Blind	Fyke
	17	Fishtown Bar Area	0.045	0.556	EFT	Distributary	Seine
	18	Freshwater SI s20	0.045	0.556	EFT	Distributary	Seine
	19	FWP New Site	0.036	0.444	EFT	Blind	Fyke
	20	FWP Old Site	0.036	0.444	EFT	Blind	Fyke
	21	Grain of Sand	0.081	1.000	FRT	Blind	Fyke
	22	Ika	0.034	0.420	EEM	Blind	Fyke
	23	Swin Ch Old Bridge	0.017	0.210	EEM	Blind	Fyke
	24	Swin Ch Site 55	0.017	0.210	EEM	Distributary	Seine
	25	Tom Moore	0.023	0.284	EEM	Blind	Fyke

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Table 2.2, continued.

System	#	Site	Landscape Connectivity	Max Std Conn	Tidal wetland	Channel type	Gear used	
Snohomish	26	Big Bend	0.027	0.077	EFT	Distributary	Seine	
	27	BigTree	0.15	0.427	FRT	Distributary	Seine	
	28	Biringer	0.023	0.066	EEM	Distributary	Seine	
	29	Deadwater	0.048	0.137	EFT	Distributary	Seine	
	30	Ebey Is Fyke	0.018	0.051	EEM	Blind	Fyke	
	31	Fields Riffle	0.351	1.000	FRT	Distributary	Seine	
	32	Heron Pt Fyke	0.019	0.054	EFT	Blind	Fyke	
	33	Langus-Outside	0.036	0.103	EFT	Distributary	Seine	
	34	LMainstem- RB/Weyerhauser	0.027	0.077	EEM	Distributary	Seine	
	35	Lower Ebey	0.013	0.037	EEM	Distributary	Seine	
	36	LSteamboat	0.019	0.054	EEM	Distributary	Seine	
	37	MarysvilleRestoration	0.017	0.048	EEM	Distributary	Seine	
	38	Otter Island Inside	0.026	0.074	EFT	Blind	Seine	
	39	Quilceda Fyke Big	0.012	0.034	EEM	Blind	Fyke	
	40	Quilceda Fyke Small	0.012	0.034	EEM	Blind	Fyke	
	41	UpEbey-Pumpstation-LB	0.109	0.311	FRT	Distributary	Seine	
	Nisqually	42	Animal	0.131	0.452	EEM	Blind	Fyke
		43	Control	0.09	0.310	EEM	Blind	Fyke
		44	I-5 RB	0.29	1.000	FRT	Distributary	Seine
		45	Lookout	0.215	0.741	FRT	Blind	Seine
		46	Madrone	0.076	0.262	EEM	Blind	Fyke
47		MCA RB	0.063	0.217	EEM	Distributary	Seine	
48		N1	0.081	0.279	EEM	Blind	Seine	
49		NEEM 1	0.15	0.517	EEM	Distributary	Seine	
50		NEEM 2	0.135	0.466	EEM	Distributary	Seine	
51		Nugies	0.185	0.638	EFT	Distributary	Seine	
52		Phase 2	0.059	0.203	EEM	Blind	Fyke	
53		Ring Dike Slough	0.182	0.628	EFT	Blind	Seine	
54		RSS LB	0.087	0.300	EEM	Distributary	Seine	
55		RSS Point	0.088	0.303	EEM	Distributary	Seine	

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Fyke trap

We used fyke traps following Levy and Northcote (1982) to capture juvenile Chinook salmon rearing in smaller blind channels. Fyke traps were constructed of 0.3 cm mesh knotless nylon with a 0.6 m by 2.7 m diameter cone sewn into the net to collect fish draining out of the blind channels. Nets featured a lead line that sank the bottom of the net to the channel floor and a float line that maintained the top of the net at the water surface. All nets were sized to completely span the channel and block fish access at high tide.

We set fyke traps across channel mouths at high tide and captured fish as they exited the dewatering channel on the ebbing tide. Fyke traps were used at most blind tidal channels in the Skagit, Snohomish, and Nisqually deltas (Table 2.2). Sampling occurred during spring tide series to take advantage of large ebb tidal drops. Catches were adjusted by trap recovery efficiency (RE) estimates derived from multiple mark-recapture experiments, using fish released upstream of the trap at high tide. RE estimates were unique to each site and were related to hydraulic characteristics of the site during trapping (e.g., the change in water surface elevation during trapping or water surface elevation at the end of trapping). Typically, multiple mark-recapture tests were completed at each site to either calculate an average RE at the site or to develop a regression model to convert the “raw” juvenile Chinook salmon catch to an estimated population size within the habitat upstream of the fyke trap on any sampling day. The RE-adjusted Chinook salmon catch was divided by the bankfull surface area of the blind channel network, upstream of the trap, to calculate a juvenile Chinook salmon density for each fyke trap set. Channel surface area was surveyed in the field.

Statistical Analysis

Fish abundance (i.e. count data) can be difficult to evaluate, because the patchiness (schooling) of fish produces a high number of zeros in the data. Thus, we used a two-stage model, a common tool for handling zero-inflated data (Barry and Welsh 2002), to evaluate how landscape characteristics influenced juvenile Chinook salmon densities in the four deltas. The first stage used logistic regression to estimate the probability of a non-zero response, i.e., presence during a sampling event. The second stage used only positive (i.e. fish present) density values to evaluate magnitude changes in biweekly local density among and within each delta. Because two-stage models include two fits to the data, final model predictions are the product of both the probability (i.e. first stage) and the estimated magnitude as a function of the selected covariates (second stage). Large system differences exist within our dataset for overall juvenile Chinook presence, but there is good system overlap in the frequency of density levels for both NOr and HOOr juvenile Chinook when present (Fig. 2.3).

Juvenile NOOr Chinook salmon display nuanced seasonal patterns reflecting complex life history variation within the species. Given the non-linear nature of these complex seasonal patterns, we used generalized additive models (GAMs; Hastie and Tibshirani 1990) to fit the presence/absence and the positive density data. GAMs are analogous to generalized linear models with the added flexibility of model covariates using a set of “smoothing functions” to capture the non-linear trends. Smoothing functions, although free to take any form, are penalized for excessive overfitting to maximize the trade-off between fit and the degree of smoothness for

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each predictor (Wood 2017). Thus, GAMs provide a robust tool to evaluate changes in density while accounting for complex non-linear trends. Two-stage models were fit separately for natural origin (NOr) and hatchery origin (HOr) juvenile groups.

The models and list of particular effects included in each stage of analysis were selected to best represent the natural system based on expert knowledge. Our objective was to evaluate how juvenile Chinook presence and density varied as a function of landscape attributes—specifically wetland vegetation type, channel type, and Max.Std.Conn within and among the four deltas. To evaluate landscape effects, all candidate models included a Week term to account for known seasonal trends of outmigrating juvenile salmon and a System term to account for known system-level differences (Table 2.1). A Year term was also included to account for inter-annual variation. The model with the lowest AIC score was selected as the best fit model (Akaike 1973). Models with delta AIC < 2 were considered to have similar support, so we used model weights to evaluate their probability as the correct model based on likelihood estimates.

First-stage models took the form:

$$\text{Eq.2.2} \quad \text{Logit}(\text{density} > 0) = f_1(\text{Week}) + \text{System} + \mathbf{X}\theta$$

where, $f_1(\text{Week})$ represents the smooth function of week, System represents the individual deltas, and \mathbf{X} is the row of the model matrix for the parametric landscape attributes with their corresponding parameter vector, θ . Model fit, or predictive capability, was evaluated based on the proportion of deviance explained by the best fit model.

Initial analysis of the positive density data suggested a more complex structure for fitting juvenile Chinook density among the four deltas in our second stage model. We used a hierarchical GAM to explore how the non-linear components differ within the levels, or groups, of our selected landscape attributes (Pedersen et al. 2018). Within this structure we could estimate a global fit for each of our parameters of interest including Week and System as well as estimate a fit for each level or group as it varied seasonally (interaction with Week term) or within each system (interaction with System term). Due to the complexity of the models and the number of potential terms, we chose to use a double penalty selection procedure (Marra and Wood 2011) on the full model including all terms and their first order interactions with Week and System. The double penalty selection procedure imposes an extra penalty on smooth terms, such that those smooth components tending toward zero and thus a straight line (reflected in effective degrees of freedom (EDF)) do not contribute toward model fit. In contrast, terms with positive EDF values and p values less than 0.05 contribute significantly toward model fit. The magnitude of EDF values indicates complexity of the smooth function used for model fit.

Our second-stage model took the form:

$$\text{Eq. 2.3} \quad \ln(\text{Density} > 0) = f_1(x_1) \dots + f_i(x_i) + f_{1,i}(x_1, x_i) + \mathbf{X}\theta + \epsilon_i$$

where, f_i represent the smooth function for single terms and interactions, and \mathbf{X} is the row of the model matrix for the parametric landscape attributes with their corresponding parameter vector,

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θ . To evaluate the importance of each individual term in our models we used a deviance decomposition, or partitioning, method similar to Reum et al. (2011). The portion of the deviance attributable to each single term, including their interactions, was the deviance of the model with all terms that included the one of interest minus the deviance for the model with all the terms of interest removed.

During model fit we also needed to account for the autocorrelation in biweekly observations of juvenile Chinook density. Prior to analysis, we evaluated autocorrelation plots and determined a lag-1 autoregressive error structure and estimated $\rho = 0.445$ fit the data sufficiently. All models were fit with this error structure and standard diagnostic procedures were used to assess fit and residual structure. All analyses were executed using R statistical software (R Core Team 2019) and specifically the mgcv package (Wood 2011). All plots were produced using the ggplot2 package for R (Wickham 2016).

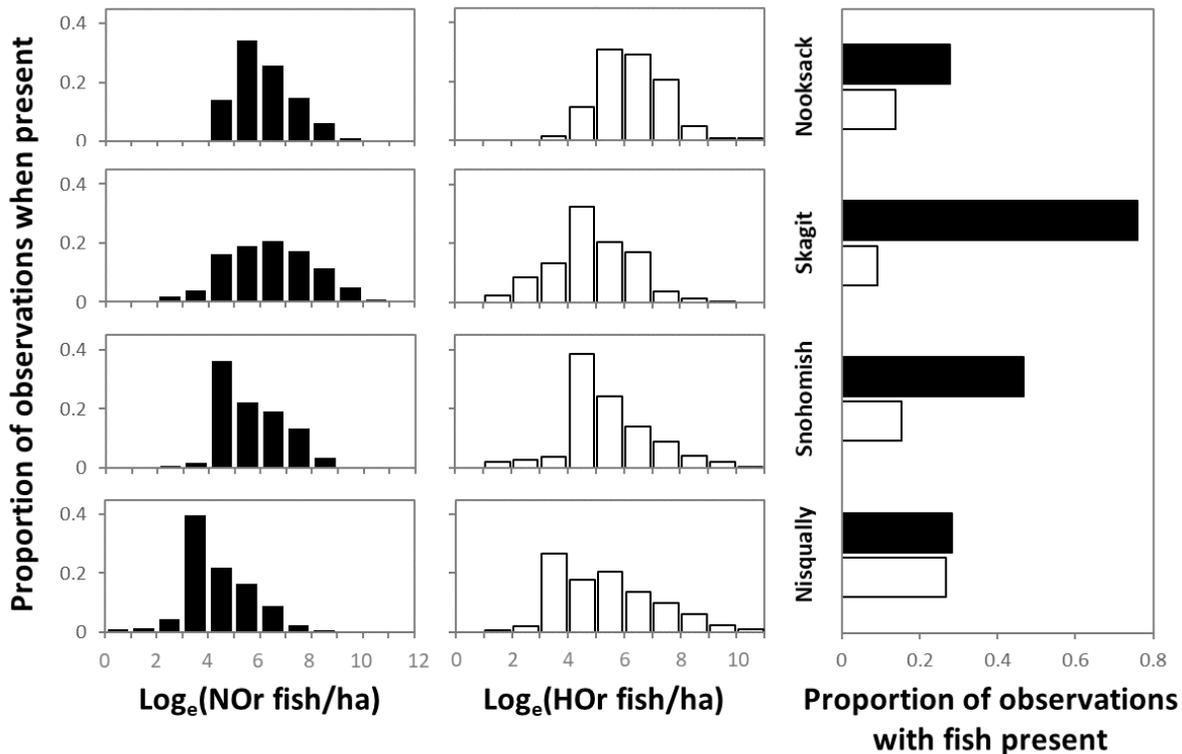


Figure 2.3. Proportion of all observations of juvenile Chinook density in Nooksack, Skagit, Snohomish, and Nisqually delta systems (top to bottom) of natural-origin (NOr) (black bars) and hatchery-origin (HOr) (open bars) when juvenile Chinook salmon were present, and proportion of observations of fish presence (right column).

Results

NOr presence/absence

The statistical model that best explained NOr presence/absence included the variables: delta system, week, channel type, and the interaction between channel type and delta system (Table 2.3). Both system and week explained the majority of the variability in presence/absence of NOr Chinook (Figure 2.4. upper left panel). Max.Std.Conn was not included in the model, although it

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was for the NOr density analysis (see below). Thus, when juvenile NOr Chinook are present in the delta, local density but not probability of presence tracks Max.Std.Conn (see also Chapter 3, Fig. 3.3).

As expected from the well-known natural history of juvenile salmon migration, there was a strong seasonal effect on the probability of NOr juvenile Chinook presence in all delta systems (Fig. 2.4, 2.5). The Skagit Delta had the highest probability of NOr Chinook presence, and this high probability was more broadly sustained over time than in the other deltas, spanning from week 8 through week 27 (mid-February to July). All four delta systems had peak probabilities of presence around week 22 (end of May), after which there were steep declines. The Skagit and Snohomish deltas had higher probability of NOr Chinook presence in blind channel habitat than in distributary channels; the reverse was true for the Nooksack. The Nisqually did not exhibit any difference by channel type. The different channel type by system results may be explained by systemic difference in outmigrant abundance and life history types. The Skagit and Snohomish outmigrants are comprised of a large fry component (Zimmerman et al. 2015; Kubo et al. 2013) that reside for weeks to months in the deltas (Simenstad et al. 1982; Beamer et al. 2000; Larsen et al. 2016); fry residents typically rear in blind tidal channels. However, the Nooksack is dominated by parr that migrate quickly through the delta (Beamer et al 2016).

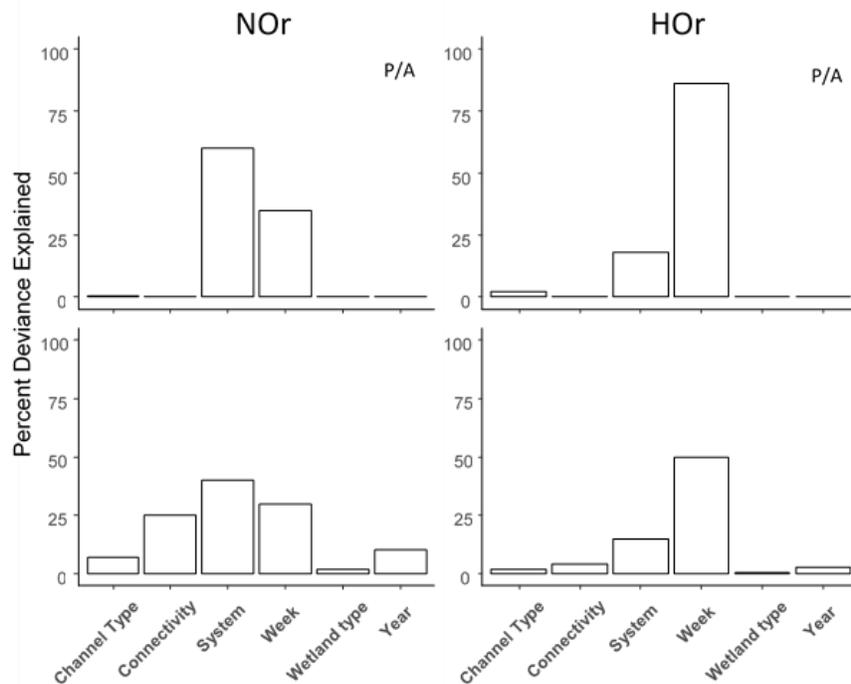


Figure 2.4. Percent deviation explained by factors for the best fit model for NOr (left column) and HOr (right column) Presence/Absence models (top row) and Chinook density when present models (bottom row). Total deviance explained by each factor includes the proportion attributable to each single factor and all interactions for which that particular factor is included.

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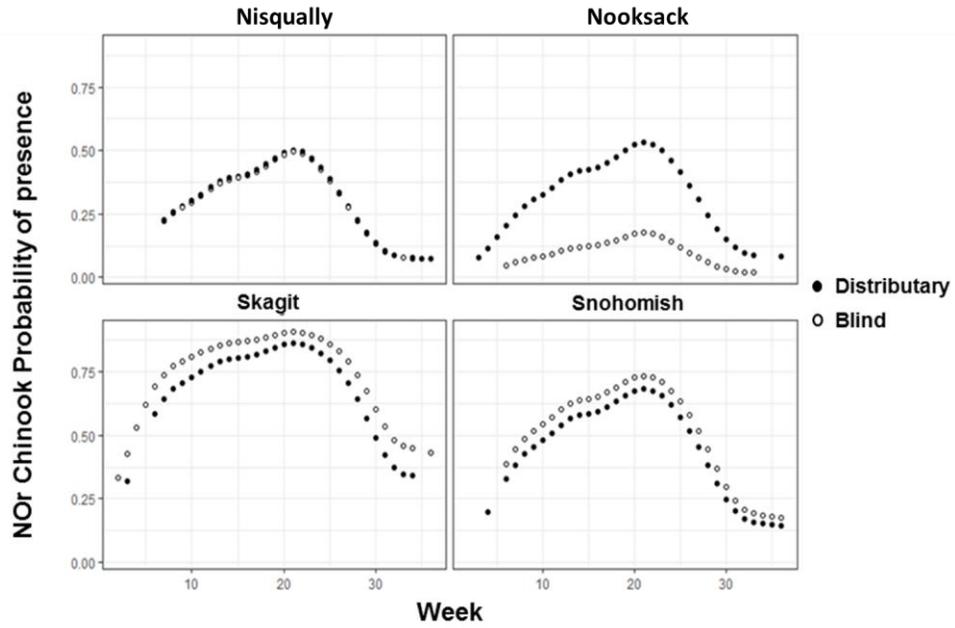


Figure 2.5. Best model fit outputs for the probability of presence of NOR juvenile Chinook by system, week, and channel type.

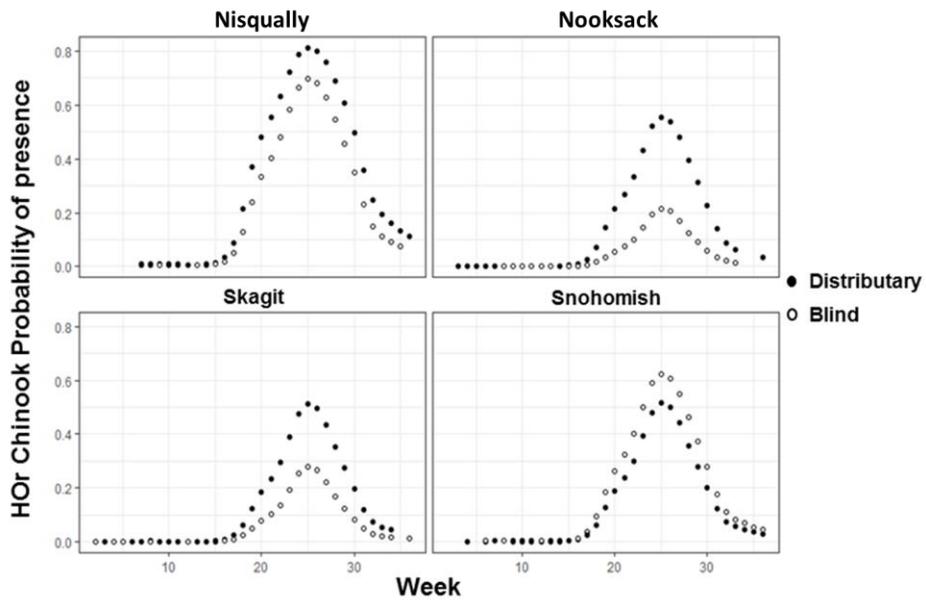


Figure 2.6. Best model fit outputs for the probability of presence of HOR juvenile Chinook by system, week, and channel type.

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Table 2.3. Model selection table for NOr presence/absence in all systems. Best fit model is indicated in bold.

Model	Week	System	Year	Max.Std.Conn	Channel Type	Wetland Type	Max.Std.Conn x System	Channel Type x System	Wetland Type x System	df	ΔAICc	weight
1	X	X	X							14	89.25	0
2	X	X								13	102.86	0
3	X	X		X						14	88.46	0
4	X	X			X					14	104.25	0
5	X	X				X				15	105.1	0
6	X	X		X			X			17	74.95	0
7	X	X			X			X		17	0	1
8	X	X				X			X	21	56.46	0

Table 2.4. Model selection table for HOr presence/absence in all systems. Best fit model is indicated in bold.

Model	Week	System	Year	Max.Std.Conn	Channel Type	Wetland Type	Max.Std.Conn x System	Channel Type x System	Wetland Type x System	df	ΔAICc	weight
1	X	X	X							15	95.84	0
2	X	X								14	94.1	0
3	X	X		X						15	95.08	0
4	X	X			X					15	55.92	0
5	X	X				X				16	62.13	0
6	X	X		X			X			18	97.06	0
7	X	X			X			X		18	0	1
8	X	X				X			X	22	23.86	0

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HOr presence/absence

The statistical model that best explained HOr presence/absence was the same as for NOr, which included the variables: delta system, week, channel type, and the interaction between channel type and delta system (Table 2.4). Similar to NOr presences/absence, system, and especially week, explained the majority of the variability in HOr presence (Fig 2.4. upper right panel). Max.Std.Conn was again not included in the model, just as for NOr presence/absence.

There was a strong seasonal effect on the probability of HOr Chinook presence in all delta systems. Probability of HOr presence peaked around week 25 (mid-June), three weeks later in the year than did the NOr peak, and the HOr curves were more compressed (Fig 2.6). These differences reflect a later and more acute release of hatchery Chinook and shorter cohort residence time in the delta compared to the broader and earlier outmigration timing of NOr migration, especially the fry life history (Zimmerman et al. 2015), from natal streams to the river delta. (Fig. 2.5).

The Skagit Delta had the lowest probability of HOr migrant presence, the Nisqually Delta had the highest, which likely reflects differences in hatchery releases and area of estuarine habitat (Table 2.1). The Skagit, Nisqually, and Nooksack deltas had higher probability of HOr Chinook presence in distributary habitat compared to blind channel habitat. Most HOr fish are similar to NOr parr in their size and migration timing, so higher presence of HOr fish in distributaries compared to blind channels reflected the strong migratory tendency of parr-sized fish. In contrast to the other deltas, Snohomish Delta HOr Chinook were more likely to be present in blind channels than distributaries. Despite these patterns, NOr and HOr exhibited strong co-occurrence during time periods after HOr releases (See Chapter 3, Fig. 3.4)

NOr density when present

The statistical model that best explained NOr density (when present) included year as the most important single effect, likely due to varying outmigrant population sizes across years. The four additional significant effects in decreasing order of importance were: Max.Std.Conn*system > week*channel type > week*system > week*wetland type (Table 2.5). System was the single most important variable (Fig. 2.4, lower left panel) though the manifestation of system effects was included with other important variables, such as Max.Std.Conn, week, and channel type.

Overall, NOr density had a unimodal relationship to week and was greater in blind tidal channels than distributaries, although the pattern varied by week and system and is described in detail below (Fig 2.7). We originally hypothesized that some wetland types may be more important than others to juvenile Chinook salmon in tidal deltas, but interestingly, we only found support for this idea as an interaction with week (Table 2.5; Figure 2.8). In general, NOr density varied seasonally by wetland type, with FRT habitat having higher densities early in the season (< week 10, early March) and EEM habitat having the lowest densities for the bulk of the season (Figure 2.8). The system*wetland type interaction reflected stronger differences in wetland types in the Snohomish compared to other systems.

One of the strongest effects on NOr density was the interaction between system and Max. Std. Conn, which was generally positive but varied by system (Fig 2.9). The week*channel type

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interaction likely reflects behavioral changes in juvenile Chinook from rearing within blind tidal channels early in the season to migration from the delta via distributaries later in the season. Similarly, the week*wetland type interaction likely results from the natural sequence of habitat encounters from FRT and EFT wetland habitats to EEM wetlands as juvenile salmon rear, grow, and move in the delta. This hypothesized wetland type relationship with NOr density may also be reflected through the system*Max.Std.Conn term because Max.Std.Conn correlates with the sequence of wetland types within river deltas (upstream to downstream: FRT>EFT>EEM).

NOr Chinook densities were highest in the Skagit Delta, lowest in the Nisqually Delta (Fig. 2.7), likely as a function of total outmigrant population size and available channel habitat area (cf. Table 2.1). Three systems clearly had higher NOr densities in blind channel habitat early in the curve, indicating extensive rearing behavior. The periods ranged from week 7 to 20 (mid-February to mid-May) for the Skagit and week 10 to 15 (early March to mid-April) for the Snohomish and Nisqually deltas. The Nooksack Delta pattern was distinct in having little difference in NOr density between blind and distributary channels during mid-season. Two reasons may account for this: first, the Nooksack is dominated by relatively large and physiologically mature parr outmigrants rather than relatively small and immature fry migrants, and parr spend relatively little time rearing in tidal marshes; second, the Nooksack Delta has relatively little blind channel habitat available for rearing (Hood 2015), requiring more rearing in

Table 2.5. Smoothed term (s) parameters from global model fit to positive NOr densities in all systems. Terms in bold contributed significantly to fit and define the best model.

Model Terms	edf	Ref.df	p-value
s(week)	0.001	24	0.001
s(system)	0	3	0.159
s(Year)	20.25	24	0.000
s(max.std.conn)	0.571	39	0.003
s(max.std.conn,system)	15.71	62	0.000
s(week,wet.type)	3.712	27	0.000
s(week,chan.type)	10.77	18	0.000
s(week,system)	4.675	39	0.001
s(chan.type):systemNisqually	0.855	2	0.012
s(chan.type):systemNooksack	0.366	2	0.169
s(chan.type):systemSkagit	0	2	0.361
s(chan.type):systemSnohomish	0	2	0.835
s(wet.type):systemNisqually	0	3	0.888
s(wet.type):systemNooksack	0	3	0.316
s(wet.type):systemSkagit	0	3	0.486
s(wet.type):systemSnohomish	1.047	3	0.004
s(wet.type)	0	3	0.420
s(chan.type)	0	2	0.483

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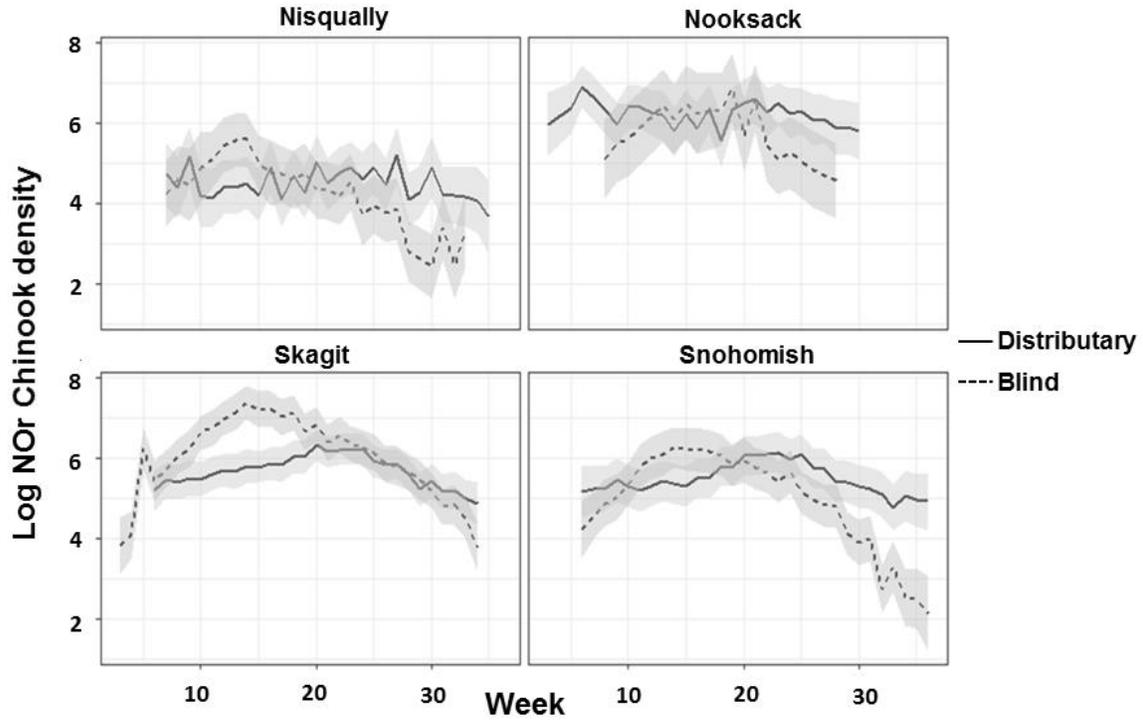


Figure 2.7. Model fitted estimates of NOR juvenile Chinook density when present by system, week, and channel type. Fish density is \log_e transformed fish/hectare. Shaded area reflects values within the 95% confidence interval based on the model's standard error.

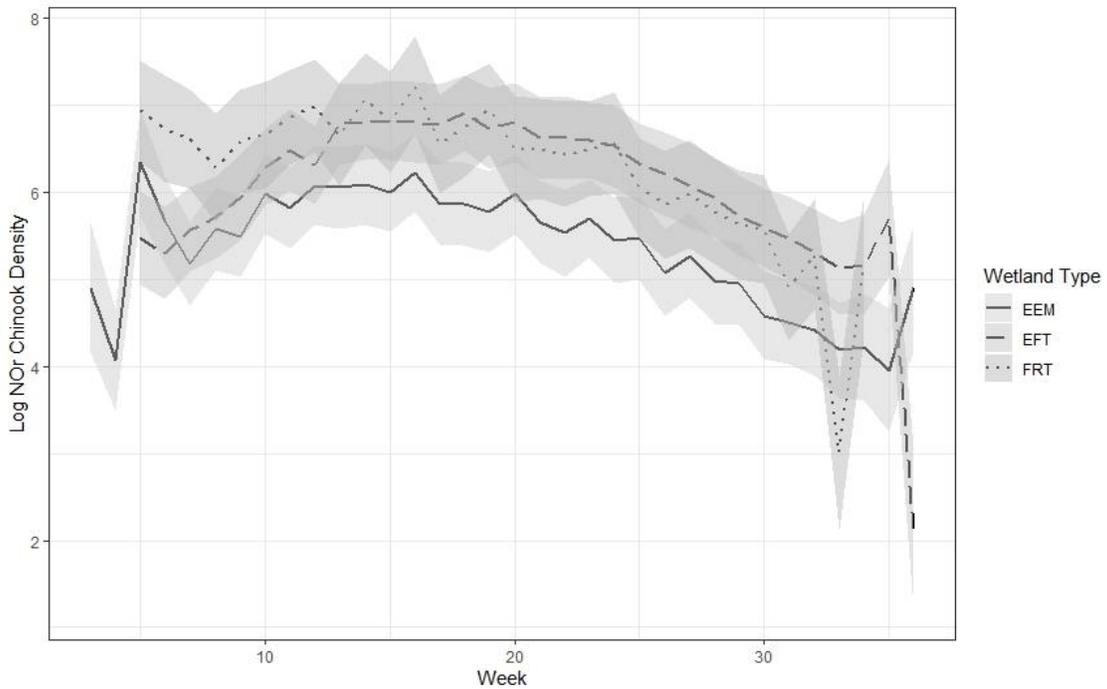


Figure 2.8. Model fitted estimates of NOR juvenile Chinook density when present by week and wetland type. Fish density is \log_e transformed fish/hectare. Shaded area reflects values within the 95% confidence interval based on the model's standard error estimates.

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distributaries. For all deltas later in the season, NOr densities became increasingly higher in distributaries compared to blind tidal channels, suggesting seaward migration became increasingly important and reflecting the later outmigration of parr from rivers (Beamer et al. 2016; Zimmerman et al. 2015). Densities in both channel types declined over time as fish left each delta to access Puget Sound nearshore and pelagic ecosystems.

The interaction between system and Max.Std.Conn was the strongest effect on NOr density (Table 2.5). The model did not find a significant interaction between channel type and Max.Std.Conn. In general, this was a positive effect for all four delta systems, as NOr juvenile Chinook density increased with increasing connectivity (Fig. 2.90, top panel). The y-axis is the landscape connectivity effect on normalized NOr Chinook density. The magnitude of shifts (i.e., the lines at different “levels”) are the consequence of two visualization techniques. First, all the model smooth functions were centered on the Y-axis at 0. Next, we treated the effect of landscape connectivity to include the differences in overall mean NOr Chinook density at the Y intercept for each system. Therefore, the Nisqually was shifted lower than the rest of the delta systems; the Nisqually had a lower mean NOr Chinook density than all other delta systems (Figs. 2.3 and 2.7).

The bottom panel of Figure 2.9 shows the frequency distribution of samples by landscape connectivity for each delta system that informed the model. All systems have some form of skew or gap in their landscape connectivity observations. For example, the Nooksack system didn't have observations with connectivity values on the lower end of the connectivity spectrum while the Snohomish system didn't have observations on the high end of the spectrum. The Nisqually and Skagit delta systems had observations ranging over the full connectivity spectrum, but both systems had gaps in observations for the upper part of the connectivity spectrum but not the lower end. Additionally, sampling from the Nooksack and Snohomish systems are heavily weighted by a narrow range of connectivity values. In the Nooksack system, one site (W Chan Saltmarsh, Max.Std.Conn = 0.619) dominated observations, while in the Snohomish system it was three sites (Quilceda Fyke Big, Quilceda Fyke Small, Lower Ebey, Max.Std.Conn ranging from 0.034 to 0.037).

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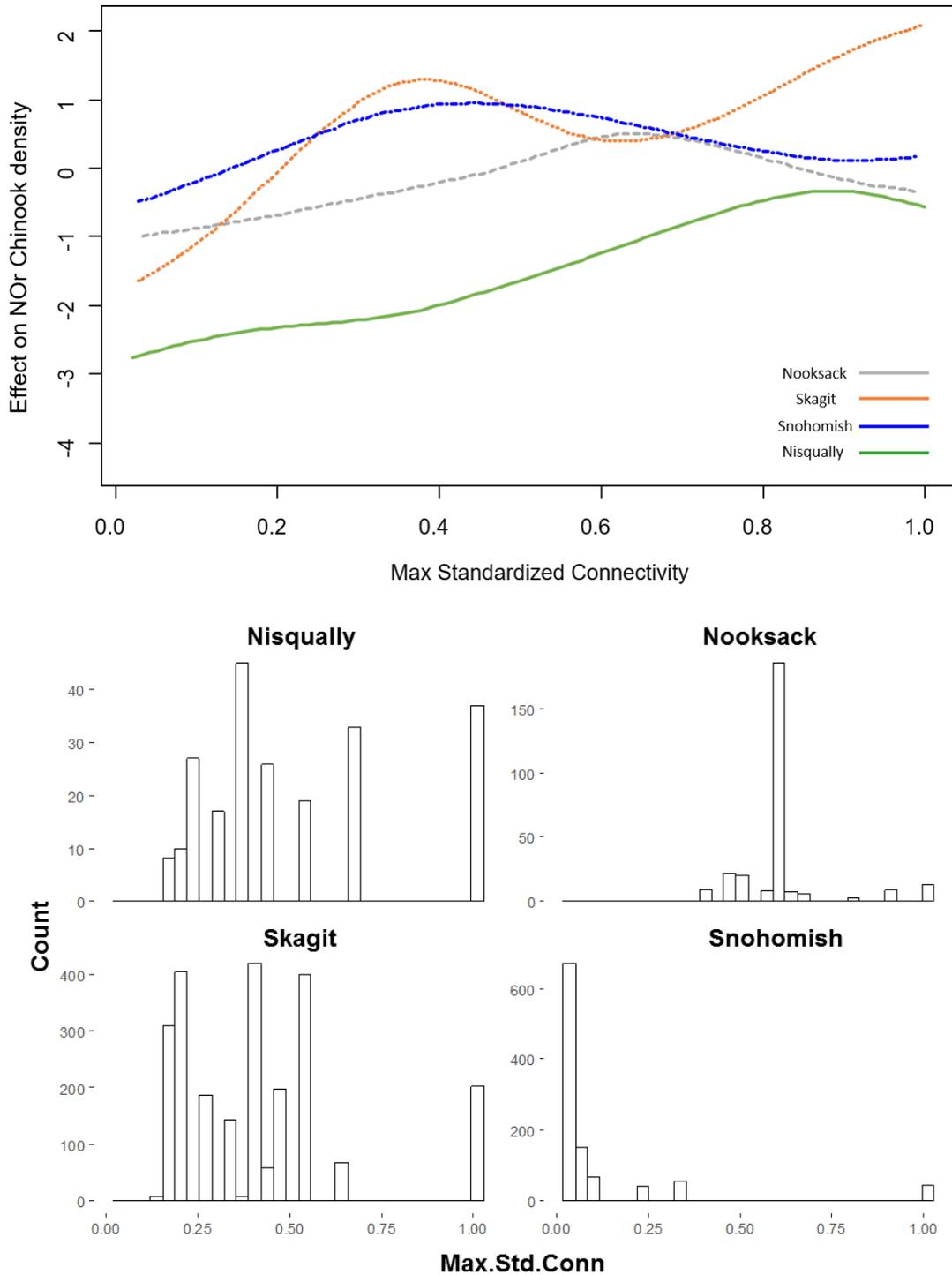


Figure 2.9. Estimated effect of landscape connectivity (standardized by maximum value within each system) on NOr juvenile Chinook density when present by system (Skagit = orange, Snohomish = blue, Nooksack = gray, Nisqually = green) (top panel) and the frequency distribution of samples by landscape connectivity and delta system used in the model Note different Y-axis scales by system (bottom panels),

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HOr density when present

The statistical model that best explained HOr density (when present) was dominated by the interaction term week*system (Table 2.6), which likely reflects system differences in the release timing and abundance of hatchery fish. Four additional significant effects, in decreasing order of importance, were year > Max.Std.Conn > week*channel type > week*wetland type. Week was by far the single most important variable in the model, suggesting HOr density was strongly influenced by release timing (Fig. 2.4, lower right panel). However, week effects were also included in other important variables such as system, Max.Std.Conn, and channel type.

Overall, the Skagit Delta had the lowest HOr Chinook densities and the Nisqually Delta the highest; the Nisqually and Nooksack HOr densities peaked around week 22 (late May), earlier than the Skagit and Snohomish systems which peaked around week 25 to 27 (mid-June to early July) (Figs. 2.10, 2.11). HOr densities in the different deltas were consistent with differences in the numbers of fish typically released by hatcheries in the different systems (Table 2.1). For the Nisqually, Nooksack, and Skagit deltas, HOr Chinook densities were similar between channel types for much of the ascending density curve, but distributary channels had higher HOr densities at peak times and on the descending portion of the curve (Fig. 2.10). This channel-type pattern likely reflects the migration behavior of HOr salmon. The release size and timing of HOr

Table 2.6. Smooth term parameters from global model fit to positive HOr densities in all systems. Terms in bold contributed significantly to fit and define the best model.

Model Terms	edf	Ref.df	p-value
s(week)	1.513	14	0.000
s(system)	0.767	3	0.000
s(Year)	7.159	24	0.015
s(max.std.conn)	4.252	19	0.000
s(max.std.conn,system)	3.946	50	0.187
s(week,wet.type)	2.428	27	0.021
s(week,chan.type)	2.856	18	0.000
s(week,system)	20.42	39	0.000
s(chan.type):systemNisqually	0	2	0.712
s(chan.type):systemNooksack	0	2	0.861
s(chan.type):systemSkagit	0	2	0.909
s(chan.type):systemSnohomish	0.976	2	0.000
s(wet.type):systemNisqually	1.046	3	0.001
s(wet.type):systemNooksack	0	3	0.702
s(wet.type):systemSkagit	0	3	0.665
s(wet.type):systemSnohomish	0	3	0.286
s(wet.type)	0	3	1.000
s(chan.type)	0	2	1.000

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salmon is similar to that of natural parr migrants which tend to rear little in natal delta blind channel habitat. Instead, their densities are higher in distributaries which they use to move through the delta to marine waters. The Snohomish system was unique (Table 2.6) in that it had higher densities of HOr Chinook in blind channel habitat than distributary channel habitat on the ascending curve and equal densities by channel type at the peak and descending portion of the curve. This result is most pronounced in the Snohomish delta's EEM blind channels (Fig. 2.11).

Seasonal patterns in HOr density also varied by wetland type (Fig. 2.11) though the differences were less discernible than those for NOr juveniles (Fig 2.7). In contrast to patterns observed for NOr density among wetland types, HOr density was generally higher in EEM and FRT habitats earlier in the season while densities in EFT were considerably lower. The observed pattern continued through the period of peak densities in all habitats (week 25-26). After the period of peak HOr density there was no apparent difference in observed differences among the wetland types and densities consistently decreased throughout the remainder of the rearing period.

Similar to NOr Chinook, we did not find overall statistically significant differences in HOr density by wetland type, although one system (Nisqually) had a unique pattern (Table 2.6). Graphically, there was no obvious trend for NOr densities across wetland types, although the HOr density differences among systems are easily observed (Figure 2.10).

Max.Std.Conn was a significant part of the statistical model, but it explained only a minor part of the deviation in HOr density and did not differ by delta system (Fig. 2.12 top panel). The same imbalances in connectivity values by delta system within the data (Fig. 2.12 bottom panel) described above for NOr Chinook densities undoubtedly hinders our ability to detect the influence of landscape connectivity on HOr juvenile Chinook densities too. However, it is reasonable to expect less effect from the delta systems because HOr Chinook across systems have more similar timing and densities than NOr Chinook across systems (compare Figs. 2.7 and 2.10). Overall, HOr juvenile Chinook were less influenced by Max.Std.Conn than NOr juvenile Chinook (Figs 2.9, 2.12), probably because HOr juvenile Chinook migrate more quickly through deltas, rather than rearing within them.

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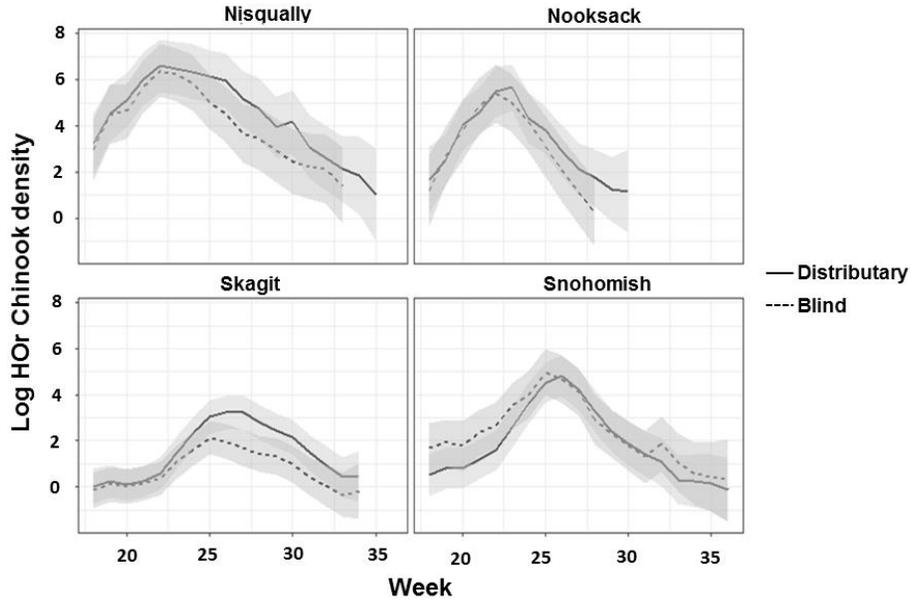


Figure 2.10. Model fitted estimates of HOr juvenile Chinook density when present by system, week, and channel type. Fish density is log transformed fish/hectare. Shaded area reflects values within the 95% confidence interval based on the model's standard error.

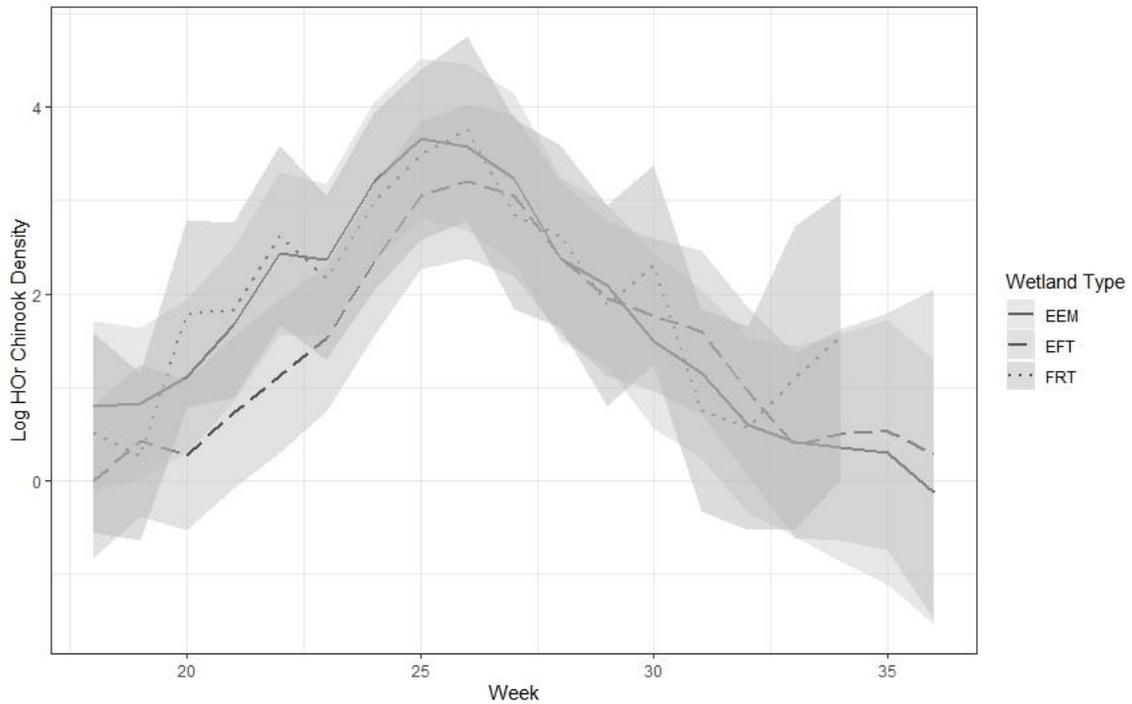


Figure 2.11. Model fitted estimates of HOr juvenile Chinook density when present by week and wetland type. Fish density is \log_e transformed fish/hectare. Shaded area reflects values within the 95% confidence interval based on the model's standard error.

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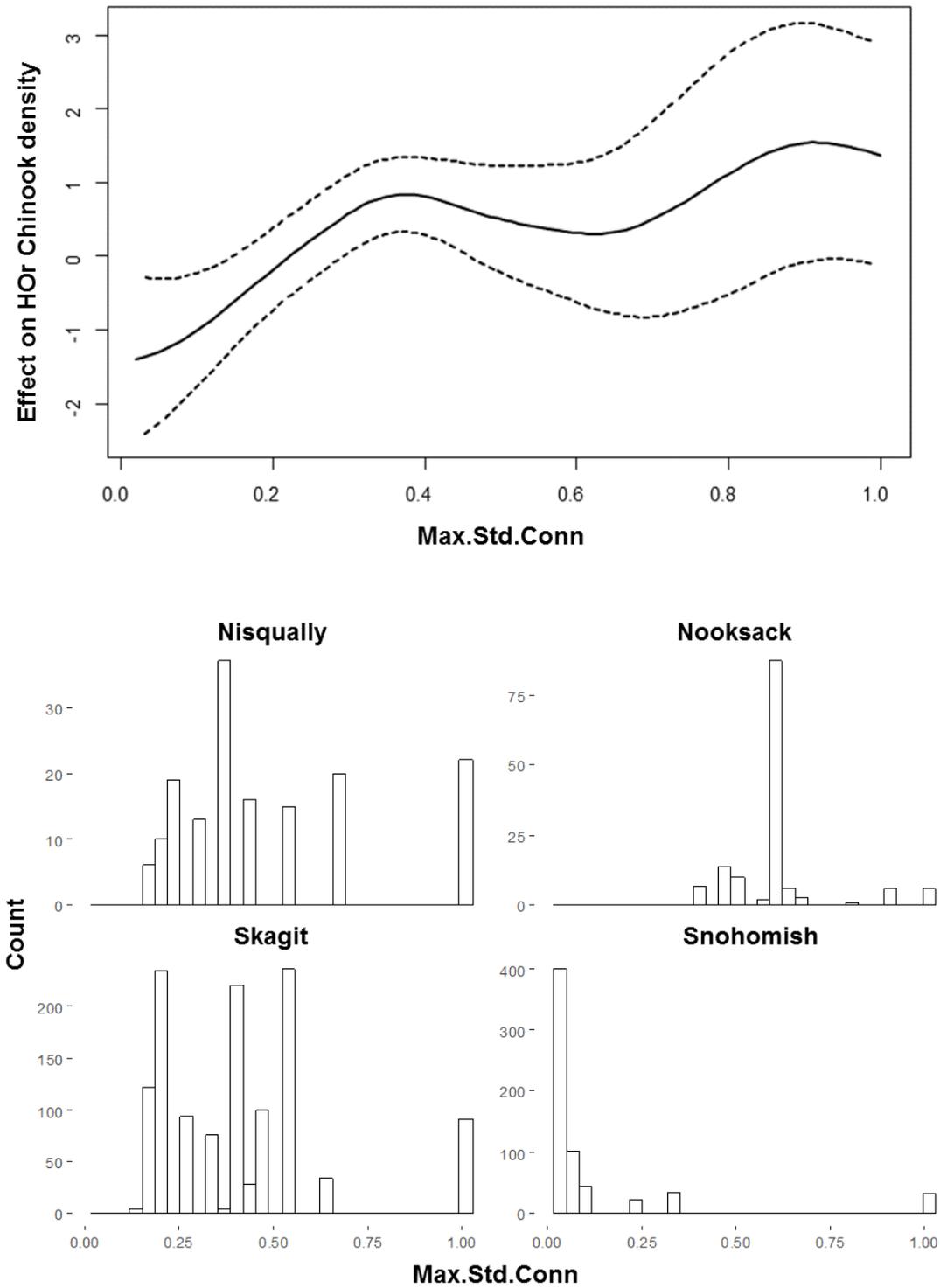


Figure 2.12. Estimated effects of landscape connectivity (standardized by maximum value within each system) on HOr juvenile Chinook density, when present for all systems combined (**top panel**) and the frequency distribution of samples by landscape connectivity and delta system used in the model; note different Y-axis scales by system (**bottom panels**).

Discussion

Our analysis of unmarked, natural-origin, and marked, hatchery-origin juvenile Chinook salmon density revealed strong landscape-based patterns, as well as strong intra- and inter-annual effects. Landscape effects included delta system, channel type, landscape connectivity, and their interactions. Seasonal effects were expected from the well-known natural history of juvenile salmon seaward migration timing through river deltas (Healey 1982). Intra-annual density can also vary greatly (Beamer et al. 2005, Ellings et al. 2016) depending on seasonal variation in local habitat characteristics such as depth (Bottom et al. 2005), temperature (Neilson et al. 1985), salinity (Levings 2016), and dissolved oxygen (Beamer et al. 2017). These characteristics likely produce variation around the central tendencies generated by landscape features (e.g., channel type and tidal wetland type, Fig. 2.6). Inter-annual variation can be caused by variation in out-migration population size (see Chapter 3) and by inter-annual climate variation impacting habitat quality, e.g., through variation in river discharge, water temperature, and salinity (Greene et al. 2005).

Landscape effects

We focus on why landscape features might directly influence juvenile Chinook salmon rearing patterns. We recognize the potential to over-estimate the strength of correlations in analyses of fish abundance, and therefore discuss our interpretations considering the strength of the correlation; its consistency across multiple populations or units of observation (i.e., systems); plausible mechanistic explanations, and alternative/competing explanations (Hilborn 2016).

System

Delta system effects explained the largest amount of deviance for natural origin Chinook and the second-largest amount for hatchery origin Chinook (after week). Two types of system differences could contribute to this result: idiosyncratic differences between river delta systems and systemic differences related to river basin size.

Idiosyncratic differences include differences in river hydrology. Most of the Skagit basin is snow dominated and has a hydrograph that shows a late spring/early summer peak; most of the Snohomish and Nisqually basins are rainfall dominated with winter peak hydrographs; and most of the Nooksack is transitional between rainfall and snow dominated. These hydrographic differences affect Chinook salmon life history traits, such as spawn timing, age at spawning, age at outmigration, and body size (Beechie et al. 2006). Tidal range also varies among the deltas with a mean range of 2.6 m for mouth of the Nooksack, 3.4 m for the Skagit and the Snohomish, and 4.1 m for the Nisqually. This tidal variation affects tidal channel geomorphology, such that blind tidal channels are few and small in the Nooksack, large and abundant in the Nisqually, and intermediate in the Skagit and Snohomish, after accounting for the effects of delta surface area (Hood 2015). Thus, differences in tidal range between systems affects delta rearing habitat availability for juvenile Chinook and may thus affect fish densities differently in each system.

Additionally, variables related to dynamic environmental features such as water temperature, dissolved oxygen, turbidity, river discharge, and tidal range vary between systems. For example, systems with large mudflats (e.g., Skagit Bay and large restored areas in the Nisqually delta) might be expected to warm faster than systems with greater vegetation coverage, and estuaries in

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watersheds that drain abundant, large glaciers (e.g., Skagit) would be expected to have protracted freshwater inundation during the latter portion of the rearing season. Finally, hatchery practices likely vary idiosyncratically among river systems, especially with respect to release abundances.

Systemic effects of basin size may be a significant unaccounted factor, with multiple pathways for influencing fish densities and rearing habitat (Hood 2007). When the maximum observed fry migrant population size (from Table 2.1) is plotted against river drainage basin area (from Czuba et al. 2011); a power function nicely describes the positive correlation, with $R^2 = 0.93$ and a scaling exponent of 3.2, which indicates a strongly non-linear (allometric) increase in outmigrant population size with increasing basin size (Fig. 2.13). The scaling exponent of 3.2 indicates that migrant fry population size increases three times faster than basin size. This is likely the result of other non-linear consequences of basin size on spawning and rearing habitat abundance in the basin. For example, in tropical systems large rivers have been shown to have disproportionately larger floodplains than do smaller rivers, and this has been related to scaling of fisheries catches with river size (Perez Filho and Christofolletti 1977, Welcomme 1979). In Puget Sound rivers, the lengths of braided and side channel habitats in river floodplains scale with mainstem river length (Fig. 2.14, data from Appendix S1 of Hall et al. 2018), with braided channel length and side channel length increasing 50% and 30% faster than mainstem length, respectively. Wood jams, which create pool habitat for many fish species, including salmon, also scale with mainstem channel length (Fig. 2.15, data from Appendix S1 of Hall et al. 2018), with jam area increasing 60% faster than mainstem length.

However, when we compare the scaling of fry migrant population size with river size to the scaling of river delta tidal wetland area with river size (data from Simenstad et al. 1982), it is apparent that modern tidal wetland rearing habitat area does not scale as steeply as does maximum migrant fry population size, although the difference with historical tidal wetland area is much less (Fig. 2.13). Consequently, juvenile Chinook salmon density effects might be stronger in larger deltas, because they produce disproportionately more fish and because, at least in the case of the four river deltas that we examined, larger deltas have had disproportionately greater tidal marsh habitat loss. Thus, basin size and its cascading and interacting effects on habitat abundance and diversity, as well as on salmon productivity and life history diversity, is likely part of what explains system effects in our analysis.

Until now, differences in salmon ecology between watersheds have been seen as idiosyncratic. Each watershed has its quirks and those can affect salmon ecology in ways that are difficult to predict. An allometric perspective on watershed size and its consequences for habitat abundance and salmon production and natural history, could allow partitioning of delta system differences in salmon ecology into predictable watershed size effects and perhaps unpredictable idiosyncratic effects. With an allometric approach one could account for systemic basin differences by using basin size as a covariate in statistical analysis rather than as a categorical variable. Any statistical differences unaccounted by the covariate could then be further examined for idiosyncratic signatures. Such an allometric approach, however, depends on a larger sample size of systems than we could accomplish in this study.

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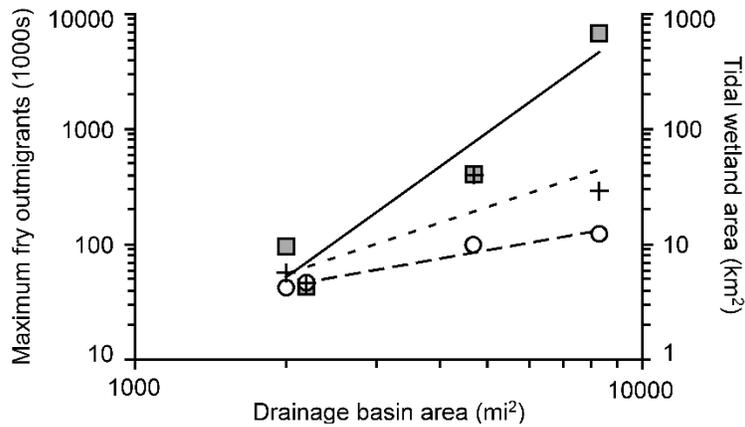


Figure 2.13. Scaling of maximum observed fry outmigrant population size (solid gray squares and left axis, $y = 4 \cdot 10^{-8} x^{3.2}$, $R^2 = 0.93$) with river drainage basin area. Scaling of late 19th century tidal wetland area (crosses, $y = 0.0004 x^{1.5}$, $R^2 = 0.78$) and 1980 tidal wetland area (white circles, $y = 0.24 x^{0.8}$, $R^2 = 0.95$) with river drainage basin area is shown for comparison on the right axis.

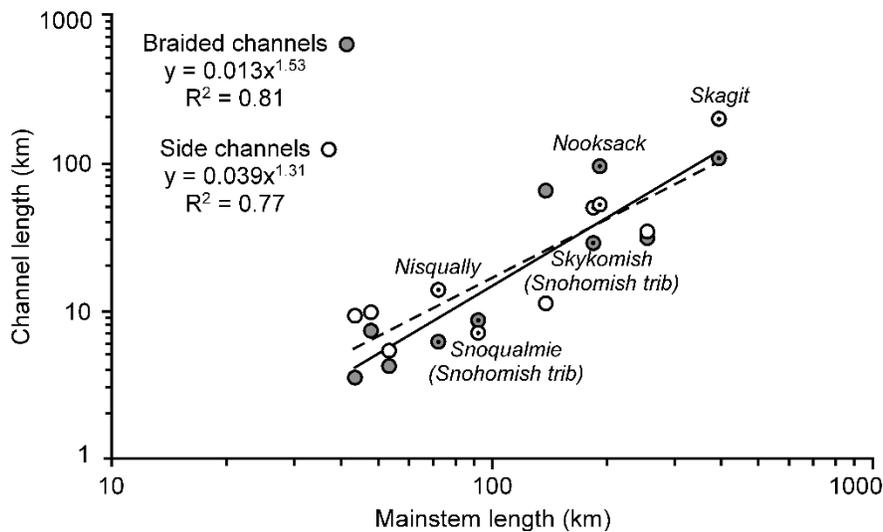


Figure 2.14. Scaling of braided channel length (dark circles) and side channel length (white circles) with mainstem river length, for a variety of Puget Sound rivers. Data from Appendix S1 of Hall et al. 2018. Braided and side channel lengths, which are often correlated with fish habitat, increase 53% and 31%, respectively, faster than does mainstem river length.

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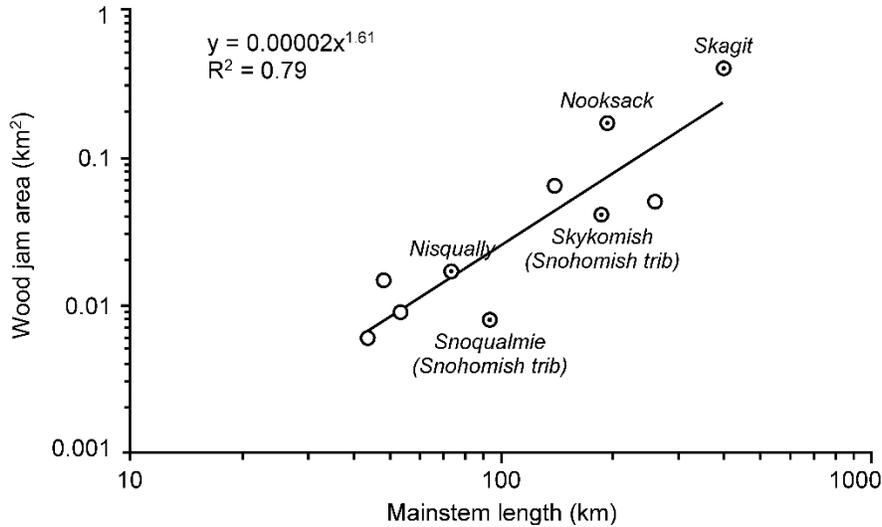


Figure 2.15. Scaling of wood jam area mainstem river length, for a variety of Puget Sound rivers. Data from Appendix S1 of Hall et al. 2018. Wood jam area, which is often correlated with pool habitat for fish, increases 61% faster than does mainstem river length.

Landscape Connectivity

This study reveals that landscape connectivity is an important predictor of NOr and HOr juvenile Chinook salmon density but not presence in all four river deltas. Overall, the landscape connectivity effect on HOr and NOr Chinook density is positive and not different between deltas for HOr Chinook but unique in each delta for NOr Chinook. Our method of calculating landscape connectivity, based on distance fish must travel and distributary channel branching, may not capture unique features within each delta that influences fish movement and residence. Our results show the Skagit and Nisqually deltas were best represented overall by our landscape connectivity method, while the Snohomish and Nooksack deltas had more non-linear results (Fig. 2.8 top panel). The Nooksack and Snohomish deltas have sampling site bias across the landscape connectivity gradient (Fig. 2.8 bottom panel). Despite data flaws, the non-linearity of our results may be exposing biological hotspots (or depressions) within each delta system. These may be related to delta system difference in habitat opportunity across deltas longitudinally (upstream to downstream) or differences in non-linear branching patterns of distributary channels across deltas which effects fish migration pathways.

We observed positive effects of landscape connectivity in all systems for NOr juvenile Chinook, as well as a strong system-connectivity interaction that reflect some non-linear aspects of connectivity for some deltas. Landscape connectivity tracks with tidal wetland type (as characterized by dominant vegetation types), because FRT sites are closer to the freshwater mainstem, while EEM sites are farther away and generally dispersed over a greater area of the delta along a network of serial distributary bifurcations. Additionally, because landscape connectivity describes the gradient from river to sea, it is a good predictor of physical habitat attributes, such as temperature and salinity, which interact with vegetation as well as the fish community (Beamer et al. 2005). Thus, connectivity can describe the physical dispersal of seaward-migrating fish over the delta as they travel along a ramifying distributary network, and

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it can describe spatial gradients in biotic and physical habitat attributes. Any variation in fish densities explained by characteristic vegetation communities and physical habitat attributes can also be explained by landscape connectivity. This autocorrelation likely reduced our ability to detect significant tidal wetland effects, independent of connectivity effects.

Effects of channel type

Juvenile natural origin Chinook salmon clearly exhibit higher densities in blind channel areas, consistent with extensive observations of utilization of these areas for rearing (David et al. 2014), which is likely due to their value as refuge from fish predators and areas of low velocities (Beamer et al. 2005) that reduce bioenergetic costs. Later in the migration season, natural origin Chinook use distributaries more than blind channels as they transition out of rearing habitats and into migratory pathways prior to moving to marine waters. Hatchery origin fish, which are released later in the year than the early part of the NOR outmigration curve and at a larger and physiologically more mature size, generally spend little time in blind channel rearing habitat, instead quickly migrating through distributaries to marine nearshore and offshore habitats.

Uncertainties

Like many efforts to document landscape effects on populations, our approach relies on determining associations between fish and their habitat. However, two natural experiments add to our confidence in landscape connectivity effects. In the Nooksack, a large log jam disconnected sites along a distributary; afterward the sites had lower fish densities (Beamer et al. 2016). Channel avulsion on the North Fork Skagit distributary increased landscape connectivity to some delta and adjacent nearshore locations, which thereafter had increased fish densities (Beamer and Wolf 2016).

We have mainly documented correlative patterns between channel types and juvenile rearing densities. Performing experiments to demonstrate cause-and-effect can be difficult at landscape scales, but it is possible in association with habitat restoration projects, as long as comprehensive effectiveness monitoring is used to document results. To better confirm the causal nature of our findings, we recommend comprehensive analysis of effectiveness monitoring across multiple projects (Flitcroft et al. 2016). For example, our results predict that increasing habitat complexity along distributaries would have smaller effects than enlarging blind channel networks for NOR Chinook migrants, especially the early component which are comprised of fry. Likewise, effectiveness monitoring could be used to evaluate whether reconnection of estuarine emergent marsh results in lower rearing densities than reconnection of forested riverine tidal areas.

An alternative to empirical evaluation of restoration experiments is modeling the movements of fish in estuary systems to determine whether landscape effects are emergent properties of individual behavior. For example, Haas et al. (2004) used an individual based model to infer habitat characteristics that increased estuary rearing by brown shrimp. While these models can further corroborate empirical patterns, the assumptions concerning individual behavior and how habitat variation affects behavior are often complex. Nevertheless, movement models afford a means to systematically test how various “rules” of fish movement and residence, based in part on landscape features, can produce systematic patterns in rearing density and other population

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attributes. As knowledge of fish behavior dynamics improves (Hering et al. 2010, McNatt et al. 2016), more accurate rules will emerge to verify these assumptions.

Our analysis assumed unmarked fish represented natural-origin migrants. For much of the rearing season, this assumption is valid, as migrant fry immigration into deltas generally precedes hatchery releases by one to three months. However, later in the season, unmarked fish may be NOR migrant fry that have reared extensively in the delta and grown to parr size, NOR parr migrants swimming to the sea from the river, or unmarked hatchery releases. Marking effort varies across hatchery programs; larger hatchery releases will have more accidentally unmarked fish simply because the small percentage of lost tags or missed marks result in a higher abundance than in smaller hatchery releases. To avoid errors in assigning NOR Chinook that are really unmarked HOr fish, we included data only for years with near-complete marking of hatchery releases. For example, from 2006 to 2015 unmarked hatchery Chinook releases in the Nooksack River have averaged <6,000 fish/year (Beamer et al. 2016). For hatchery Chinook salmon originating from the Skagit, 99.9% of the 764,570 fish released in 2002 (yearling and subyearlings combined) could be identified as hatchery fish based on the presence of an adipose fin clip or electronic wand for presence of a coded-wire tag (Beamer et al. In review). Marking practices in the Skagit have been similar to 2002 starting in 1995 to present. Even with near-complete marking of HOr migrants, NOR parr migrants can be expected in catches later in the season, particularly if sampling occurs in distributaries conveying NOR parr migrants to the sea. Despite this biological “noise” in our analysis, we believe the observed patterns are robust, as we obtained similar model results when using total Chinook salmon density (marked and unmarked combined). Further efforts to refine analyses could focus on earlier sampling and body size cut-offs for fry observations.

Future study

Numerous questions for future research arise from this study. However, we want to highlight one local system specific issue (the unique Snohomish delta HOr density pattern) and one broader issue to study (improved prediction capability for landscape connectivity effects on NOR Chinook abundance).

Landscape connectivity: Because landscape connectivity has such a strong influence on NOR Chinook density and because of its utility for restoration planning and monitoring, we suggest systematically examining alternate models of landscape connectivity for multiple deltas. We suggest study be organized around the following four nested fish migration hypotheses to ensure models make ecological sense:

1. Distance of migration pathways taken by fish predicts fish densities best.
2. Complexity of migration pathways taken by fish predicts fish densities best.
3. Distance & complexity of migration pathways taken by fish predicts fish densities best.
4. Distance, complexity & accumulation of rearing habitat of migration pathways taken by fish predicts fish densities best.

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The four hypotheses provide a framework to collect landscape data to calculate a measurement of landscape connectivity. Additional hypotheses should be nested within each general hypothesis. For example, ‘distance’ of migration pathways could be linear in the downstream direction based on distributary channel branches or based on hydrodynamic model results which may find flow directions within some deltas are not uniformly downstream. Additionally, for hypotheses using a ‘complexity’ of migration pathways component, fish migration could be considered ‘equal’ or ‘unequal’ after each distributary bifurcation in the two downstream channels. In this study, landscape connectivity was based on the ‘distance and complexity’ general hypothesis and considered (a) the distance of migration pathways to be linear based on a downstream direction and (b) the complexity of migration pathways to be unequal (based on differences in the downstream distributary channel widths) at bifurcation nodes.

Snohomish delta HOr Chinook density patterns: The Snohomish delta had a unique pattern for HOr juvenile Chinook presence and density compared to the three other deltas which were not predicted by systemic differences in the watersheds or deltas. Specifically, Snohomish Delta HOr Chinook were more likely to be present in blind channels than distributaries (Fig. 2.4) and had higher densities of HOr Chinook in blind channel habitat than distributary channel habitat on the ascending part of the seasonal timing curve (Fig. 2.10). Both results are the opposite pattern compared to the three other deltas. We speculate these unique results may reflect the location of a non-natal river hatchery near the mouth of the Snohomish Delta (releases not reported in Table 2.1), in addition to the hatchery releases from within river (releases reported in Table 2.1). Fish released from the nearby non-natal hatchery enter estuarine waters immediately, and some of these fish are known to utilize blind channels located in the lower Snohomish delta where there is an abundance of blind channel habitat (compared to the upper delta) prior to outmigration into more marine waters. We did not attempt to quantify the importance that any non-natal NOr or HOr fish migration pathways may have on deltas. The Snohomish is a good system to compare non-natal habitat use to what has already been studied in the Nisqually delta by Hayes et al. (2019).

Implications for science-based restoration

Our results suggest four general rules are likely applicable across Puget Sound estuary systems: 1) restore landscape connectivity, 2) reconnect blind channel habitats, 3) restore the diversity of estuarine wetland types, and 4) improve monitoring.

Restore landscape connectivity

Increasing landscape connectivity will improve the probability that large numbers of migrant fry will find blind channel rearing habitats. This has long applied to salmon and other diadromous fish at a variety of life stages and continues to be a focus of restoration in freshwater, estuarine, and nearshore habitats (Beamer et al. 2005). In many cases, increased landscape connectivity will accompany blind channel restoration, but this is not necessarily true for some projects. For example, plans for increasing the connectivity of the Swinomish Channel to the North Fork Skagit River distributary simply require breaching a man-made causeway or jetty; no additional restoration of historical tidal marsh from current agricultural use is necessary for this particular project (SRSC and WDFW 2005). Similar connectivity restoration has been recently

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implemented in the Fraser River Delta. It involved only breaching the Steveston jetty to allow juvenile salmon to access an otherwise inaccessible stretch of tidal marsh along Sturgeon Bank. Juvenile salmon responded instantly and dramatically to the jetty breach (The Narwhal, 2019). Hence, restoring landscape connectivity pathways provides an additional conceptual tool for restoration.

Reconnect blind channel sites

Blind channel sites offer the greatest opportunities for rearing fry, so increasing blind channel habitat will benefit natural-origin Chinook salmon populations dominated by subyearling migrants. Whether by means of large-scale dike removal/setback or breaches, restoring blind channel rearing areas should have greater benefits than “softening” existing channel margins or minor dike setbacks that create broader and shallower distributaries. Our recommendation may sound simplistic, but we want to emphasize restoration of blind channels must be done in the context of restoring natural processes over a large enough footprint to ensure success. Following allometry norms for Puget Sound delta systems (e.g., Hood 2007, 2015) will help ensure restored blind channel habitat features are both functional and sustainable.

Restore a diversity of estuarine wetland types

We originally hypothesized that some estuarine wetland types may be more important than others to juvenile Chinook salmon in tidal deltas, but interestingly, we did not find overall statistically significant differences in NOr or HOr presence or density by wetland type. While all wetland types were well used by juvenile Chinook in all delta systems, we did find some seasonal differences in densities among habitat types for both NOr and HOr juveniles that are likely important and suggest maintaining habitat diversity rather than advocating for specific habitat types is beneficial. Potential reasons for the observed differences, as they relate to growth potential, specifically, and the importance of habitat diversity are explored in depth in Chapter 4. The importance of habitat diversity for population productivity is well-documented (Schindler et al 2010, Brennan et al. 2019). Diverse habitat portfolios likely support increased life history diversity (Campbell et al. 2017), which in turn supports population resilience (Greene et al. 2010). The results of this chapter, and the supporting analysis in Chapter 4, suggest restoring habitat diversity be a primary focus of restoration planning in tidal deltas. Restoration planning that incorporates the spatial extents of habitats within each delta compared to historical conditions may help identify missing, or under-represented (i.e., gaps) wetland habitats specific to an individual delta that could improve conditions for individuals and promote population resilience

Improve effectiveness and status monitoring

Our results should help improve monitoring efforts. For example, use of a quantitative landscape connectivity metric as a covariate allows more accurate comparison of reference sites to treatment sites (Beamer et al. 2017), by acknowledging that low landscape connectivity sites will have lower fish densities than high landscape connectivity sites. Likewise, tidal wetland and channel type differences argue for better stratification in long-term monitoring programs tracking fish abundance, particularly when monitoring the effects of habitat changes caused by restoration or climate change (e.g., Greene et al. 2015).

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Appendix 2.1. Four Delta System Channel Area Estimates

Methods

We extracted estuarine river delta polygons from NOAA's habitat status and trends (Beechie et al. 2017) data layer for the four delta systems (Nooksack, Skagit, Snohomish, Nisqually). The Beechie et al. (2017) data layer was created from 2011 orthophotos and we refer to it as the '2011 delta layer.' We applied three steps to these data in order to calculate an estimate of channel area for juvenile Chinook salmon rearing for each delta.

First, we trimmed the dataset of unneeded polygons. The 2011 delta layer categorizes wetted areas as: distributary, industrial, primary distributary, tidal channel, tidal complex, and tidal flat. We excluded from analysis non-channel habitat types which are: industrial, tidal complex, and tidal flat. Excluded 'industrial' polygons areas were: 3.9 ha in the Snohomish delta and 28.5 ha in Swinomish Channel corridor. These polygons are all dredged boat harbors and are not part of our study's habitat types. Excluded 'tidal complex' polygons areas were: 0.92 ha, 38.12 ha, 16.41 ha, 10.21 ha for the Nooksack, Skagit, Snohomish, and Nisqually deltas respectively. Excluded 'tidal flat' polygons areas were: 0.00 ha, 0.00 ha, 0.64 ha, 14.90 ha for the Nooksack, Skagit, Snohomish, and Nisqually deltas respectively.

Second, we examined the 2011 delta layer to determine if it had a reasonable representation of the geographic extent for 'vegetated tidal delta' channel habitats, spanning the three possible estuarine vegetative zones: EEM, EFT, and FRT. To do this, we verified the accuracy and consistency of the (1) EEM zone on its seaward boundary and (2) FRT zone on its upstream boundary for all four delta systems.

1. For the seaward boundary, we found only Snohomish delta polygons needed to be trimmed on its marine boundary because the 2011 delta polygons included large areas of unvegetated tidal flat habitat, which are not part of our study. The other three deltas' marine side boundaries were fine, ending along the vegetated tidal delta boundary with unvegetated flats seaward and EEM habitat riverward. We also found the marine boundaries in the 2011 delta layer compared favorably with similar habitat status and trends delta polygons for the Nooksack (Beamer et al. 2016) and the Skagit delta (Beamer et al. 2015).
2. For the upstream boundary, we found all deltas did not include channel polygons for the full tidal upstream extent in the 2011 delta layer. The missing habitat was mostly mainstem or primary distributary channel habitat. Very little smaller distributary or tidal blind channel area exist in these unmapped areas. Because very little prime tidal rearing habitat is represented by these missed regions, and the omissions were consistent across systems, we did not edit the 2011 delta layer to include these omitted upstream habitats.

Third, we looked for omitted areas of known channel habitats within the 2011 delta layer polygons or adjacent to the lateral sides (not upstream or downstream) of each delta. We found two delta systems with significant omitted regions that needed to be included for our study.

2. Landscape determinants

1. The Nooksack delta was missing a complex of channels in the Silver Creek area upstream of Marine Drive. We included habitat results for this area using data for the 2013 habitat status from Beamer et al (2016).
2. The Skagit delta was missing channel habitat within the Swinomish Channel corridor and had assigned delta habitats located between the southern boundary of the South Fork delta (near the outlet of Big Ditch) to an area on the northern side of Camano Island known as English Boom as Stillaguamish delta. Since Skagit origin juvenile Chinook are known to dominate in these two areas (Beamer et al. 2007; Beamer et al. 2009), we included them using polygons from Beamer et al (2015).

We summed the area “tidal channel” polygons because juvenile Chinook salmon are known to utilize their entirety. For the two distributary polygon types, we calculated juvenile salmon rearing area based on perimeter length, assuming a 2-m buffer along polygon perimeters is prime rearing habitat. Total channel area results were summed by delta system (Table 1).

Table 1. Prime juvenile salmon rearing habitat area estimates by tidal delta.

Channel Type	Nooksack	Skagit	Snohomish	Nisqually
Distributary	10.41	34.62	28.05	4.51
Primary Distributary	4.52	4.03	10.14	1.83
Tidal Channel	29.02	255.31	98.41	242.48
Distributaries & tidal channel only	43.95	293.96	136.60	248.82

We noted the Nisqually delta has some very large and wide tidal channels, which results in a large total tidal channel area for such a small geomorphic delta. We reviewed the classification of these polygons with local experts and believe the large tidal channel area estimate for this system is appropriate.

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Appendix 2.2. Four Delta Landscape Connectivity Site Calculations

Methods

Landscape connectivity was defined as a function of both the length, width, and complexity of the pathway that out-migrating juvenile Chinook salmon must follow to access particular estuarine locations. Habitat connectivity decreases as the complexity and distance of the migratory path increase.

We created GIS layers of point data representing all sites used in this study. For each point, we calculated a landscape connectivity value according to the methods described in Beamer and Wolf (2011), utilizing a fish pathway arc layer. The GIS arc layer uses width measurements of distributary channels to calculate landscape connectivity for each site in this study. It reflects the pathways juvenile Chinook salmon are expected to move through the delta channel network and along the nearshore to find and colonize habitat represented by the fish sampling sites. Per methods described in Appendix D.V, page 79 of Beamer et al. (2005), values for channel bifurcation order were assigned to each channel polygon.

$$LC = \frac{1}{1 + \sum_{j=1}^{j_{end}} (O_j * D_j)}$$

where O_j = bifurcation order for distributary channel or nearshore segment j , D_j = distance along segment j of order O_j , j = count (1... j_{end}) of distributary channel or nearshore segments, and j_{end} = total number of distributary channel or nearshore segments at destination or sample point. One minor change in the calculation for this report, compared to Beamer et al. (2005), was that 1 was added to the denominator to insure the maximum value for LC equaled 1.

Channel width was measured at each bifurcating channel, and used to determine channel order per Table D.V.1. in Beamer et al. (2005) and repeated here as Table 1.

In a bifurcating tidal distributary network, multiple possible pathways exist to reach the same location. We focused on the maximum connectivity value of a site to the freshwater mainstem. Possible landscape connectivity values ranged 0 (completely isolated) to 1 (mainstem river at the head of tide). Higher values of landscape connectivity have a shorter and/or less complex pathway to the river mainstem, the source of fish.

Rules for determining bifurcation order (and subsequent channel-specific values of $O_j * D_j$) are as follows:

Arcs were digitized on-screen roughly down the center of distributary channels.

Measure (on-screen) each bifurcating (splitting) channel at head ($hdwid_ft$) and upstream channel just upstream of bifurcating channel ($uplkwid_ft$).

Divide $hdwid_ft$ by $uplkwid_ft$ and multiply by 100 to get the percentage of head width to upper width (PCT_value).

2. Landscape determinants

Use PCT_value to ascertain 'PlusBi' value from Table D.V.1. (Assignment of Distributary Channel Order for Channels that Split into Unequal Widths) from the Chinook Plan (SRSC & WDFW 2005). Please note that the table was edited in 2011 to include a "Plus 0" option if the PCT_value is greater than 75%.

Assign 'uplk_Bi' value for each arc that already has a Bi value for its upstream arc (this process is repeated as you work your way downstream).

Compute Bi for arc by adding uplk_Bi and PlusBi.

The following rules apply to Bi value determinations:

When two or more arcs come together, the Bi value of the resulting (joined) arc is the same as the smallest value of the incoming arcs (6,4=4). If the incoming arcs have the same Bi value, the value of the resulting arc is the value of the upstream arcs minus 1 (7,7=6).

Arcs to blind channel mouths are given a Bi value of the nearby distributary arc plus 1 (no measurements are made as outlined above).

In some cases, GIS Arc pathway locations and directions outside of the delta are needed to connect delta areas to each other. For arcs outside of the delta's region with defined distributary channels (i.e. downstream of the edge of the vegetated tidal delta), the Bi was determined following these rules:

Arcs flowing out of the delta into the bay get the Bi of the upstream arc plus 1.

When two or more arcs with the same Bi value come together, the Bi value of the resulting (joined) arc is the value of the upstream arcs minus 1 (7,7=6).

When two or more arcs of differing Bi values come together, the Bi value of the resulting (joined) arc is the same as the smallest value of the incoming arcs (6,4=4).

When an arc splits into two or more arcs, the Bi value of the downstream arcs is the Bi value of the upstream arc plus 1 (2=3,3).

Any arcs running along the front of the delta, out in the bay, are assigned the same Bi value all the way along, regardless of how many times it split off into truncated channels in the delta.

Short arcs were added from each nearby arc to snap to each sampling site. These arcs were given a Bi value of the nearby arc plus 1.

Fish migration pathway maps for each delta are shown as Figures 1-6. Significant natural changes in distributary channel pattern occurred within the period of fish data used in this study for the Nooksack and Skagit deltas. Thus, we created fish migration pathway for multiple time periods for these deltas to account for the distributary channel changes. In the Nooksack delta a large log jams formed during our analysis time period so we created fish migration pathway results representing the before/after logjam best orthophotos for each period. The before logjam period is represented by the 2008 orthophotos (Figure 1). The after logjam is represented by the 2013 orthophotos (Figure 2). In the Skagit delta a new distributary channel began to form in the

2. Landscape determinants

North Fork region of the tidal delta well upstream of any pre-existing distributary channels (Figure 3). This new channel has widened each year since becoming a dominant flow path within the North Fork tidal delta. The before the new distributary period is represented by the 2004 orthophotos (Figure 4 top panel). The after the new distributary period is represented by the 2013 orthophotos (Figure 4 bottom panel).

Table 1. Assignment of distributary channel order for channels that split into unequal widths.

Bifurcation order of downstream channel equals:	Downstream channel head-end width (% of upstream channel mouth width)	Low end of range	High end of range
Upstream channel order plus 1	60%	75%	45%
Upstream channel order plus 2	36%	45%	27%
Upstream channel order plus 3	22%	27%	16%
Upstream channel order plus 4	13%	16%	10%
Upstream channel order plus 5	8%	10%	6%
Upstream channel order plus 6	5%	6%	3%
Upstream channel order plus 7	3%	3%	2%
Upstream channel order plus 8	2%	2%	1%
Upstream channel order plus 9	1%	1%	1%

2. Landscape determinants

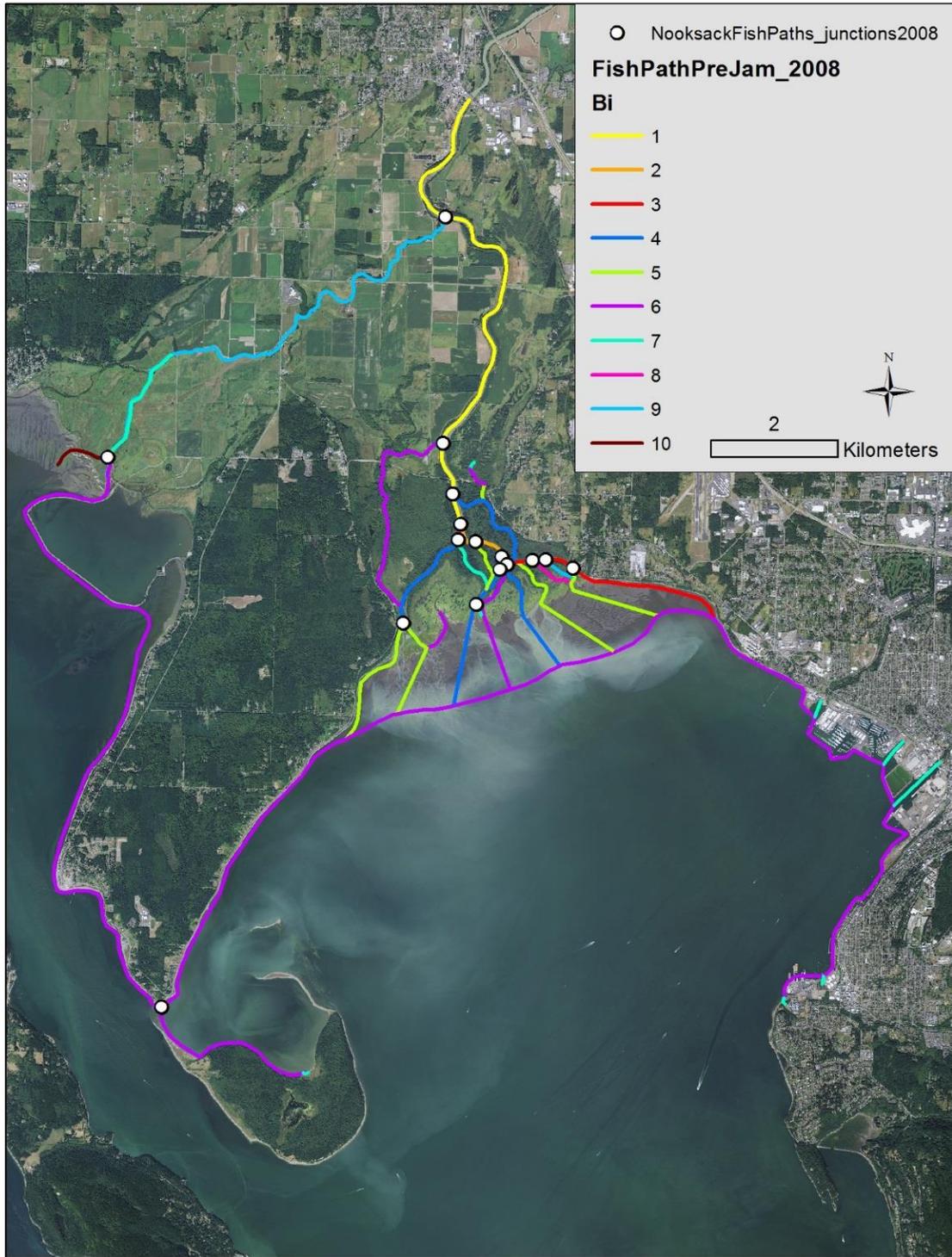


Figure 1. Nooksack Delta fish pathways arcs based on 2008 orthophoto.

2. Landscape determinants

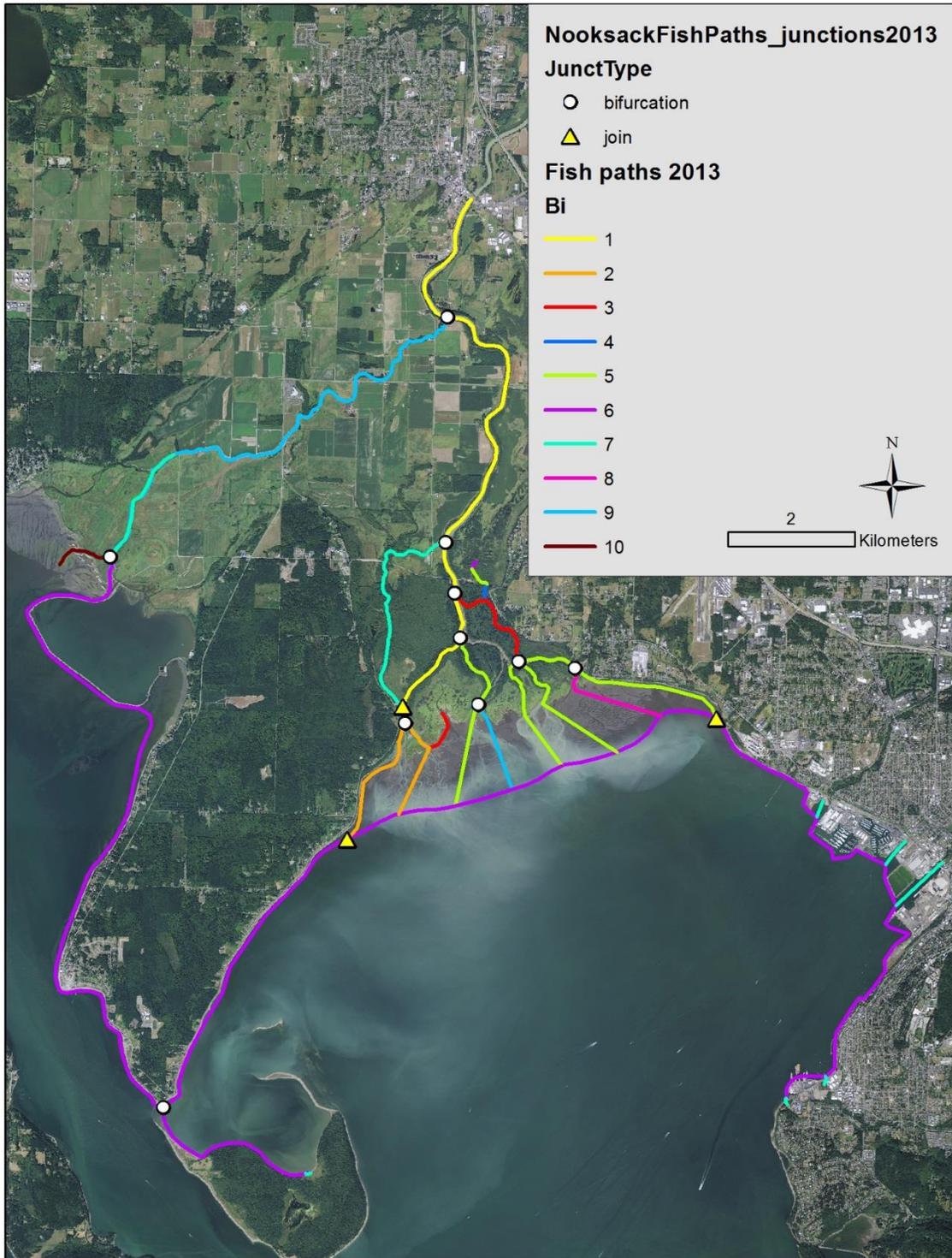


Figure 2. Nooksack Delta fish pathways arcs based on 2013 orthophoto.

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Figure 3. Fish migration pathway GIS data layers for the Skagit River tidal delta for 2004 (upper panel) and 2013 (lower panel).

2. Landscape determinants

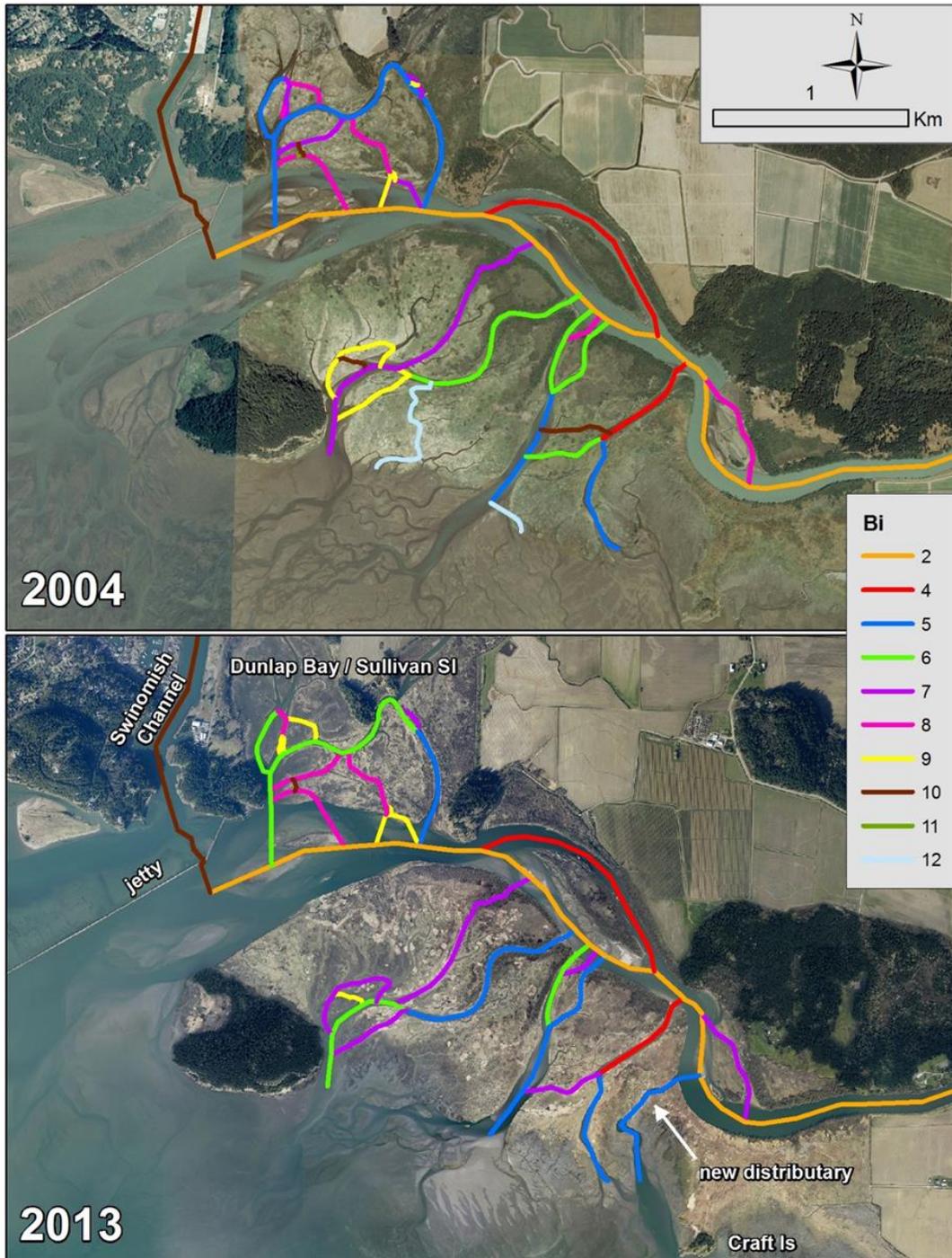


Figure 4. Distributary channel bifurcation order in the North Fork Skagit tidal delta before (top panel) and seven years after (bottom panel) the formation of the new distributary channel.

2. Landscape determinants

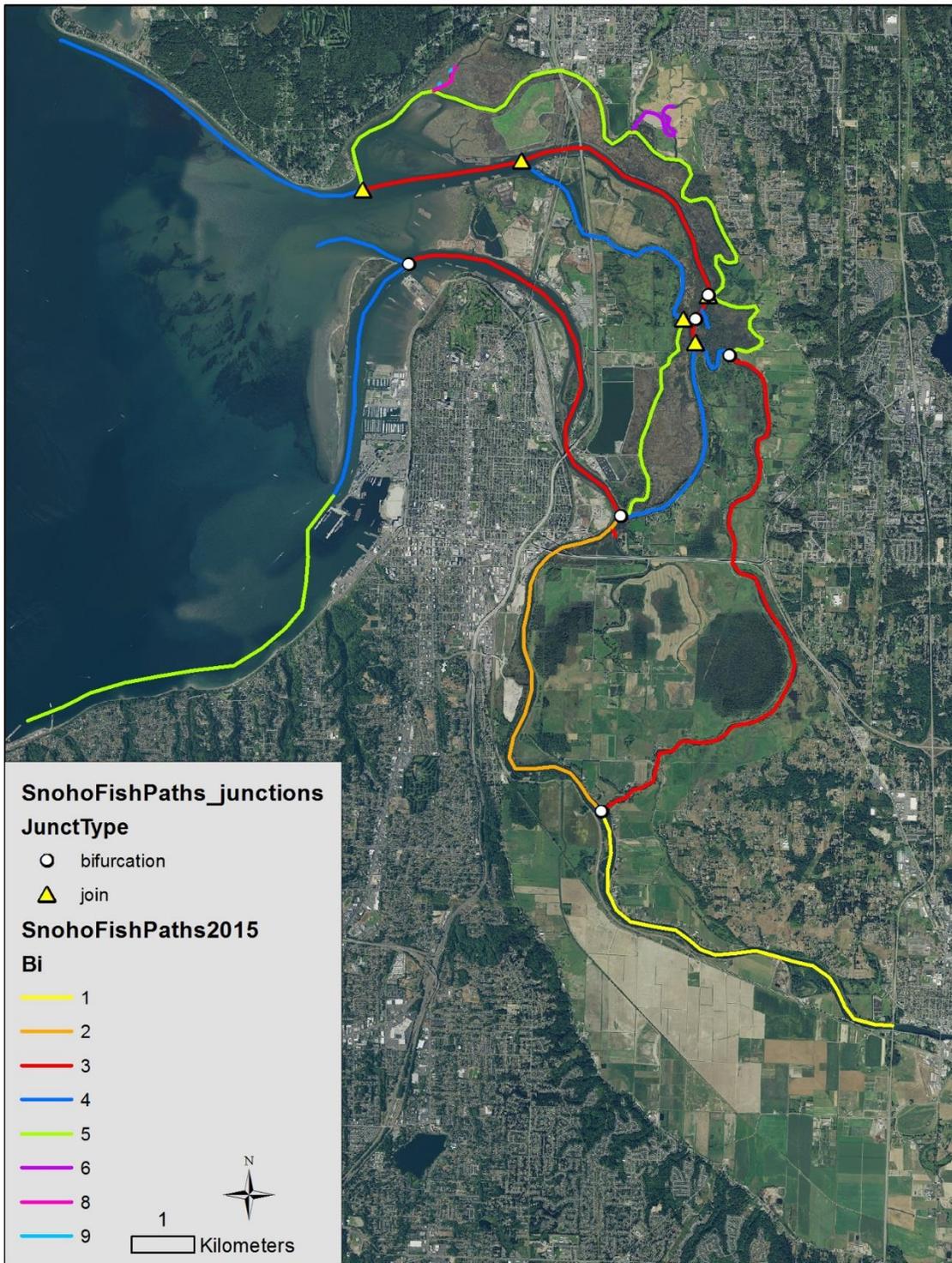


Figure 5. Snohomish Delta fish pathways arcs based on 2015 orthophoto.

2. Landscape determinants

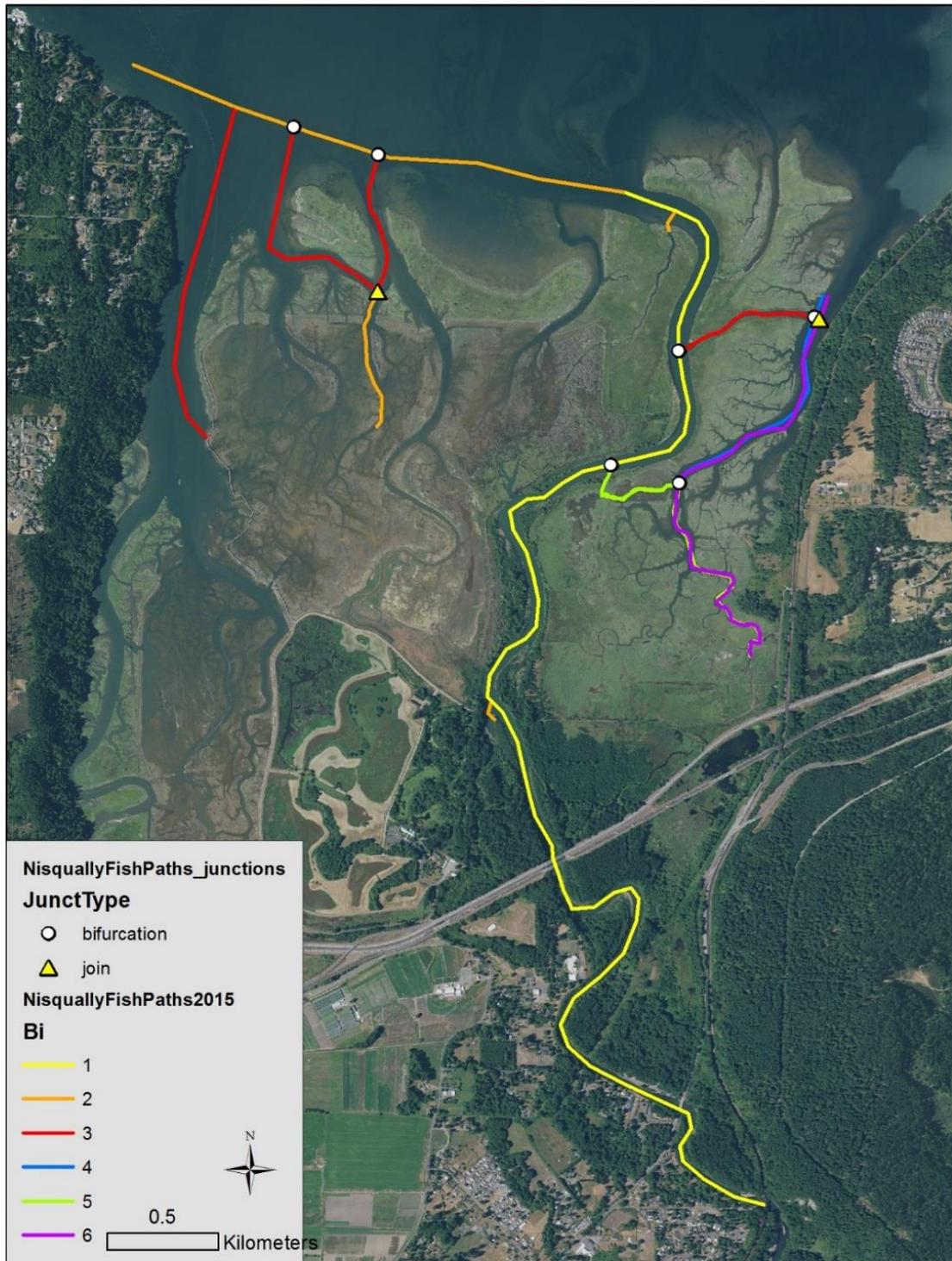


Figure 6. Nisqually Delta fish pathways arcs based on 2015 orthophoto.

2. Landscape determinants

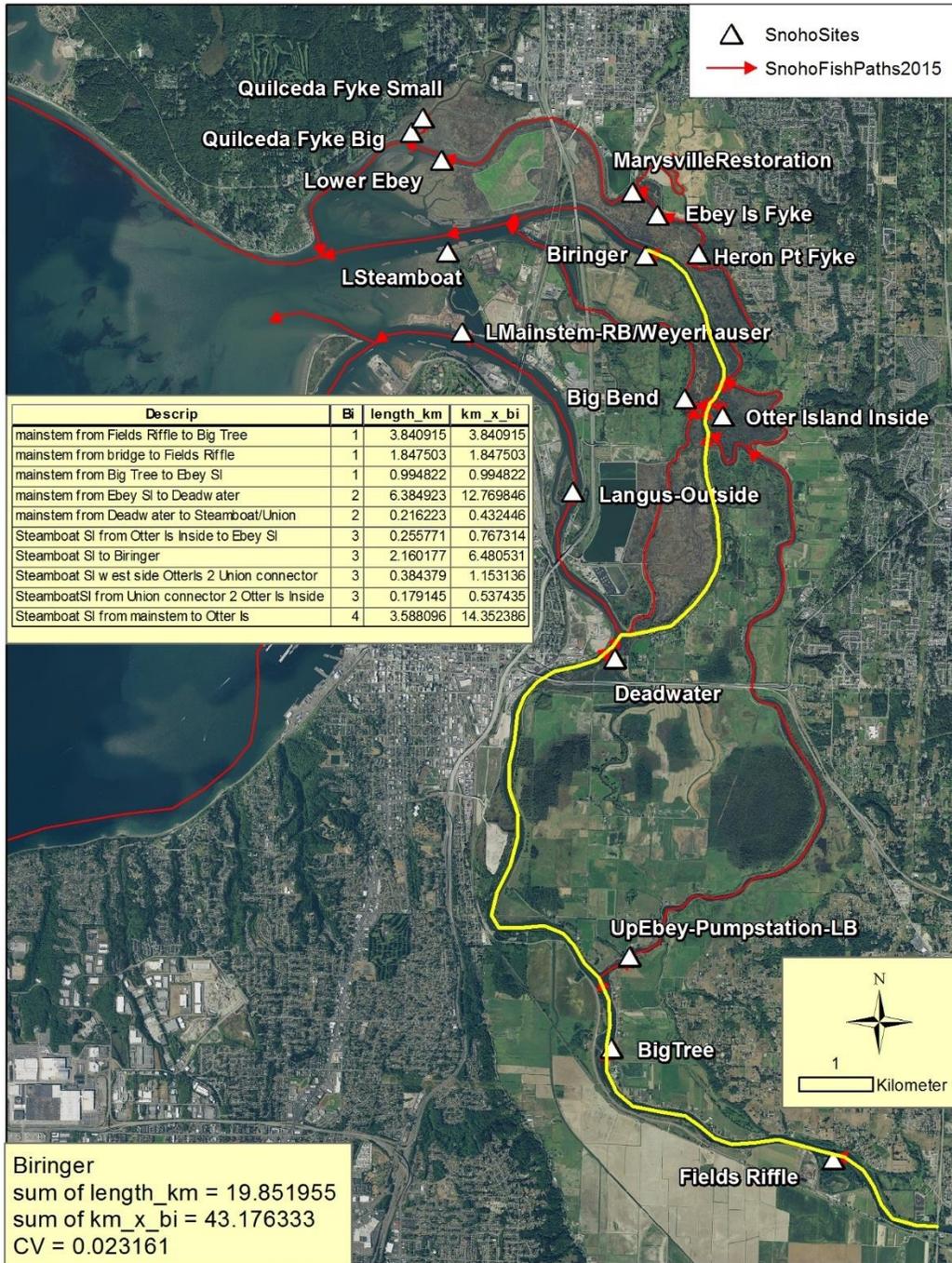


Figure 7. Example of the calculation of Landscape Connectivity for the Biringner site in the Snohomish delta from multiple pathways along different channel bifurcations (see inset Table).

Results

For each delta, the landscape connectivity values are oriented to juvenile Chinook salmon originating from within the delta's natal Chinook salmon river, i.e., Nooksack, Skagit, Snohomish, and Nisqually Rivers.

2. Landscape determinants

To calculate Landscape Connectivity to any given fish sampling site, we selected the arcs with the shortest and least complex route and used attributes associated with each selected arc to calculate Landscape Connectivity. Specifically, the length (in kilometers) of each arc (length_km) was multiplied by Bi (km_x_bi). These values are summed for each route to a fish sampling sites divided into 1 to give a Landscape Connectivity value to that site. Table 2 shows attributes used for Landscape Connectivity calculations. Possible Landscape Connectivity values range from greater than 0 to less than 1, but never achieving 0 or 1. Higher values of Landscape Connectivity are more connected (i.e., have a shorter and/or less complex pathway) to the source of fish. By example, calculation of Landscape Connectivity from upstream to the Biringer site in the Snohomish delta involves 10 pathways on 9 channel bifurcations (Fig. 7).

Table 2. Attributes used to calculate Landscape Connectivity, and their descriptions.

Attribute	Description
Bi	Index bifurcation order of route arc
Length_km	Length of route arc in kilometers
Km_x_bi	“Length_km” multiplied by “Bi”
Sum	Sum of all “Km_x_bi” values for a specific fish migration
Landscape	1/Sum

Detailed maps showing how Landscape Connectivity is calculated to each fish sampling site for each delta are listed below and are organized in alphabetic order by delta.

Mapped results to each site used in this study for the Nooksack and Skagit deltas was previously completed in earlier works (Nooksack – Beamer et al. 2016a; Skagit – Beamer and Wolf 2016 and Beamer et al. 2016b) and not repeated here.

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Nooksack Delta Sites

Mapped results to each site used in this study for the Nooksack delta was previously completed in Beamer et al. (2016a) and are not repeated here. Please see Beamer et al. 2016a for these maps. Landscape Connectivity varied by two time periods during our study due to the formation of a logjam within the delta (Table 3).

Table 3. Landscape connectivity values by site and year for the Nooksack delta.

Site	Lat	Long	Landscape Connectivity pre-logjam (<2010)	Landscape Connectivity post logjam (2010-pres)
Airport Creek	48.7780	-122.5607	0.063144	0.049068
Fish Pt	48.7722	-122.6007	0.061209	0.09033
Kwina Sl 1	48.7954	-122.5957	0.064896	0.100315
Kwina Sl 2	48.7934	-122.6053	0.064896	0.06015
Kwina Sl.Smokehouse	48.7868	-122.6047	0.049249	0.044708
Silver Cr 1	48.7897	-122.5837	0.084249	0.090661
Silver Cr 3	48.7798	-122.5649	0.06786	0.053926
Silver Cr Upper	48.7939	-122.5856	0.064196	0.070805
Tidal Delta 2	48.7724	-122.5922	0.04187	0.069248
W Chan Forested	48.7724	-122.6008	0.065944	0.092724
W Chan Saltmarsh	48.7673	-122.5957	0.051863	0.082232

Skagit Delta sites

Landscape Connectivity varied by year for four sites within the Skagit delta because of the development of the North Fork Skagit delta avulsion channel (Table 4). Mapped results to each site used in this study for the Skagit delta was previously completed in earlier works and are not repeated here. Please see Beamer and Wolf 2016 and Beamer et al. 2016b for these maps.

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Table 4. Landscape connectivity values by site and year for the Skagit delta.

Site	Lat	Long	Year	Landscape Connectivity
Browns Sl Barrow Ch	48.334061	-122.415512	all other years	0.015263
			2010	0.014487
			2011	0.013709
			2012	0.01439
			2013	0.014972
			2014	0.015651
			2015	0.016329
			2016	0.016329
Browns Sl Diked Side	48.337980	-122.414056	all other years	0.014584
			2010	0.013807
			2011	0.013612
			2012	0.013028
			2013	0.014196
			2014	0.014875
			2015	0.015554
Cattail Saltmarsh	48.363408	-122.480255	all other years	0.038831
			2010	0.039201
			2011	0.039477
			2012	0.039477
			2013	0.039477
			2014	0.039108
			2015	0.038739
DW Old Site	48.326473	-122.355113	all years	0.052133
DW Reference E Blind	48.308412	-122.367172	all years	0.029315
Fishtown Bar Area	48.360294	-122.468690	all years	0.045528
Freshwater Sl s20	48.326336	-122.369545	all years	0.044616
FWP New Site	48.314188	-122.377873	all years	0.035587

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FWP Old Site	48.314269	-122.378818	all years	0.036145
Grain of Sand	48.366068	-122.415199	all years	0.080967
			all other years	0.03391
			2010	0.034003
			2011	0.034003
Ika	48.365720	-122.503696	2012	0.034003
			2013	0.033349
			2014	0.03391
			2015	0.032788
			2016	0.032788
Swin Ch Old Bridge Blind	48.392042	-122.499144	all years	0.017392
Swin Ch Site 55	48.393101	-122.498307	all years	0.017199
Tom Moore	48.281397	-122.377935	all years	0.022865

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Snohomish Delta sites

Table 5. Landscape connectivity values for Snohomish delta sites.

Site	Lat	Long	Landscape Connectivity
Big Bend	48.0133	-122.1577	0.026195
BigTree	47.9333	-122.1690	0.149515
Biringer	48.0308	-122.1654	0.022674
Deadwater	47.9812	-122.1696	0.0478
Ebey Is Fyke	48.0358	-122.1632	0.017585
Fields Riffle	47.9201	-122.1281	0.351197
Heron Pt Fyke	48.0312	-122.1556	0.019319
Langus-Outside	48.0017	-122.1778	0.035866
LMainstem-RB/Weyerhauser	48.0209	-122.1976	0.027427
Lower Ebey	48.0421	-122.2029	0.012833
LSteamboat	48.0308	-122.2015	0.018838
MarysvilleRestoration	48.0386	-122.1679	0.016909
Otter Island Inside	48.0128	-122.1513	0.026195
Quilceda Fyke Big	48.0454	-122.2086	0.012151
Quilceda Fyke Small	48.0472	-122.2065	0.01176
UpEbey-Pumpstation-LB	47.9446	-122.1660	0.10778

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Nisqually Delta sites

Table 6. Landscape connectivity values for Nisqually delta sites. Multiple dominant pathways exist for some sites. We show results for two logical pathways for these sites.

Site	Lat	Long	Landscape Connectivity (higher)	Landscape Connectivity (lower)
Animal	47.0975	-122.6983	0.130888	
Control	47.0893	-122.6935	0.091074	0.087175
I-5 RB	47.0702	-122.7028	0.289773	
Lookout	47.0775	-122.7079	0.214762	
Madrone	47.0893	-122.7151	0.075871	
MCA RB	47.0886	-122.7255	0.062617	
N1	47.0963	-122.7227	0.080629	
NEEM 1	47.0920	-122.6979	0.150527	
NEEM 2	47.0977	-122.6980	0.134499	
Nugies	47.0857	-122.7080	0.184805	
Phase 2	47.0803	-122.6927	0.064459	0.053658
Ring Dike Slough	47.0867	-122.7073	0.182138	
RSS LB	47.0950	-122.6890	0.109528	0.063056
RSS Point	47.0895	-122.6912	0.092559	0.083494

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Appendix 2.3. Beach seine net dimensions and standard set areas

Table 1. Nets used in this study. Table shows dimensions, set style and set area covered by the net during various sampling protocols.

Net description	Net dimensions	Set style	Standard set area (m ²)
Small net beach seine	3 mm mesh, 1.8 m deep by 24.4 m long	small net beach seine method	96
Large net beach seine	3 mm mesh, 3.7 m deep by 36.6 m long	large net beach seine method	235
		Puget Sound Protocol method	206
LNRD BS 9x2	1.5 mm mesh, 2 m deep by 9 m long	small net beach seine method	26
		drag and haul	26-96

3. Density-dependent habitat limitations for juvenile Chinook salmon in four large river deltas of Puget Sound, WA

Correigh Greene^{1*}, Eric Beamer², Joshua Chamberlin³, Joseph Anderson⁴, Chris Ellings⁵, Sayre Hodgson⁵, Matthew Pouley⁶, and Todd Zackey⁶

*To whom correspondence should be addressed

¹ Fish Ecology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd E, Seattle WA, 98112, USA

² Skagit River System Cooperative, PO Box 368, LaConner WA

³ Fish Ecology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, NOAA, Mukilteo Station, Mukilteo, WA

⁴ Washington Department of Fish and Wildlife, Olympia, WA

⁵ Nisqually Indian Tribe, Department of Natural Resources, Olympia, WA

⁶ Tulalip Tribes, 6406 Marine Drive, Tulalip WA

Keywords

Chinook salmon, density dependence, tidal wetlands, estuary restoration, hatchery-wild interactions

Abstract

Efforts by people to restrain tidal inundation to promote agriculture and development has led to large amounts of tidal wetland habitat loss in large river deltas across the Pacific coast. These losses are one of multiple threats facing estuary-dependent species such as Chinook salmon, yet concomitant declines in these populations have raised questions about the extent to which juvenile Chinook salmon compete for limited estuary habitat and how estuary restoration will help recover populations. To examine the potential for habitat limitation, we used a cross-system approach to combine outmigrant and population density data in four large river deltas of Puget Sound. By adjusting outmigration abundance to natural-origin outmigrants/ha of delta channel, we were able to develop a statistical stock-recruit model that standardized outmigrations across all four estuaries. Our analysis revealed evidence for negative density dependence throughout the range of observed outmigration sizes. This was despite substantial variation in densities in deltas, even when outmigrations from rivers were high. Within each large river delta system, fish densities approached predicted capacity levels at some site or time in most years, although the frequency with which this occurred varied greatly by system. Furthermore, exceedance frequencies systematically varied across the season and in different habitat types. Capacity exceedance depended in part on hatchery releases, which have the potential to contribute to density dependence due to co-occurrence with natural-origin fish. Habitat-specific variation also

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existed in the highest observed population densities (90th and 95th quantiles) within deltas, and these levels were not greatly influenced by densities of hatchery-origin migrants in tidal deltas. These findings have important implications for monitoring programs, estuary restoration, and hatchery management.

Introduction

The idea that competition among individuals structures dynamic changes in a population's abundance and other attributes has a long history in the field of ecology (Lack 1954, Ricker 1954). Competitive dynamics come in many forms and can have important population consequences such as reduced growth (Chapman 1966), early migration at high densities (Chapman 1966, Reimers 1973, Greene and Beechie 2004), higher mortality (Ricker 1954), and population regulation (Turchin 1999). Such density-dependent phenomena are especially relevant to populations of managed species where individuals are harvested, or their habitats have been lost through natural and anthropogenic pressures. Analyses examining density dependence in specific life stages are particularly useful for linking field biology to management actions because the analysis can isolate whether a population is limited by conditions occurring within that life stage.

Density dependence has long been measured using a stock-recruit perspective: i.e., a nonlinear relationship between a population's abundance at a given time (stock) and the population at a future time (recruits) (Ricker 1954, Beverton and Holt 1957). While this approach is often conceptualized for density dependence between successive cohorts, it has also been used to address density-dependent transitions within cohorts (Mousalli and Hilborn 1986). For example, Barrowman et al. (2003) examined 14 stocks of coho salmon and found strong evidence for saturating relationships between spawners (i.e., stock) and juvenile outmigrants (i.e., recruits), typical of Beverton-Holt or hockey stick models.

Stock-recruit approaches have been criticized for a number of reasons, (e.g., temporal invariance of parameters despite dynamic environmental conditions, Walters 1990), and often fail to provide strong fits to data (Simmonds et al. 2011). Despite these weaknesses, numerous studies (e.g., Hilborn and Walters 1992, Myers 2001, Barrowman et al. 2003) note that stock-recruit approaches are important in multiple management contexts such as harvest forecasts because they provide an important basis for understanding how self-limiting populations will dynamically respond to management actions. Likewise, concepts of density dependence underpin views of management strategies to restore and protect habitat. If a population is considered to be nearing the capacity of habitats that support it, these habitats may be considered limiting factors to population recovery (Nickelson and Lawson 1998).

These concepts are particularly relevant for estuarine aquatic systems, which have undergone huge losses worldwide and now provide a fraction of productive habitat to fish and other species compared to what was historically available. For example, in urbanizing portions of Puget Sound and elsewhere in the Pacific Northwest, estuarine habitat loss has been estimated between 60-99% in large estuaries (Simenstad et al. 2011). This range mirrors summaries for the Pacific Coast (Brophy et al. 2019) and in other portions of the world (Lotze et al. 2006). For species that rely on estuaries during early rearing, these high levels of habitat loss may have exacerbated

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intra- and inter-specific competitive interactions, causing them to occur at lower levels of abundance. In this context, restoring wetland habitat (e.g., reconnecting isolated systems, restoring large areas of habitat to tidal inundation) should translate into improving productive capacity, and therefore allow declining estuary-dependent populations to rebound.

Here, we examine evidence for density dependence in Chinook salmon using thousands of observations in four large river tidal deltas in Puget Sound. Chinook salmon are an anadromous species listed as Threatened under the Endangered Species Act in many parts of its Pacific Coast range, including Puget Sound. Critical habitat for early life stages include tidal wetland environments for their safe, highly productive, and low energy rearing conditions (Healey 1980, David et al. 2016, Ellings et al. 2016, Davis et al. 2019, Levings 2016). Understanding the conditions under which Chinook salmon experience density dependence in different habitats can inform estuary restoration planning and implementation as a tool to recover populations. For example, results from the Skagit Intensively Monitored Watershed Project have documented multiple density-dependent mechanisms. As shown by the generalized relationships in Figure 3.1, density dependence in the tidal delta, as measured by transitions from river outmigrations of migrant fry to local densities in delta's wetlands (A), correspond to reductions in size (B), residence (C), and the frequency of fry migrating to Skagit Bay (D) and thereby bypassing an extended residence period in the delta (Greene et al. 2016). Notably, density dependence in size and residence occurred at much lower levels of outmigrant abundance compared to the pattern of density-dependent migration. These density-dependent relationships explain 44% of the variation in marine productivity as measured by adult returns relative to all subyearling migrants, indicating that density dependence in this particular stage can have important life cycle consequences.

While analysis of long-term data in the Skagit provides important perspective on density-dependent mechanisms for estuarine dependent species like Chinook salmon, it remains difficult to broaden these conclusions to other systems that vary in the size of their outmigrations as well as the size of available wetland habitat in their tidal deltas. Comparative analyses of different populations can help further improve understanding of density dependence by providing a broad range of habitat areas and levels of population density in different habitats. We take advantage of long-term monitoring of both juvenile outmigrations from rivers and subsequent rearing in the Nooksack, Skagit, Snohomish, and Nisqually deltas to examine whether estuarine rearing habitats for juvenile Chinook salmon exhibit similar patterns of density dependence across various outmigration population sizes.

Methods

Fish monitoring data

As noted in Section 2, Chinook salmon are characterized by extensive juvenile life history variation (Reimers 1978, Healey 1991). Three broad groupings based on size and age are yearlings (reared at least one year in freshwater), parr migrants (subyearlings that have exhibited growth in freshwater and outmigrate after 2-4 months), and migrant fry (fish <50 mm that have spent very little time in freshwater after hatching). While yearlings and subyearling parr migrants rear in freshwater before migrating to the sea, they are logically not expected to extensively rear

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as extensively in tidal deltas (Reimers 1973, Beamer et al 2005). Migrant fry may spend time in natal and non-natal tidal wetlands during outmigration to marine habitats. Subyearling hatchery fish appear to behave like parr migrants in that they do not extensively rear in estuaries (Lind-Null and Larsen 2010), although they are regularly recorded in sampling efforts (Davis et al. 2018), likely due to large numbers of fish released from hatcheries. Because our observations of

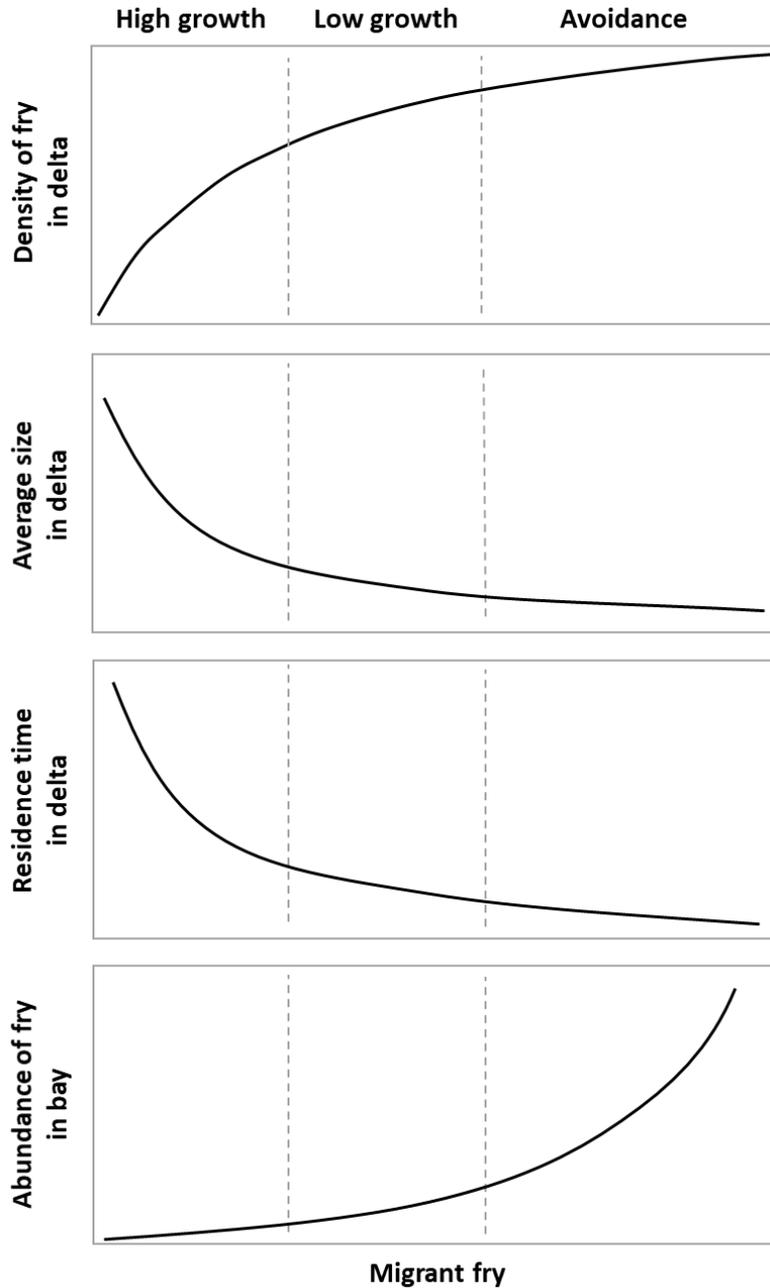


Figure 3.1. Generalized density-dependent relationships observed in natural-origin juvenile Chinook salmon using the Skagit delta, illustrating ranges of outmigrants (separated by dashed lines) supporting residency and growth, and density-dependent avoidance or migration (Greene et al. 2016).

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fish in tidal delta prevented us from separating parr migrants from fry with extensive rearing, we focused our analyses on all subyearling migrants (i.e., parr and fry) in analyzing the potential for density dependence.

The focus of this paper is on density dependence occurring in tidal deltas, using outmigrants as the “stock” and local densities of juveniles in large river deltas as the “recruits.” Our approach differs from other analyses of density dependence (e.g., Barrowman et al. 2003, Greene et al. 2016) in that we used data on fish densities summarized at the smallest spatial (site) and temporal (sampling event) resolution to build analyses of density dependence. Hence, rather than summarizing overall recruitment in a given year, we assessed what we considered instantaneous density dependence occurring throughout the season and years available, examining a considerable range of both number of downstream migrants entering large river deltas and local density of fish at different sites.

Outmigrants

Analyses of density dependence necessitated estimation of outmigrants from rivers. These include both natural-origin (NOr) juveniles and hatchery releases. For NOr juveniles, we used data from outmigrant trapping in all river systems. The methods for estimating outmigrants are summarized in Zimmerman et al. (2015), Klungle et al. 2018, and Hall et al. (2019), and include estimates of both fry and parr outmigrants from rivers. Briefly, fish were enumerated at screw traps during the outmigration season (February-July), and multiple capture efficiency tests of marked groups were used to expand trap counts. Fry and parr proportions were estimated based on size frequencies measured each week. Hatchery-origin (HOr) migrants were not systematically monitored at all outmigrant traps, so we did not attempt to estimate outmigration abundances of HOr migrants.

To match biweekly and monthly sampling of juveniles in estuaries with outmigrant data in rivers, we examined several possible summaries of the outmigrant data. The simplest summary is the weekly estimate of outmigrants observed the same time that juveniles were sampled in the delta. However, this match ignores extended residence of juveniles in estuaries that migrated downstream in previous weeks, which can range from 1 to 15 weeks in estuaries (Beamer et al. 2000, Lind-Null and Larsen 2010). Hence, we also summarized weekly outmigration estimates into two-week, four-week, and eight-week rolling sums. We examined the performance of these four summaries of outmigrants using raw correlations between outmigrants and estuary density and determined that eight-week rolling sums had the highest correlation compared with other summaries of outmigrant abundance.

In order to properly relate outmigrant abundance data with density estimates in the four tidal deltas, we converted outmigrants to outmigrants/channel area based on GIS analysis of total channel area within each tidal delta. This procedure resulted in density values (fish/ha) for both the “stock” and “recruit” variables in our analysis and corrected for differences across systems with differing outmigrant population sizes and estuary wetland extents. Total channel area included estimates of total blind channel area as well as distributaries. Data on channel area came from the Puget Sound Status and Trends project (Beechie et al. 2017), modified based on checks with independently derived estimates of channel area from the Nooksack and Skagit estuaries

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(Beamer et al. 2016, Table 3.1, Appendix 2.1). We focused on summations of distributaries and tidal channels, ignoring tidal complexes and flats, because they were not as associated with the habitat types in which fish densities were measured. We used total channel area (as opposed to

Table 3.1. Total channel areas (in ha) in four estuaries synthesized from cross-walked analyses in Beamer et al. 2016 and Beechie et al. 2017 of area in distributaries, primary distributaries, tidal channels (including blind tidal channels), tidal complexes, and tidal flats. The sum of distributaries and tidal channels (*italics*) were used for this analysis.

Channel Type	Nooksack	Skagit	Snohomish	Nisqually
Distributary	10.41	34.62	28.05	4.51
Primary Distributary	4.52	4.03	10.15	1.83
Tidal Channel	29.02	255.31	98.41	242.48
Distributaries & tidal channels	43.85	293.86	136.60	248.82
Tidal Complex	0.92	38.12	16.41	10.21
Tidal Flat	0.00	0.00	0.64	14.91
Total	44.87	332.08	153.65	273.83

wetland- or channel-specific subsets) because when outmigrants are enumerated at smolt traps, we have little means to predict where fish will later reside in estuaries, other than to expect dynamic movements among habitat types during outmigration.

Densities in large river deltas

We used all observations summarized in Chapter 2 of juvenile Chinook salmon captured at index sites in The Nooksack, Skagit, Snohomish, and Nisqually large river deltas (Table 2.1). As all fish captured in these sampling efforts were monitored for marks indicating HOr, we were able to calculate two density measurements: unmarked (presumed NOr) and total density (unmarked + marked density).

Habitat variation

We used data from Section 2 to describe three wetland vegetation types (forested riverine tidal (FRT), estuarine forest transition (EFT), and estuarine emergent marsh (EEM)) and channel type (distributaries and blind channels) in the fish density dataset and to determine whether these habitat types exhibited different density-dependent patterns. We considered landscape connectivity as a covariate, to control for site-specific sources of variation while testing for systematic differences in habitat types. This assumption followed from the results of Chapter 2 (see Fig. 2.6), whereby local density but not probability of presence of chinook was structured by connectivity. These results suggested the ability of the delta network geography to influence abundance in a density-independent fashion.

Statistical analysis

We combined data from all four systems into a stock-recruit analysis evaluated at the level of individual sampling event. This enabled us to detect levels at which density within tidal deltas might exceed predicted capacity at an instantaneous level, and to use this relationship to determine seasonal and landscape-dependent patterns of density dependence at larger spatial and

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temporal scales. Stock-recruit models incorporated data only for sampling events when fish were captured, but we included observations of absence when making predictions at larger spatial and temporal scales.

We modeled stock-recruit patterns as a Beverton-Holt relationship:

$$\text{Eq. 3.1} \quad \log_e(R_{t,i}) \sim \log_e((A*S_t/(B*S_t + 1)) + C*L_i + e)$$

where, $R_{t,i}$ is the density measured within the delta in a given time t (by year and week) at a site i , A and B are the fitted Beverton-Holt parameters, and S_t is the outmigrant density based on the rolling 8-week sum of outmigrants including and previous to the week in which estuary density was sampled. C is a covariate describing an assumed linear effect of landscape connectivity L_i .

To determine the likelihood that a density-dependent model is a better explanation than a linear relationship, the Beverton-Holt model can be compared with a density-independent model lacking the B term:

$$\text{Eq. 2} \quad \log_e(R_{t,i}) \sim \log_e(A*S_t + C*L_i + e)$$

Model assumptions common to both models are independence of data points, homoscedasticity, and log-normal distribution of error (e). Unlike model estimation of Eq. 2, the nonlinear model estimation for Eq. 1 does not assume additivity of parameters. We evaluated these predictions by visual inspection of covariance and residual patterns. We tested for density dependence by comparing the fit of the data to statistical models based on Eqs. 1 and 2 using likelihood ratio tests (Ogle 2016). All models and statistical tests were run using the FSA module in R (Ogle 2016).

Like all statistical models, stock-recruit models are designed to provide a fit of central tendency. In a well-performing model, the resulting fit will produce positive and negative error across the range of the independent variable describing the “stock”, and an estimate of “capacity” – the theoretical asymptote of the Beverton-Holt curve – determined by A/B . Positive error values at high levels of the “stock” are assumed as noise around the fit, yet they represent observations of fish densities exceeding the level of “capacity”. Recognizing the existence of landscape variation (Section 2) and the potential for different density-dependent processes to occur at different portions of the range of outmigrant abundances (Fig. 3.1), we produced several summaries of our results that helped us to address the following questions:

- 1) How does landscape variation affect habitat limitation (density dependence)? We addressed this question by producing different potential stock-recruit functions summarizing landscape variation.
- 2) Under what conditions do tidal deltas exceed their carrying capacity? To answer this, we analyzed observations of fish densities exceeding the stock-recruit function.
- 3) How do landscape variables affect the frequency of extremely high densities? We addressed this question by summarizing the 90th and 95th percentiles of density in different habitat types.

How does landscape variation affect habitat limitation (density dependence)?

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We examined several possible models incorporating density dependence in a landscape context. At the largest spatial scale, our observations were segregated by system. To examine whether our observations of density dependence were system-dependent, we compared a model combining data from all systems to “leave-one-out models”, in which data from each system were removed. Because these models differed in sample size, they could not be compared using information theoretical criteria such as Akaike’s Information Criterion (AIC). However, they were compared by examining root-mean square error (RMSE) as well as the estimate of theoretical capacity (A/B) produced by each sub-model.

At the smallest spatial scale, individual tidal delta sampling sites were characterized by wetland and channel type. We examined whether models summarizing data from particular wetland or channel types explained the data better than a single model estimated across all systems and habitat types. For this analysis we assumed that channel and wetland types might vary in terms of both A and B parameters. Hence, unlike the connectivity parameter, we modeled separate stock-recruit functions for different combinations of wetland and channel types. Each density-dependent model required four parameters – A, B, C, and e. Initial runs of the three wetland types indicated that models sometimes did not converge for FRT or EFT wetland types, so data from these sites were combined. Hence, when treating both wetland type and channel type (distributary and blind channel) independently, two separate curves (one for each wetland type and one for each channel type) could be produced, yielding a total of 8 parameters estimated. If examined in combination, four curves could be estimated (16 parameters estimated). We compared these models using Akaike’s Information Criterion (AIC), which weights the best models as those that explain the most variation using the fewest number of parameters (Burnham and Anderson 2000).

How frequently do tidal deltas exceed instantaneous capacity?

The capacity parameter (A/B) produced in the Beverton-Holt equation is a theoretical asymptote of population density within the delta, and therefore is predicted to occur only during the largest outmigrations. Therefore, we examined the predicted probability of the four systems to approach carrying capacity by comparing individual observations in each year to the 95% level of carrying capacity estimated in the best model. Because this threshold is in terms of outmigrant density, it can be applied to other systems with outmigrant trapping but lacking observations in the river delta. Furthermore, the model can be used to predict the delta densities when the 95% outmigration density threshold is exceeded. These values would be useful if sampling occurred within delta habitats in the absence of outmigration numbers and could be used to simulate whether addition of HOr migrants increases the likelihood of density dependence.

How do landscape variables affect the frequency of extremely high densities?

While the Beverton-Holt best fit provides a measure of central tendency in populations subject to density dependence, values of density with positive error represent observations of density above the capacity limit of the Beverton-Holt equation. As noted in Fig. 3.1, these may correspond to conditions of high competition and therefore low density-dependent productivity (e.g., as measured by individual growth). We examined whether observations of high density (90-95th quantiles of all density observations) varied by channel or wetland type.

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Results

Patterns of outmigrant and delta resident density across estuaries

The number of subyearling outmigrants varied greatly by week and year among the four large river deltas. Median weekly subyearling migrations ranged from over 2,000 in the Nisqually to over 60,000 in the Skagit, but in certain weeks and years, these numbers topped 45,000 and 1.5 million, respectively. Outmigrations from the Nisqually and Nooksack rivers were generally 5 to 25 times lower in outmigrant abundance compared to Snohomish and Skagit Rivers. Converting these numbers to outmigrant density by dividing by tidal wetland channel area increased the overlap of data among systems (Fig. 3.2, left column), but Nisqually outmigrant data nevertheless stood out as having a much lower outmigration density than the other three systems.

Weekly densities of NOr and HOr measured within deltas varied less than outmigration numbers when fish were present. However, presence/absence (observations of at least 1 fish present) varied greatly among large river delta systems (Fig. 3.2). This was true regardless of whether NOr or total density was considered, primarily because NOr numbers dominated the total density calculation. While these differences in presence/absence did not figure into stock-recruit estimation described below, they are important for determining the likelihood of population density approaching capacity as described below.

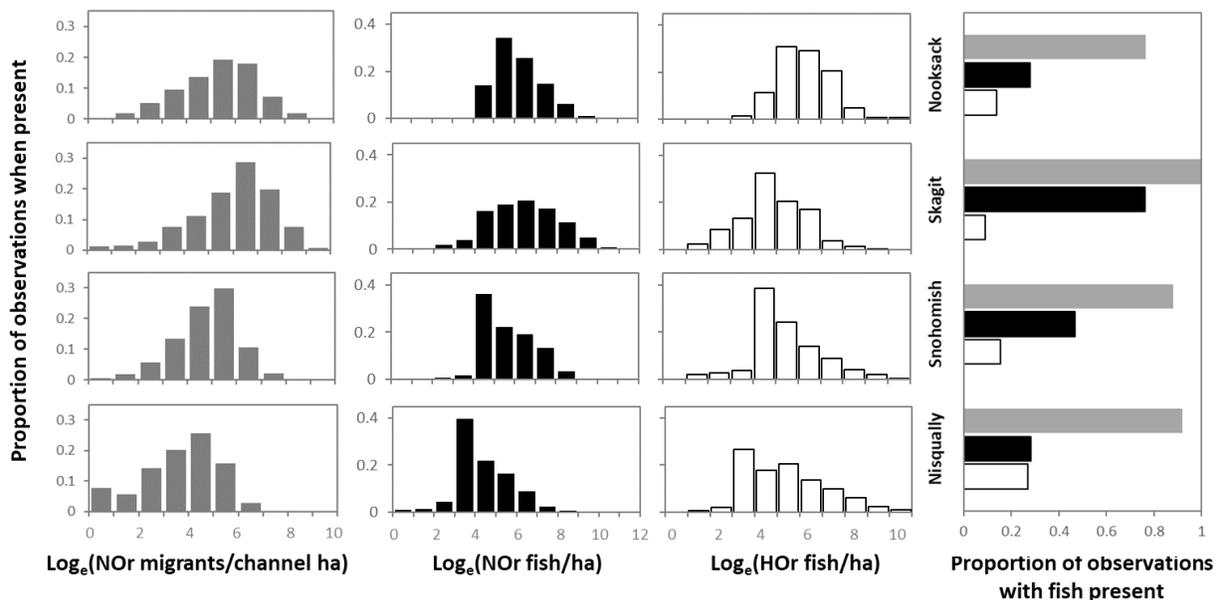


Figure 3.2. Proportion of all observations in Nooksack, Skagit, Snohomish, and Nisqually systems (top to bottom) of natural-origin (NOr) outmigration densities (gray bars), NOr delta densities (black bars), and hatchery-origin (HOr) delta densities (open bars) when juvenile Chinook salmon were present, and proportion of observations of fish presence (right column).

Variation in presence/absence of NOr juveniles and density when present was largely independent of outmigration size. In theory, one would expect presence/absence to be low for small outmigrations, and increase at higher ones. While this pattern was apparent for the Nooksack and to some extent for the Skagit (Fig. 3.3. left column), presence/absence generally showed strong stability within systems, such that 25-90% of sampling attempts captured 0

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Chinook salmon even during the highest outmigrations. Variation in log-transformed density was fairly similar across the range of different outmigrations (Fig. 3.3 right column), ranging from 5-30% of the mean. Translating back into actual densities implies substantial variation in local densities across the range of outmigration sizes.

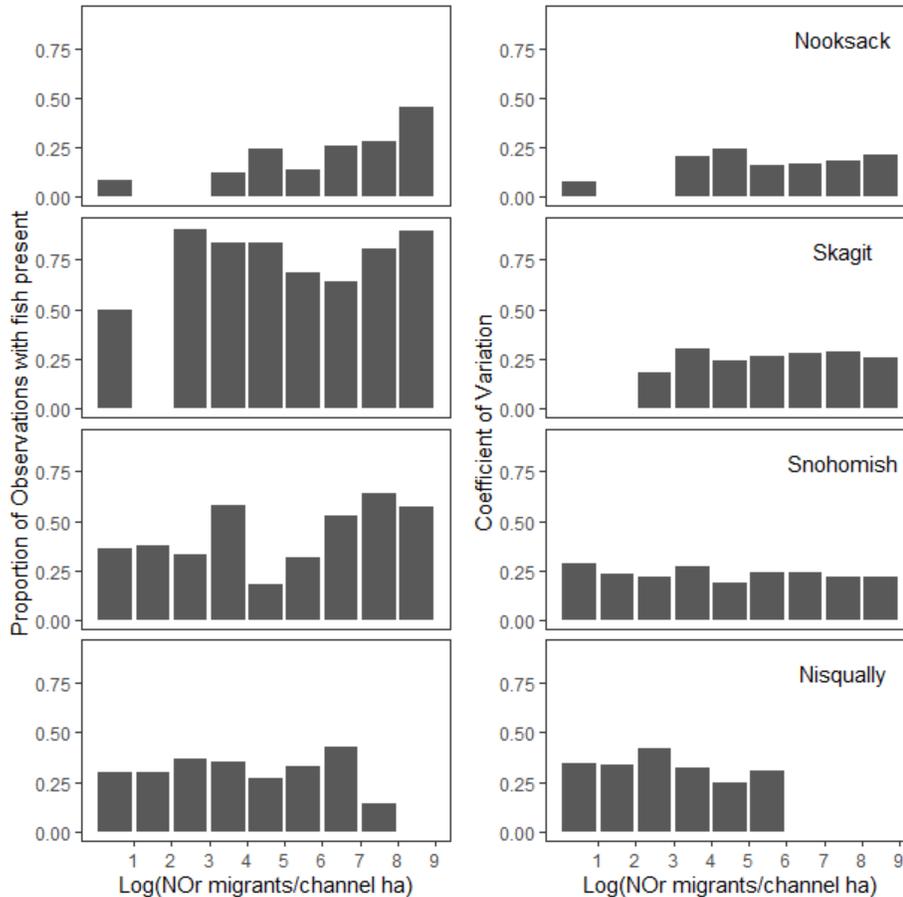


Figure 3.3. Left column: proportion of all observations with natural-origin (NOr) juveniles present in Nooksack, Skagit, Snohomish, and Nisqually (top to bottom) deltas as a function of 8-week rolling sums of outmigration densities (NOr migrants/delta channel area). Right column: coefficient of variation of log-transformed density when present as a function of outmigration densities. Data for ranges of the x-axis with < 3 observations were excluded.

We observed substantial overlap between presence of NOr and HOr salmon during management weeks (week of January 1 = week 1) associated with hatchery releases (Fig. 3.4). Within the subset of observations in which either NOr or HOr juveniles were present (4,158 observations across all years), the weekly proportion exhibiting co-occurrence peaked between weeks 17 and 36 in all four systems, significantly overlapping NOr residence (weeks 10-27, Fig. 2.5). Furthermore, the duration and peak level of co-occurrence varied by system, with Nisqually showing the largest co-occurrence and Skagit exhibiting the least. Within this time period, similar levels of co-occurrence existed within all three wetland types and two channel types, although levels differed across systems. Hence, NOR and HOR fish considerably overlapped in time and space between one quarter to over half of the typical NOR rearing period.

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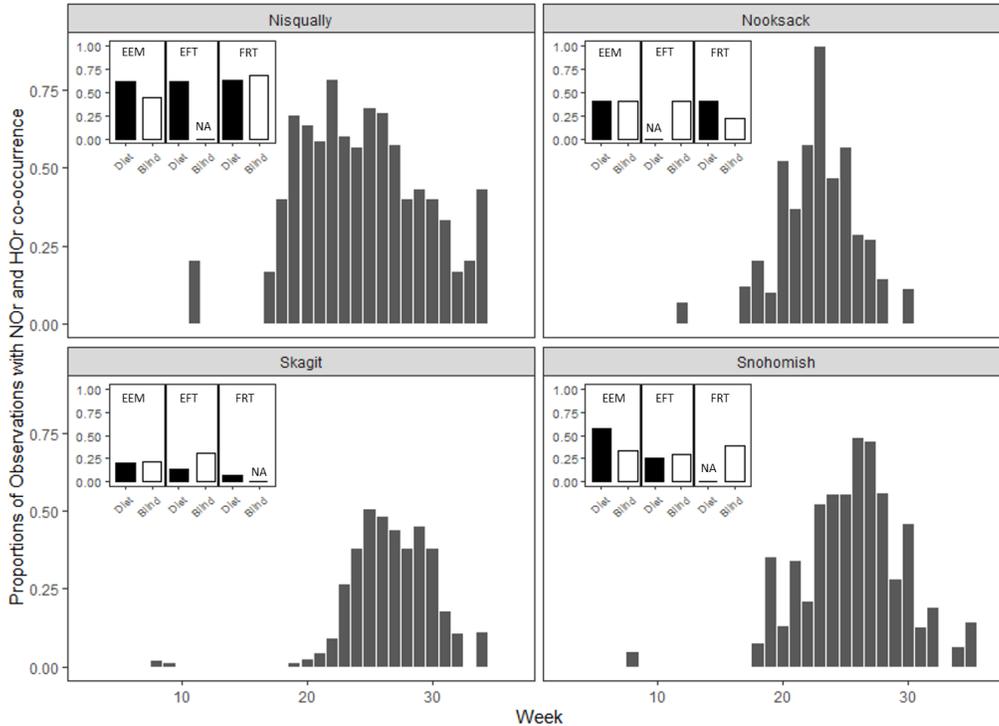


Figure 3.4. Proportion of all observations by management week of co-occurrence of natural-origin (NOR) and hatchery-origin (HOR) juvenile Chinook salmon in Nisqually, Nooksack, Skagit, and Snohomish systems. Inset bar graphs illustrate the same proportion limited to the period of co-occurrence (weeks 17-36) in three wetland types (EEM, EFT, and FRT) and two channel types (distributary and blind). NA indicates habitat types which were not sampled in each delta.

How does landscape variation affect habitat limitation?

System level patterns. We first asked whether inclusion of different river systems had a strong effect on model predictions by comparing a model including all systems with “leave-one-out models.” The model including all systems revealed strong evidence for density dependence compared to the density independent model without parameter B (likelihood ratio test $p < 0.001$), and included a moderate effect of landscape connectivity (Table 3.2). This model predicted habitat capacity at 252.7 fish/ha when connectivity was held constant at 0 (Fig. 3.5). This density is within the range in which we observed density-dependent declines in individual growth based on otolith microstructure (Appendix 4.3).

Predicted capacity did not strongly depend on data from particular systems. We found that leaving out Skagit data from the model reduced RMSE by nearly 15% and removed the effect of landscape connectivity (C). However, the difference in the estimate of capacity (A/B) was negligible compared to that predicted when all systems were included, and the total sample size was reduced by over 60%. Conversely, removing Snohomish observations increased RMSE by 5%, increased the effect of C, and reduced the estimate of capacity by nearly 8%. Leaving out Nisqually or Nooksack data had negligible effects on RMSE, C and capacity. Leaving out Skagit

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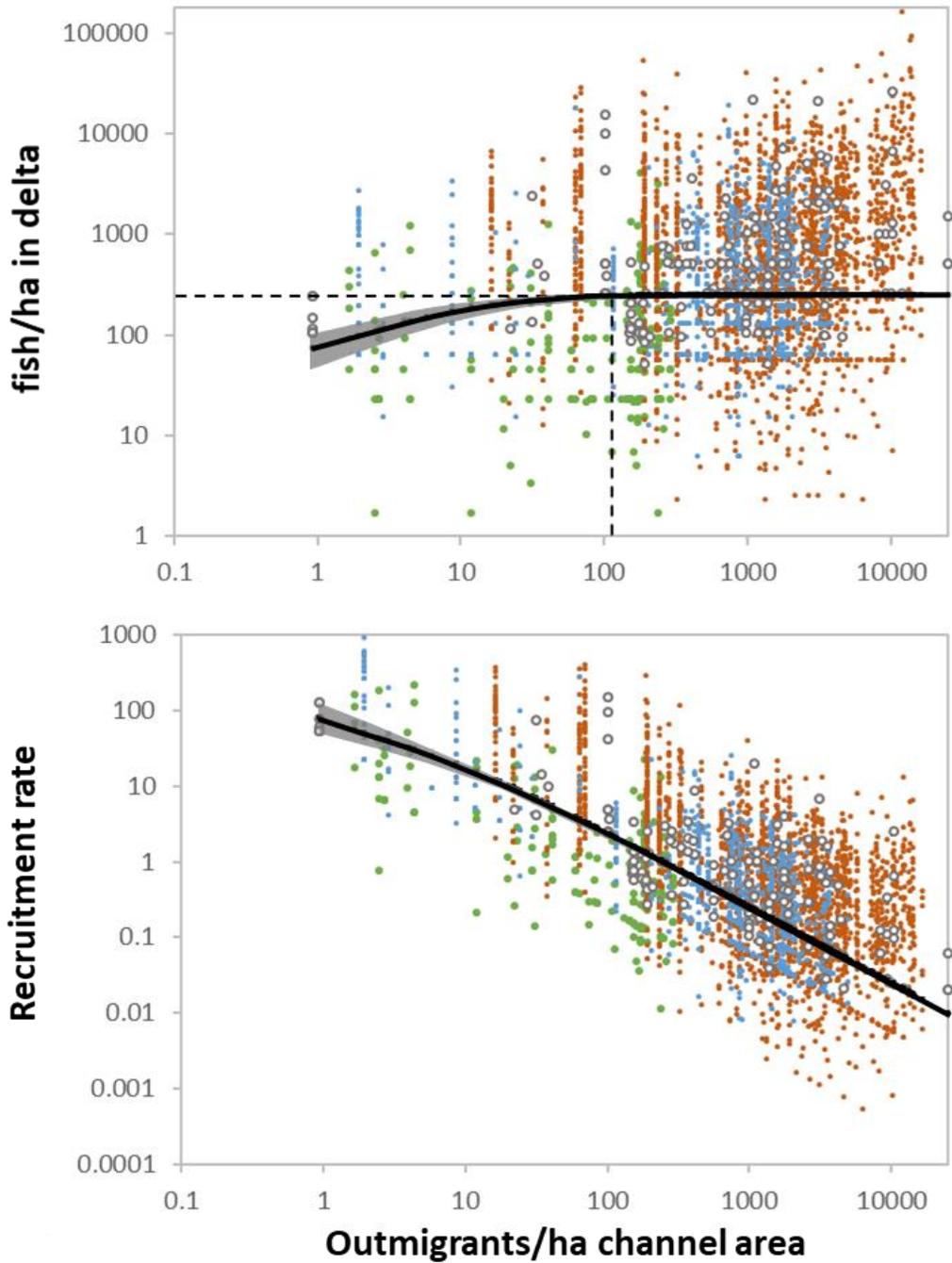


Figure 3.5. Beverton-Holt stock-recruit fit to combined data from four large river deltas (orange = Skagit, blue = Snohomish, open gray = Nooksack, green = Nisqually). The top panel shows the fit to the raw density data in terms of in-river natural-origin (NOr) Chinook salmon subyearling outmigrants standardized by hectares (ha) of delta channel area and corresponding density of fish captured in the delta. Black line indicates best fit (\pm 95% confidence intervals denoted by gray shading) of the Beverton-Holt relationship. Horizontal and vertical black dashed lines indicate 95% of habitat capacity estimated by model fit, and corresponding outmigrants/ha at that level of density in the delta. The bottom panel shows the recruitment rate (delta fish \cdot ha $^{-1}$ / outmigrants \cdot ha $^{-1}$), indicating negative density dependence across the range of observed outmigrants/ha.

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Table 3.2. Comparison of Beverton-Holt models combining data from all systems with “leave-one-out models.” A and B are the parameters in the stock-recruit function, capacity (A/B) is the asymptote of the function in terms of fish/ha, and C is the parameter for the landscape connectivity covariate. Root mean square error (RMSE) and sample size (number of observations in which fish were recorded as present) provide information on model diagnostics.

Model	A	SE	B	SE	Capacity (A/B)	C	SE	RMSE	Sample size
NOr density									
All systems	54.88	14.05	0.22	0.07	252.70	1.61	0.10	1.62	3588
Leave one out									
No Nooksack	51.29	13.82	0.21	0.06	247.28	1.74	0.11	1.63	3405
No Skagit	196.58	83.24	0.77	0.33	253.79	0.02	0.13	1.38	1354
No Snohomish	10.58	2.50	0.05	0.01	231.63	1.97	0.15	1.71	2607
No Nisqually	174.89	86.76	0.70	0.35	249.87	1.89	0.10	1.57	3398

or Nisqually data greatly increased the standard error of estimates for A and B parameters in the model. All “leave-one-out models” provided strong evidence for density dependent relationships (parameter $B > 0$, based on likelihood-ratio tests, $p < 0.001$).

Based on these results, we determined that all river systems contributed information to the overall analysis of density dependence; therefore, we included all systems in our remaining analysis. Within each river delta, the model included observations of densities exceeding capacity levels (Fig. 3.5) and showed strong density dependence throughout the range of outmigrants (Fig. 3.5, lower panel). The stock-recruit curve approached the asymptote at relatively low outmigrant levels, resulting in many observations of outmigrants/ha that corresponded with delta fish/ha greater than 95% of predicted capacity (i.e., exceeding the intersection of the dashed lines in Fig. 3.5 upper panel).

Habitat differences. All models produced strong density-dependent relationships (likelihood ratio tests, $p < 0.001$ for all fitted curves). Comparison of models using AIC (Table 3.3) indicated strongest support (AIC-based model probability = 0.49) for a single stock-recruit function (Model 1), and less support for models with multiple curves for either wetland type or channel type (model probabilities 0.25 and 0.23, respectively). Model 2 predicted the combined FRT and EFT wetland type to have a higher capacity than EEM (480 vs 175 fish/ha, respectively) and Model 3 revealed off-channel sites to have a higher capacity compared to distributaries (260 vs 249 fish/ha, respectively). Although Models 2 and 3 received about equal support, separate

Table 3.3. AIC analysis of a Beverton-Holt models combining data from all systems with submodels based on multiple wetland or channel types (2 curves fit) or the combination of wetland and channel types (four curves fit). Δ AIC is the difference of each model from the best model (lower is better), and probabilities of each model (higher is better) are calculated from Δ AIC values (Burnham and Anderson 2000).

Model Number	Model	Parameters	AIC	Δ AIC	Probability
1	Single	4	0.06	0	0.49
2	By wetland type	8	1.37	1.32	0.25
3	By channel type	8	1.52	1.47	0.23
4	By wetland & channel type	16	5.62	5.56	0.03

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relationships for all four wetland and channel type combinations received much less support (probability = 0.03). Due to the ~2-fold higher probability of the best model, we used Model 1 for further analysis but note that Models 2 and 3 are informative in terms of understanding variation in productive capacity.

Conditions in which densities exceeded 95% instantaneous capacity

We used the best Beverton-Holt function to evaluate circumstances when and where densities within large deltas exceeded 95% of predicted capacity (240 fish/ha) across systems, and to what degree HOr fish increased densities above capacity within the tidal delta. We refer to these observations as “exceedance frequency.”

We first asked when capacity was likely to be exceeded within the outmigrant season by combining observations of local delta density observations across years and examining by management week. Predicted capacity was exceeded at least some of the time in each river system. The frequency of observations varied greatly, from < 20% in the Nisqually to > 60% in the Skagit (Figure 3.6). Regardless of system, observations of NOr migrants exceeding 95% capacity were twice as likely during weeks 13-27 (March 24 – June 30) compared to observations before or after the seasonal tails (weeks < 13 and > 27). The time period of highest density values varied by system, with the Skagit exhibiting high densities prior to week 20 (May) primarily due to large pulses of migrant fry) while Nooksack and Snohomish peaked between weeks 20 (May) and 26 (June), primarily due pulses of migrant parr. HOr migrations increased the exceedance frequency between weeks 17-30 (April 21-July 21), although the effect was system-dependent. For example, HOr migrants had a negligible effect on exceedance frequency in the Skagit delta, but tripled this value in certain weeks in the Nisqually.

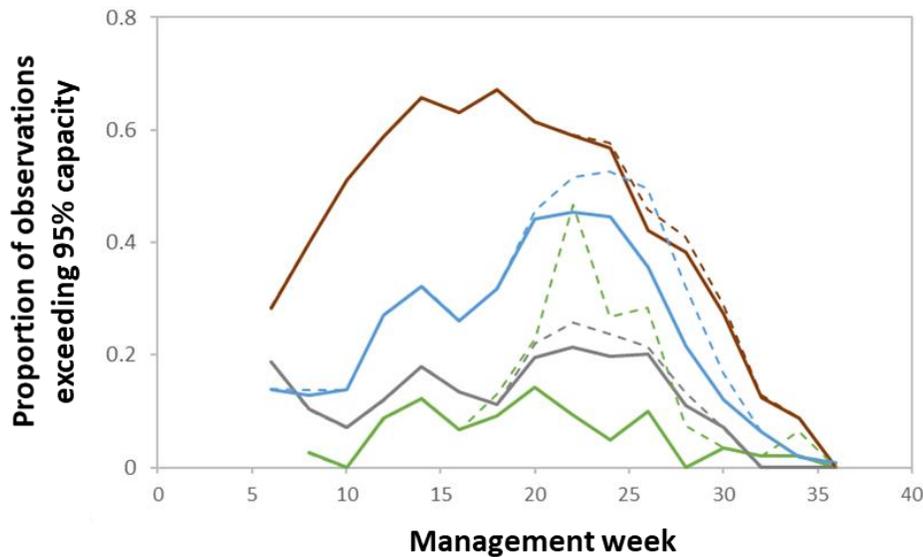


Figure 3.6. Seasonal summaries of proportion of observations exceeding 95% predicted capacity the Beverton-Holt model illustrated in Fig. 3.5 in the Skagit (orange line), Snohomish (blue), Nooksack (gray), and Nisqually (green) large river deltas. Observations were totaled by management week (January 1 = week 1) across years. Dashed lines indicate changes in exceedance frequency when accounting for increased population density from hatchery-origin (HOr) fish.

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We also found that the proportion of observations exceeding capacity varied by wetland and channel type, although these also had system-specific differences (Fig. 3.7). In the larger two river systems (Skagit and Snohomish), FRT and EFT sites were more likely to exceed capacity than EEM sites, as well as offchannel sites compared to distributaries. This pattern contrasted to some extent with the smaller two systems (Nooksack and Nisqually): distributary sites were more likely to exceed capacity than off-channel areas. Migrations of hatchery fish increased habitat-specific exceedance frequency primarily in the Snohomish and Nisqually systems, but these increases were relatively small compared to seasonal increases (compare Fig. 3.7 to 3.6).

Annual summaries of exceedance frequency revealed substantial annual variation, regardless of whether these were based on densities measured within the tidal delta (Fig. 3.8 top panel) or outmigration numbers (Fig. 3.8 bottom panel). In all systems, annual variation in exceedance frequency was extensive. For example, the highest exceedance frequency in a given system was more than twice as large as the lowest value. The annual summary of observations of exceedance frequency increased noticeably for two of four systems when HOr migrants were included. After accounting for HOr fish, the exceedance frequency increased in the Snohomish by 4-50% and in the Nisqually by 0% to over double that of NOr fish alone (Fig. 3.8 top panel).

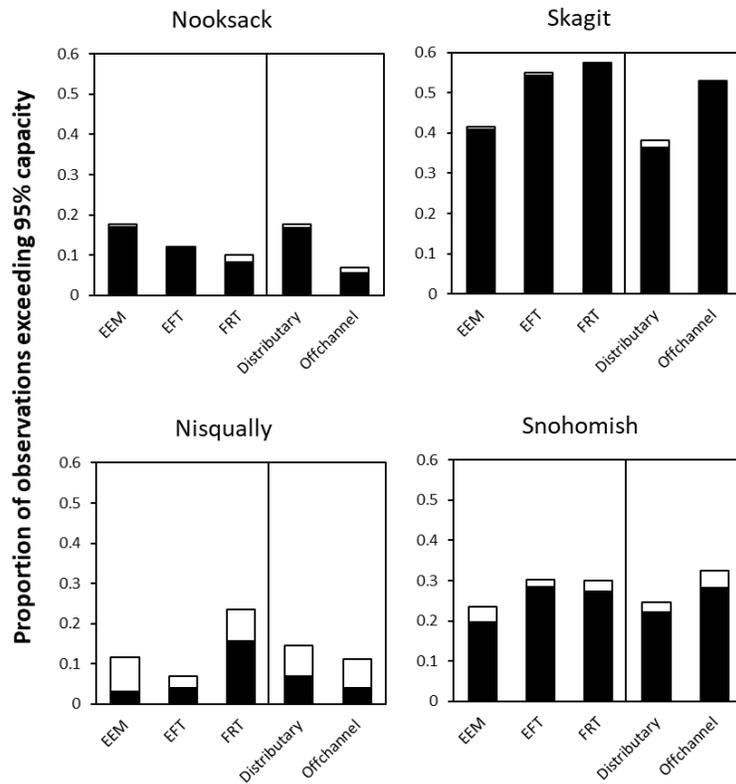


Figure 3.7. Proportion of observations exceeding 95% predicted capacity of the Beverton-Holt model illustrated in Fig. 3.5 in the Nooksack, Skagit, Snohomish, Nooksack and Nisqually large river deltas summed across either wetland type (EEM = estuarine emergent marsh, EFT = estuarine forest transition FRT = forested riverine tidal) or channel type (distributary or blind channel). Black bars represent exceedance frequency associated with natural-origin fish only, and white bars account for increased exceedance from hatchery densities.

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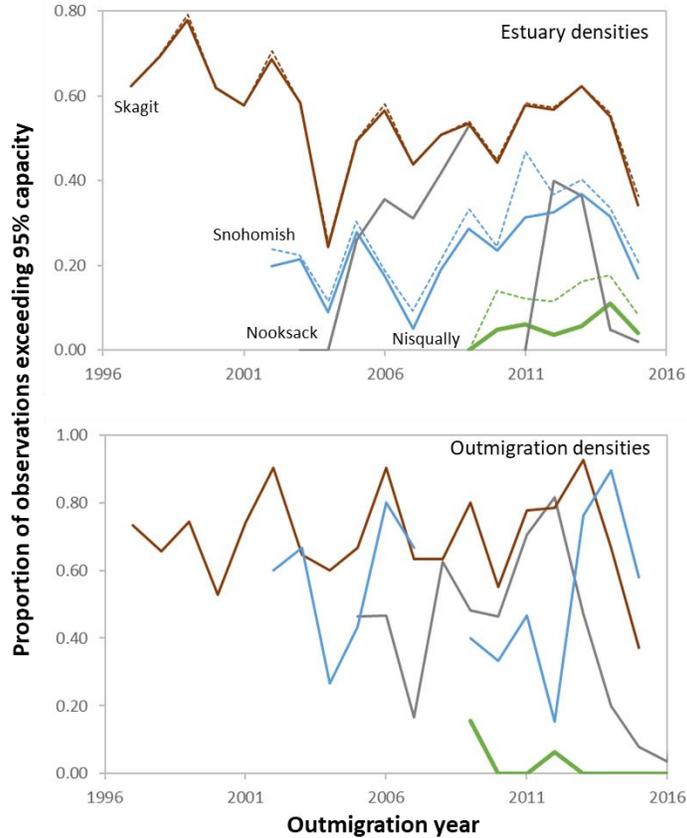


Figure 3.8. Annual summaries of the proportion of observations exceeding 95% predicted capacity of the Beverton-Holt model illustrated in Fig. 3.5 in four large river deltas. Dashed lines indicate changes in 95% capacity exceedance when accounting for increased population density from hatchery-origin fish. Top panel: proportion of observations exceeding 95% capacity based on observations within the tidal delta (horizontal line in Figure 3.5.). Bottom panel: exceedance proportion based on observations of outmigrants (outmigrants/ha of delta channel) exceeding the 95% capacity level (vertical line in Fig. 3.5). Line breaks for the Snohomish (top panel) and Nooksack (bottom panel) indicate years when sampling did not occur or was compromised.

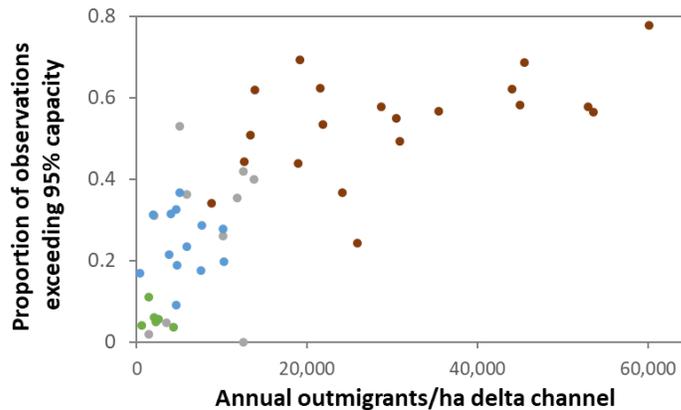


Figure 3.9. Annual proportion of observations in the four tidal deltas (orange = Skagit, blue = Snohomish, gray = Nooksack, green = Nisqually) exceeding 95% of capacity predicted by a Beverton-Holt model as a function of the annual outmigration density of natural-origin (NO) subyearling migrants/ha of delta channel area.

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Annual differences in total subyearling outmigrants accounts for much of the observed differences in exceedance frequency among systems. As shown in Figure 3.8, the annual exceedance frequency of 95% capacity was strongly linked to total outmigration densities and resembled a stock-recruit relationship of its own across data points defined by system and year. Annual summaries of exceedance from the Skagit delta appeared as variation around an upper limit, while data from the three other systems increased in much more of a linear fashion.

Extremes in local density within large river deltas

As observed in Figure 3.5, numerous measurements of local densities exceeded 95% capacity predicted by the Beverton-Holt model, reflecting substantial variation in density, particularly at high levels. To evaluate the range of systematic variation in extreme densities, we examined the 90th and 95th quantiles of local densities in the four deltas. Across all observations, these values ranged between 2,040 and 4,267 fish/ha when considering just NOR juveniles, and 2,335 and 4,841 fish/ha for total density (NOR + HOr fish, Fig. 3.10). This range was approximately 10-20 times higher than habitat capacity predicted by the Beverton-Holt model. Moreover, the 90th and 95th quantiles varied systematically with habitat: For both NOR and total densities, off-channel sites had approximately twice the extreme density as distributaries, as did

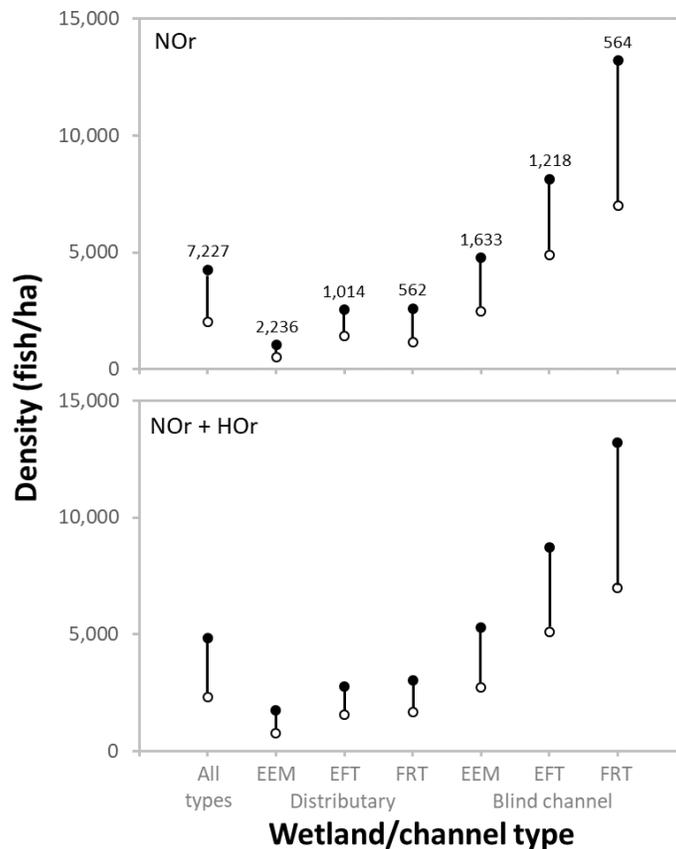


Figure 3.10. 90th and 95th quantiles (open and filled circles, respectively) illustrating the range of extreme values in estuary density of natural-origin (NOR) juvenile Chinook salmon (top panel) and total (NOR + hatchery-origin (HOr)) density (bottom panel) measured in three wetland types and two channel types across four large river deltas. Values above points in the top panel represent the number of observations.

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FRT and EFT wetland sites compared to EEM sites. In combination, these habitat differences led to roughly a 10-fold range in extreme densities characterized by the combined differences among wetland and channel types. Adding densities of HOr fish did not substantially change these patterns.

Discussion

Our analysis revealed evidence for negative density dependence throughout the range of observed outmigrations for NOr sub-yearling migrant Chinook salmon in four estuaries in Puget Sound. Adjustment of outmigration abundance to outmigrants/ha of delta channel provided a straightforward way to develop a statistical stock-recruit model that standardized outmigrations across all four estuaries. Analysis of the model indicated that observations surpassed predicted capacity levels some of the time in most years despite high variation in density, and the frequency with which this occurred varied greatly by large river delta. Furthermore, capacity exceedance was associated with conditions over the season and in different habitat types. These conditions were associated in part on densities of HOr fish, which have the potential to contribute to density-dependent relationships due to co-occurrence of NOr and HOr fish in the delta during the latter half of the migration period. Systematic spatial variation also existed in the highest observed population densities (90th and 95th quantiles) within deltas, and these levels were not greatly influenced by densities of HOr migrants in tidal deltas.

While these observations of density dependence provide important applied ecological information, they do not necessarily indicate what specific ecological mechanisms result in diminishing returns (in terms of population densities within large river deltas) at large outmigrations. The most straightforward explanation for these patterns is competition among individuals for limited prey (e.g., David et al. 2016), as suggested by declining size of individuals in the Skagit delta (Fig. 3.1). We examine this potential explanation in Section 4. However, other plausible mechanisms include density-dependent disease transmission among migrants (Rhodes et al. 2011) and apparent competition resulting from mortality when predators are attracted to large outmigrations (Anderson 2001). Density dependence could also occur in the absence of direct competition or mortality if accumulated conspecific interactions induced early migration through conspecific cueing (Hillman and Mullan 1989, McMichael et al. 1999). Regardless of the mechanisms, density dependence in the delta stage strongly predicts smolt-adult return rates (Beamer et al in prep.), indicating important life-cycle consequences of density dependence in tidal deltas.

Our modeling of the density-dependent relationship provides insight into conditions under which density-dependent impacts might be expected to predominate. The “leave-one-out” sensitivity analysis indicated that all systems contributed to a robust stock-recruit curve, particularly the Nisqually (characterizing relatively low levels of outmigrants) and the Skagit (characterizing high outmigrations). Hence, cross-system comparison allowed us to better infer a density-dependent relationship across a broader range of outmigration sizes than would be represented by an individual system. This broad range of outmigration sizes revealed that the net effect of density-dependent interactions at this life stage appears negative (Fig. 3.4 bottom panel). We found little evidence for Allee effects at low densities predominating, which would have been

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inferred from a recruitment rate index (Fig. 3.5 lower panel) with a unimodal (“hump-shaped”) function with outmigration density (Myers et al. 1995). Such patterns would occur, for example, if individuals aggregated to reduce likelihood of predation or to gain information about their environment (Liermann and Hilborn 2001). Rather, the relationship appeared uniformly negative through the observed range of outmigration sizes.

Nevertheless, we observed substantial variation in presence/absence and density when present. Even at the highest observed outmigrations when we would expect strong effects of density dependence, we observed 25-80% presence/absence, and similar levels of variation in density when present as at the lowest outmigrations. Both results suggest that any notion that delta habitat would completely fill after surpassing “capacity” – i.e., resulting in 100% presence/absence and high levels of density when present with little variation at high outmigrations – is a misconception of how density dependence plays out in tidal deltas. Instead of this “filled vessel” analogy, a better conceptualization might be a city at rush hour, where preferred routes are packed but side streets remain relatively clear. As discussed below, this latter analogy is also consistent with habitat-dependent variation of high levels of density.

Spatial and temporal variation in high population densities

We used a straightforward metric to interpret when density dependence would likely have detrimental interactions: the proportion of observations that exceeded 95% of the capacity predicted by a Beverton-Holt stock-recruit function. While the choice of exceedance threshold is arbitrary in some respect – the very notion of density dependence implies effects across the continuum of density, and there exist very few published studies documenting threshold effects at specific densities (but see David et al. 2016) – it serves as a consistent metric by which to evaluate realistic ranges in population density across systems that experience density dependence throughout the entire range of outmigration. In addition, it occurs at outmigrations that fall well within the observed range and therefore is a useful benchmark for all four systems.

We found that seasonal patterns of observations exceeding 95% capacity track the timing of migrations by NO or outmigrants into large river deltas (Fig. 3.6). Across the four deltas, these patterns coincided with peaks of both migrant fry and parr, indicating that system-specific variation in these life history types has a strong potential to influence the timing of density-dependent interactions. For example, distinct peaks exist in the Snohomish related to both fry and parr migrations, but the peak in observations exceeding 95% capacity is higher for the parr migrant portion of the migration which occurs later in the spring (weeks 20-27). In the Skagit, peaks in life history-specific migrations overlap each other much more and produce a more unimodal pattern of exceedance.

These patterns played out at a larger temporal scale in terms of variability in annual exceedance frequency. We observed high annual variability (Fig. 3.8) which was largely explained by variation in annual outmigration numbers (Fig. 3.9). These values are in part the consequence of dynamics in upstream spawning and rearing habitats, which have been shown to depend in part on annual spawner abundance (Zimmerman et al. 2015, Hall et al. 2018), incubation flood magnitude (Greene et al. 2005, Ward et al. 2015, Zimmerman et al. 2015, Hall et al. 2018), and floodplain habitat quantity and complexity (Hall et al. 2018). When downstream migrations are

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large relative to available floodplain habitat, migrant fry are likely to predominate. Because migrant fry benefit from tidal delta rearing, the interaction of habitat availability in both freshwater and tidal wetlands will likely determine the strength of density dependence in large river deltas (Reimers 1973, Greene and Beechie 2004). Nevertheless, as observed from Fig. 3.8, migrant parr and HOr releases may have important contributions to density dependence later in the season.

Likewise, seasonal and annual environmental variation within tidal deltas (e.g., prey availability, temperature) has the strong potential to affect residence time (Fig. 3.1, see Chapter 4), and thereby would be expected to affect the timing of large pulses of fish rearing in the delta. Hence, warm years could compress migrations, resulting in short periods of residency but also high densities when fish were resident (Munsch et al. 2019). Conversely, cooler years could result in a longer seasonal rearing period, resulting in the “piling up” of migrants moving downstream over the season (Munsch et al. 2020). Both patterns would be expected to be exacerbated in years of large outmigrations. Hence, dynamics related to climate change could impact the frequency of observations that exceed estimated capacity.

We also found spatial variation in the potential for populations to exceed predicted 95% capacity. Our model incorporated landscape connectivity as a covariate in the stock-recruit function, which was an informative predictor in multiple systems (see Chapter 2). In addition, FRT sites (and EFT sites to a lesser extent) were more likely to exceed 95% capacity than EEM sites, and in the two larger deltas, off-channel sites were more likely to exceed 95% predicted capacity than distributaries. These patterns were also observed in the analysis of 90th and 95th quantiles. Off-channel (Jeffres et al. 2008) and forested sites (Davis et al. 2019) may offer better conditions for growth and survival than other wetland habitats, and thereby may attract more fish. In addition, because these sites have been subjected to higher rates of anthropogenic conversion (Simenstad et al. 2011), they may be lower in areal coverage, thereby resulting in greater relative usage by migrating fry and parr.

Uncertainties

Like Section 2’s analysis of landscape features structuring juvenile Chinook salmon densities, the analyses in this section uses statistical models to infer habitat relationships. In this section, the primary concern is spatial and temporal variation in density-dependent interactions. These patterns deserve careful scrutiny to determine whether observed spatiotemporal patterns in fish abundance define causal processes. As in other fields such as epidemiology and socioeconomics where actual experiments are difficult to pursue at the appropriate scales, moving from pure correlations to better support for causation will require multiple lines of evidence. In the case of addressing density dependence in estuaries, additional work would involve more-in depth analysis of timing of movements, other metrics such as size or growth in addition to average annual densities, and additional models including individual based models and bioenergetics models (see Section 4). As shown in Fig. 3.1, some of this work has been done within the Skagit River estuary. Here, multiple lines of evidence support the hypothesis that juvenile Chinook are capacity-limited at large outmigrations (Beamer et al. 2005, Greene et al. 2016). Similar analysis of timing within years can help corroborate apparent effects of NOr fry and parr, as well as

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hatchery releases, to determine whether pulses of migrations influence dynamics within estuary habitats. Likewise, in Chapter 4 we provide additional evidence for density-dependent diet choice and growth, both of which intensified when densities reached the level that our statistical model predicted as capacity.

Stock-recruit vs quantile based perspectives on capacity

While our analysis provides a strong justification for density dependence across all systems, there were numerous observations of population density for which “habitat capacity” predicted by the model was exceeded. How then should we interpret these observations? In other fisheries analyses, variation around stock-recruit fits may reflect measurement error in either “stock” or “recruit”, in which case more complex models that incorporate such error (e.g., MacNally et al. 2010) may be warranted. Measurement error of both outmigrants and delta residents was certainly an issue in our analysis, which persisted despite our efforts to standardize both sets of data to a common currency (fish/ha). For example, higher values of density measured for Skagit compared to other systems may partially reflect differences in measurement error associated with fyke traps (more commonly used in the Skagit) or beach seines (more commonly used in the other systems), despite efforts to standardize using gear-specific capture efficiency and area sampled. That results from all four systems followed a similar stock-recruit pattern suggest that standardization techniques were at least partially successful in reducing measurement error across sampling efforts.

More commonly, high residual variation has been interpreted as stochastic conditions affecting recruitment of cohorts (Fogarty et al. 1991, MacNally et al. 2010). Similar arguments could be made in the situations we observed within and among seasons. For example, in addition to annual and seasonal variation in migration abundance, population density in tidal wetlands might exceed predicted capacity in years of low prey availability or when optimal temperatures predominate in these wetlands (David et al. 2014). Like the landscape connectivity metric, these factors could conceivably be incorporated into the model as covariates (e.g., MacNally et al. 2010, Munsch et al. 2019), but in our analysis they were unavailable for large portions of the data sets. In Chapter 4, we examine potential bioenergetics aspects in two years in which temperature data were systematically collected in the four deltas.

A third interpretation for large numbers of observations exceeding capacity is that in the face of density dependence, individuals continue to reside in adverse conditions until a particular level of density is reached, after which they begin to emigrate. This idea follows from multiple studies of density-dependent growth of estuarine-dependent fishes emerging at low levels of abundance (Martino and Houde 2012, David et al. 2016). Furthermore, observations in the Skagit indicate higher rates of decline in resident size and timing in the lower third of the distribution of outmigrants, but increased density-dependent migration only in the higher third of the distribution (Figure 3.1). In the context of patch selection (Brown 1988) and foraging ecology (Charnov 1976), these patterns may be the consequence of a high migration cost into nearshore habitats relative to density-dependent diminishing returns in high quality foraging areas of tidal wetlands.

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Alternatives for juvenile salmon to mitigate negative density dependence include moving to lower quality foraging areas within deltas, migrating to nearshore waters, or seeking non-natal estuarine rearing opportunities. The first possibility, analogous to seeking side streets when traffic is at capacity, is likely given the habitat-specific variation we observed. The latter two alternatives likely constitute high-risk alternative strategies compared to rearing at more highly competitive densities. Migrating to nearshore marine waters likely incurs a size-dependent risk of predation; for example, Duffy and Beauchamp (2011) demonstrated a strong size-dependent relationship with smolt-adult survival. Using otolith microstructure, Beamer et al. (2005, appendix D) were unable to find any returning adults that migrated to the nearshore as migrant fry, implying that size-dependent mortality is particularly strong for subyearlings lacking extensive rearing in freshwater floodplains, natal deltas, or non-natal estuaries.

What is the likelihood that juvenile Chinook subject to negative density dependence during the delta rearing stage compensate their growth response by emigrating to non-natal estuary systems? We think it is unlikely that significant compensation opportunities exist from other nearby natal Chinook estuaries. First, there is little evidence of significant numbers of natural- or HOr juvenile Chinook using non-natal large river deltas. While some observations have occurred in certain systems (particularly in lower tidal wetlands, Hodgson et al. 2016, Hayes et al. 2019), large numbers of NOr fish have not been observed to colonize non-natal deltas. What has been observed is use of small non-natal estuaries such as lagoons and other “pocket estuaries” (Beamer et al. 2003). Historically, pocket estuary habitat opportunities were abundant across Puget Sound, and these may have offered significant habitat opportunity to Chinook populations. However, under current habitat conditions, pocket estuary habitats have been reduced by $\geq 80\%$ from their historical extent for the marine basins associated with our four studied estuaries (Collins and Sheikh 2005). Put in this context, our results imply that density dependence during tidal delta rearing likely constitutes a demographic constraint with life cycle consequences. Indeed, Beamer et al. (submitted) found that the tidal delta recruitment index explained 44% of the variation in smolt-adult return rate.

Together, these findings suggest that our predicted capacity estimates appear to best represent conditions in which body size (Fig. 3.1, Beamer et al. submitted) or growth (Appendix 4.3) is affected, and therefore may represent levels at which the survival of individuals at subsequent stages is impacted via carry-over effects (Duffy and Beauchamp 2011, Gamble et al. 2018, Gosselin et al. 2018). However, if early migration is most associated with the very high levels of outmigration size as suggested by Fig. 3.1, quantile-based approaches to capacity may be better than capacity as predicted from a stock-recruit function when used for predicting habitat transitions by different life history types (Greene and Beechie 2004). As shown in Table 3.4, these values are quite disparate: quantile-based estimates of high densities across the four deltas result in fish abundance numbers that are between 10 and 20 times that predicted using the Beverton-Holt based estimate of capacity. These latter numbers compare fairly well when expanded to annual estimates. For example, using annualized numbers in a Ricker model, Beamer et al. (2005) estimated capacity at approximately 2-3.7 million fry after accounting for habitat use by other life history types. This estimate is roughly twice the 95th quantile of capacity

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predicted by the instantaneous model. Since samples occur at biweekly intervals, the discrepancy between this and the previous model could be accounted for by adjusting for individual residency averaging one month within deltas (Lind-Null and Larsen 2010). Hence, while capacity estimates likely track when density dependence intensifies, 90-95% quantiles likely represent maximum values fish are likely to tolerate before altering behavior (e.g., migrating from the delta).

Table 3.4. Instantaneous capacity (based on biweekly or monthly data) of the four large river deltas, estimated by multiplying total channel area (see Chapter 2) by either predicted capacity of NOr delta density or the 90th or 95th quantile of all observations of total density (HOR + NOr). Capacity estimates are therefore in units of juvenile Chinook salmon (fish), not fish/ha.

System	Channel area (ha)	Capacity from Beverton-Holt model	Capacity from quantiles of total density	
			90 th	95 th
Nooksack	44.87	11,339	104,771	217,216
Skagit	332.08	83,917	775,407	1,607,599
Snohomish	153.65	38,827	358,773	743,820
Nisqually	273.83	69,197	639,393	1,325,611

Implications for habitat restoration and recovery of populations

The results of this section have several additional implications for Chinook salmon populations beyond the points noted in Section 2. These questions focus on how limiting factors are addressed by estuary restoration.

At what levels of abundance do effects of density dependence occur?

Our analysis demonstrated that negative density dependence occurred throughout the range of observed outmigrations, implying that competition is an important aspect of population dynamics associated with residency in tidal wetlands regardless of whether migrations reach the levels predicted here as exceeding capacity. Our study also documented observations in all systems in where predicted capacity was exceeded, indicating a period of intense competition for at least a portion of the rearing season in most years. These results suggest that extant tidal wetlands may function as a key limiting factor for juvenile Chinook salmon in a diverse set of systems.

From a recovery perspective, the levels which we identified as “capacity” are useful as targets in effectiveness and status monitoring by providing benchmarks for addressing additive benefits of habitat restoration (Beamer et al. 2005), and in quantitative risk assessments using life cycle models and other tools (e.g., Greene and Beechie 2004). Unlike the four systems in this study, many watersheds lack either monitoring of outmigrants or monitoring of densities within their deltas. The modeling approach highlighted herein provides information for potential use where empirical data are unavailable. For example, if delta rearing densities are measured but not outmigrant abundances, the approaches used in Figs. 3.6-3.9 could be used to predict whether observed densities approach predicted capacity of 252 fish/ha to determine whether observations are likely in the range where density dependent interactions predominate. Likewise, if outmigrations but not delta rearing densities are monitored, one could use the approach in Fig. 3.8 (bottom panel) to predict similar conditions in the delta. As shown in Figure 3.8, these two

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approaches yield correlated but not identical predictions, and it appears that the latter approach has higher uncertainty than the former.

Understanding estuary habitat restoration actions in the context of habitat capacity

Estuary habitat restoration is often predicated on the assumption that habitat loss has reduced the amount of habitat area available to an estuarine-dependent population, resulting in habitat-based limiting factors (Nickelson and Lawson 1989) or a demographic bottleneck (Wahle and Steneck 1991). Our results suggest that estuary restoration offers substantial opportunity for reducing the frequency of exceeding habitat capacity by increasing area available for rearing by Chinook salmon. These findings were particularly true for the Skagit and Snohomish basins, where capacity was exceeded in greater than 20% of the observations over the seasons and years, and could be much higher in peak outmigration years.

In the Nisqually and Nooksack, which may not typically surpass capacity levels in some years, there are multiple reasons for restoring habitat area aside from just increasing habitat capacity. These include promoting resilience of populations and ecosystems (Jones et al. 2014) by providing spatial complexity, improving functions of habitat processes such as tidal prism (Hood 2014), and increasing availability of extensive wetland habitat to address recovery goals or to address impacts of sea level rise (Hood et al. 2016) and increasing temperature (Munsch et al. 2019). Moreover, many of the observations used in this analysis potentially have some restoration effects built into them. For example, multiple restoration projects have occurred in the Skagit delta during the course of the data collection used in this study (Greene et al. 2016), and all data from the Nisqually were collected after a large restoration project was completed (Ellings et al. 2016). Perhaps the declining annual exceedance frequency in the Skagit and the low frequency of observations exceeding 95% capacity in the Nisqually is indicative of very successful restoration of habitat capacity.

In addition to restoration benefits for NOr fish, it is also possible that restoration of estuarine habitat capacity could benefit HOr fish. Due to their relatively short residence in deltas (Lind-Null and Larsen 2010), HOr migrants might be expected to benefit little from estuarine residence gained from restored habitat capacity. Furthermore, analysis of growth circuli (Gamble et al. 2018) suggests little size-dependent benefit of delta rearing by HOr migrants. Nevertheless, Magnuson and Hilborn (2003) found that marine survival of Chinook as measured by hatchery coded-wire tag groups was positively associated with amount of natural wetland habitat. Likewise, David et al. (2016) found stronger density dependence in food ration in more urbanized systems (where habitat capacity was presumably reduced), and both NOr and HOr fish were included in their meta-analysis. Our study revealed both evidence of habitat partitioning (Chapter 2, see also Davis et al. 2018), as well as situations where co-occurrence was restricted (Skagit) or extensive (Nisqually, see also Hayes et al. 2019) corresponding to relative NOr outmigration size. These results suggest that where capacity is not fully utilized by NOr individuals, HOr migrants will make use of it. Hence, estuary restoration could reduce co-occurrence of HOr and NOr individuals, thereby benefiting their growth.

Nevertheless, it is possible that over the short time scales often dictated by most funding cycles, it will be difficult to document NOr or HOr population responses to estuary restoration if a

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depleted population is not using it in the way it is expected to when highly abundant. The results of our analyses may help temper criticism that estuary restoration is wasted effort without a positive population response, particularly if it can be shown that long-term restoration goals are effectively addressing some of the issues raised above. Furthermore, our results may point toward a more nuanced process for prioritizing restoration actions that have a high probability of “success” (i.e., resulting in a population response). If populations are at lower levels relative to the capacity levels documented in this report, actions such as reconnecting off-channel habitats and restoring habitat with high intrinsic productivity such as forested riverine tidal habitats would be expected to offer big benefits to small recovering populations as well as larger ones. In addition, relative predicted benefits among channel and wetland types could be used as a basis to weight habitat restoration portfolios (Maron and Cockfield 2008).

Where fish populations and their habitats are threatened, fisheries managers address recovery through various management strategies. Our study shows how science relevant to management of populations and their habitat can be integrated in a decision framework to better achieve desired future conditions (DFC), i.e., population recovery. Utilizing findings from this study, we provide an example of a decision framework to help managers select appropriate estuary habitat strategies for any specific estuary system for Puget Sound Chinook Salmon (Figure 3.11). The decision framework incorporates responses to three questions concerning juvenile Chinook

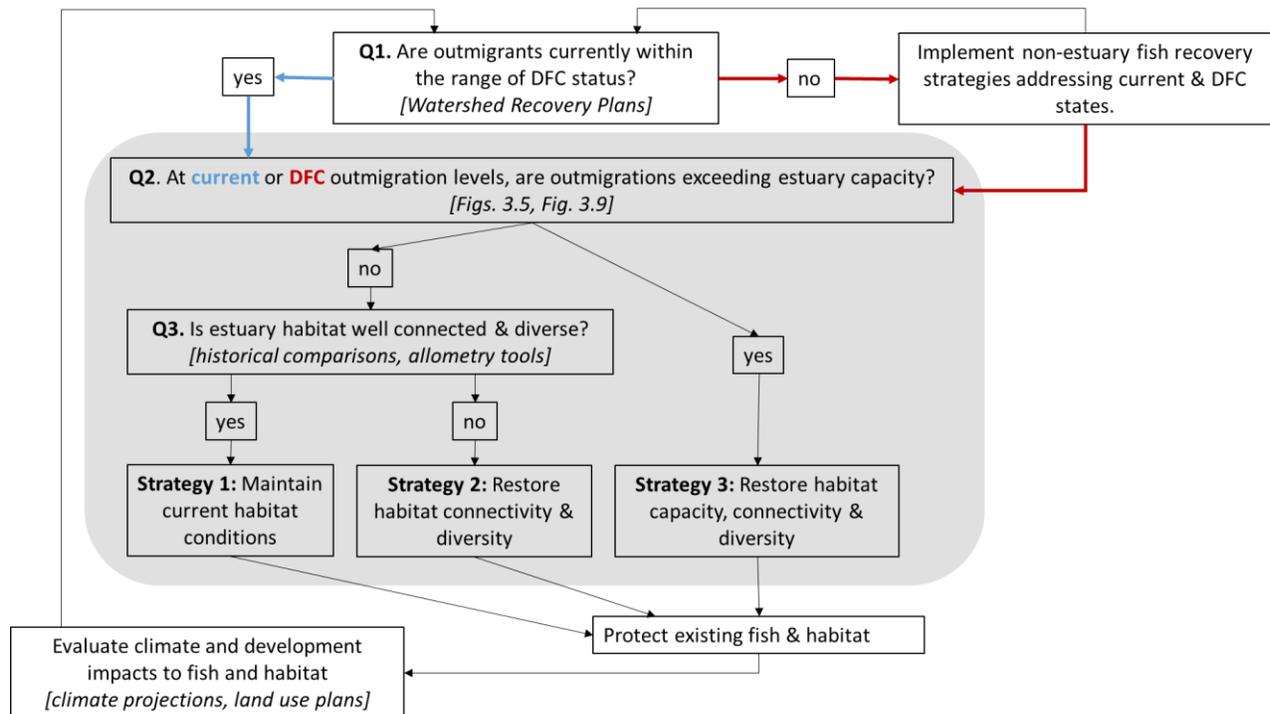


Figure 3.11. Decision diagram to evaluate what restoration strategy is appropriate for a specific estuary system for Puget Sound Chinook Salmon when populations are at current (blue arrows) or desired future conditions (DFC, red arrows), which can be addressed in parallel. The gray shaded area represents content developed within the scope of this study, and example diagnostic tools to answer questions are shown within brackets in italic. See text for more details.

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population and estuary habitat conditions to help managers identify which of the three general estuary habitat restoration strategies is appropriate for their estuary.

The response to Question 1 concerns whether current Chinook salmon outmigration population status meets its DFC goal. Answers for Puget Sound watersheds are described in watershed chapters of the Puget Sound Chinook Recovery Plan (<https://psp.wa.gov/salmon-recovery-watersheds.php>) or their updates. As all Chinook salmon populations in Puget Sound remain Threatened under the Endangered Species Act, managers in most cases may find that current Chinook salmon outmigrations are not at DFC. When that happens we recommend two simultaneous steps: 1) move on to answering Question 2 using the DFC outmigration state for question responses, and 2) implement non-estuarine fish recovery strategies aimed at moving the current state to DFC for the population because implementing habitat restoration strategies is a decades-long process and waiting until DFC population conditions are achieved will only delay implementing needed habitat work. Identifying appropriate non-estuarine strategies is outside of the scope of this study. These strategies are unique to each watershed and could be habitat restoration actions aimed increasing the number of outmigrants caused by bottlenecks at life stages prior to the estuary or strategies aimed at improving watershed “seeding” levels, such as increased escapement if watershed habitat quantity and quality are adequate.

The response to Question 2 can be ascertained by utilizing the tools developed in this study, such as results found in Figures 3.5, and 3.9, and in Table 3.4 as examples. We have provided suggested conditions for responses by these tools in Table 3.5, which could be applied to local outmigration trapping efforts (and hatchery releases) and/or direct fish sampling within estuaries. The response to Question 3 can be ascertained by comparing current habitat conditions to (a) its historical reconstruction (e.g., Collins et al. 2003; Simenstad et al. 2011) and/or (b) reference habitat norms (Hood 2007, 2015). Additionally, we recommend utilizing an ongoing adaptive management loop to the decision framework to insure continued diligence at protecting existing fish population and habitat conditions that have reached DFC states from ongoing pressures such as climate change and human development.

Table 3.5. Empirically determined conditional responses to Question 2 (Fig. 3.11): At current (or DFC) outmigration levels are/will estuary habitats exceed capacity?

Data type	Parameter	Condition for ‘yes’ response	Condition for ‘no’ response
Estuary fish sampling	local instantaneous juvenile Chinook salmon density (NOr & HOr combined) in the estuary (Fig. 3.5)	Regularly (>40% of time) ≥ 250 fish/ha of estuarine channel	Regularly < 250 fish/ha of estuarine channel
Outmigrant trapping & hatchery releases	NOr Chinook annual outmigrants & HOr Chinook releases combined	Current or DFC outmigrants $\geq 10,000$ outmigrants / ha of estuary channel	Current or DFC outmigrants < 10,000 outmigrants / ha of estuary channel

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Strategy 1 (maintain current habitat conditions) makes sense for a system where (a) the current juvenile Chinook salmon outmigration is within the range of its DFC, (b) the current outmigration does not exceed the indicators for density dependence in the estuary derived from this study, and (c) the current estuary is well connected and diverse in terms of wetland and channel type complexity. Estuaries that fit this strategy would essentially be pristine areas with Chinook salmon populations (NOr and HOr) at current (or DFC) levels where density-dependent pressures within the estuary do not occur or cannot be improved. This type of estuary does not currently exist in Puget Sound because all natal Chinook large river estuaries have a high degree of habitat change from historical conditions with large reductions in overall extent, connectivity, and complexity (Simenstad et al. 2011).

Strategy 2 (restore habitat connectivity and diversity) makes sense for a system where (a) the current juvenile Chinook salmon (NOr and HOr) outmigration is within the range of its DFC, (b) the current outmigration does not exceed the indicators for density dependence in the estuary derived from this study, but (c) the current estuary is not well connected and/or not diverse in terms of wetland and channel complexity. Estuaries that fit this strategy have reduced habitat extent but their Chinook salmon populations don't exhibit regular density dependence pressures within the estuary. Because the current (or DFC) population generally does not express density dependence conditions, habitat restoration within these estuaries does not need to focus on restoring vast areas (i.e., capacity) but should work toward restoring connectivity and the diversity of wetland types and channel types within the estuary which will support resilience in the face of extrinsic pressures such as climate change. This type of estuary could exist in Puget Sound and may be represented by the current conditions shown in our study for the Nooksack and Nisqually systems. It is outside the scope of this study to determine whether DFC outmigrant goals for the Nooksack or Nisqually reflect the current conditions observed in this study. If they do not, then these systems would fit the Strategy 3 paradigm for their DFC states.

Strategy 3 (restore habitat capacity, connectivity and diversity) makes sense for a system where the current or DFC outmigration levels exceed the indicators for density dependence in the estuary as derived from this study. Estuaries that fit this strategy have reduced habitat extent and their Chinook salmon populations regularly exhibit density dependence within the estuary. Because of this, habitat restoration within these estuaries needs to focus on restoring large areas (i.e., capacity) as well as connectivity and the diversity of wetland types and channel types within the estuary. This type of estuary does exist in Puget Sound and is represented in our study by the current conditions shown for the Skagit and to a lesser extent for the Snohomish. It is important to emphasize estuaries fitting Strategy 3 are determined based on whether either current or DFC outmigration levels are/will produce density dependence. Both types of systems ultimately need to restore capacity, connectivity, and diversity but systems under density dependence due to current outmigration levels may be more urgent to restore than systems that have yet to reach DFC outmigration levels. Nonetheless, habitat restoration at the system scale is such a long-term endeavor (decades) that we strongly recommend not waiting until DFC outmigration levels are achieved before acting on appropriate restoration strategies.

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How does hatchery management affect NOr fish rearing in estuaries?

Our results also suggest that issues of hatchery management may intermingle with issues of habitat restoration, particularly if there is spatial or diet overlap between HOr and NOr fish (Fig. 3.4, Appendix 4.2.). We observed that added densities of HOr fish could lead to increased likelihood of exceeding tidal delta capacity. In this respect, the Skagit appears least affected by hatchery releases, followed by the Nooksack, Snohomish, and Nisqually. In the Nooksack, hatchery releases had very few inter-annual effects except at the highest levels of releases. Following from these observations, increased frequency of capacity exceedance depended not only the magnitude of hatchery releases but also on the abundance of NOr Chinook salmon rearing in the delta.

Determining whether density dependence is intensified by HOr migrants as suggested by our results will require better science and monitoring of individuals and populations. While NOr individuals generally reside in deltas for longer than HOr migrants (Lind-Null and Larsen 2010), the sheer number of hatchery releases can be greater than the NOr population, raising the potential for competition, apparent competition through predator attraction (Anderson 2001), or disease transmission (Rhodes et al. 2011). Hence, additional research comparing behavioral interactions of NOr and HOr fish before, during, and after they co-occur would confirm whether hatchery releases result in competitive or other density-dependent interactions. In Chapter 4, we model whether bioenergetic-based consumption of both natural- and HOr residents impacts consumptive demand.

If our observations are indicative of actual hatchery-wild interactions in estuaries, our work may have several important management implications. All hypotheses would predict that release number, timing, body size, and location could influence the propensity of HOr migrants to interact with NOr juveniles residing in the delta. From the perspective of decreasing the absolute number of interactions, smaller hatchery releases will have less effect on NOr populations than large releases. Likewise, spreading out releases over time will lessen the intensity of interactions over short time frames. Alternately, Figure 3.6 suggests late-season release after migration of NOr parr migrants would decrease the likelihood of density-dependent effects, although these later time periods may come at the cost of HOr survival (Duffy and Beauchamp 2011, Satterthwaite et al. 2014). Other practices such as net pen rearing or other non-natal hatchery releases might similarly reduce the potential for density dependence within tidal deltas.

Finally, as NOr juveniles migrate before most hatchery releases, there may be opportunities for real-time adaptive management to optimally adjust releases so as to limit interactions with NOr outmigrants. Our results indicated that the greatest increases in exceedance frequency attributable to hatchery fish were associated with low NOr migrations. One possible explanation is that if existing capacity is not taken up by juveniles of natural origin, hatchery origin fish will exploit rearing in tidal delta wetlands. These observations suggest NOr fish in deltas may possess a prior residence advantage that limits rearing opportunities for HOr migrants. Hence, if outmigrations were expected to be small, releases could conceivably be postponed until later in the rearing season.

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Conclusions and opportunities for future research

Chinook salmon populations have been declining for over 30 years and have not shown signs of rebounding. As declining numbers of southern resident orcas illustrate, downward trends for Chinook salmon are having ecosystem consequences in the Puget Sound region. Estuary restoration is an important long-term solution for species recovery in the region, and this analysis supports the hypothesis that reduced tidal wetland habitat in large river deltas is limiting recruitment by imposing density dependence. This analysis shows that four systems currently exist on a spectrum of density dependence, with the Skagit regularly experiencing high levels of population density in deltas within and between years and the Nisqually doing so much less frequently, except possibly when large numbers of HOr fish are released. These results strongly imply that restoration of the acreage of tidal wetlands, particularly freshwater tidal and off-channel areas, will likely help remove early rearing bottlenecks and promote growth of individuals migrating into Puget Sound, and that both habitat restoration and hatchery reform management strategies can work in concert. However, these results also suggest that due to broad range of outmigration sizes in these four systems, these and other systems will not respond uniformly to restoration. Populations at the lower end of outmigration sizes relative to extant delta channel rearing area might show a more muted response to restoration than those populations at the higher end. Further cross-system comparisons integrating multiple spawning populations (e.g. Hall et al. 2018) may help elucidate whether estuary restoration is improving recruitment of juvenile fish as we predict.

This study also raises additional questions as to the consequences of density-dependent relationships within large river deltas and wetlands. As local instantaneous juvenile Chinook densities increase, the direct consequences of competitive conditions can include competition for prey and refuge habitat, which would result in poorer growth opportunities or lower survival within tidal wetlands. An indirect consequence to poorer growth in the estuary could be poorer survival at later life stages, especially if there is a critical period (Beamish and Mahnken 2001) or size-dependent survival (Duffy and Beachamp 2011) related to prey capture or marine predation. If there is competition for food or space in light of the combination of available resource (amount and quality of food and habitat) and competitors (the other fish), then individual fish must respond with one of two choices: 1) stay and compete or 2) move and search for other safe feeding opportunities. For juvenile Chinook salmon, moving can occur at several spatial scales, including moving to nearshore environment including non-natal lagoons or “pocket estuaries. In the Skagit delta, large density-dependent migrations to nearshore environments occur when outmigrations and delta rearing densities are high, and these patterns are correlated with lower smolt to adult return rates. While these further linkages are beyond the scope of this study, they represent information that will be critical to determine the relative benefits of restoration of natal and non-natal tidal wetlands.

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3. *Density-dependent habitat limitations*

4. Evaluating habitat-specific growth potential and consumption demand for Chinook salmon across multiple tidal deltas

Joshua Chamberlin^{1*}, Correigh Greene¹, Eric Beamer², Melanie Davis³, Joseph Anderson⁴, Todd Zackey⁵, Chris Ellings⁶, Sayre Hodgson⁶, and Isa Woo⁷

*To whom correspondence should be addressed

¹ Fish Ecology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd E, Seattle WA, 98112, USA

² Skagit River System Cooperative, PO Box 368, LaConner WA, 98257

³ U S Geological Survey, Western Ecological Research Center, Olympia Substation, Billy Frank Junior Nisqually National Wildlife Refuge, 100 Brown Farm Rd NE Olympia, WA 98516

⁴ Washington Department of Fish and Wildlife, Olympia, WA

⁵ Tulalip Tribes, 7515 Totem Beach Road, Tulalip WA, 98271, USA

⁶ Nisqually Indian Tribe, Department of Natural Resources, 12501 Yelm Highway Southeast, Olympia, WA 98513, USA

⁷ U S Geological Survey, Western Ecological Research Center, PO Box 158, Moffett Field, CA 94035-0158

Keywords

Chinook salmon, individual growth, consumption demand, bioenergetics, river deltas

Abstract

Habitat influences the conditions and resources that are available to individual consumers which may ultimately affect growth. As conditions and/or resources vary, individuals may use multiple habitat types to maximize growth benefits. However, if competition for resources increases in a particular habitat, growth may become limited, especially where abundance varies greatly and prey is limited. Juvenile Chinook salmon use estuaries to varying degrees during the outmigration period. Individuals that enter at different periods may experience variable conditions (environmental and demographic) that can affect growth. We used fish abundance, fish diet, prey availability, and temperature data from four tidal deltas in Puget Sound to evaluate wetland-specific growth potential and consumption demand. To evaluate variability in individual growth among cohorts and wetland types we used bioenergetics models to estimate individual growth for multiple cohorts of juvenile Chinook salmon entering the estuary at different times and sizes. Estimated individual weekly energy consumption was scaled to population abundance for each life history type in four tidal deltas to assess whether consumption demand was limited,

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indicative of potential density dependent growth processes within each delta. Lastly, we used estimates of overlap between diet and prey assemblages to evaluate whether similarity increased or decreased with changes in local density or individual size. Growth potential among cohorts and across wetland types was highly variable. No single wetland type offered consistently higher growth throughout the rearing period. Consumption demand never surpassed estimated prey availability, but demand approached availability in some systems during periods of peak Chinook abundance. Consumption demand was not evenly distributed among life history types through time or among systems. Diets became more similar (less selective) to prey assemblages as density increased, and results suggested extensive variability, creating a direct relationship on the upper limit of prey/diet overlap. Prey/diet overlap was not strongly associated with changes in individual size, although the relationship suggested a negative relationship between overlap and size. Our analysis highlights the importance of habitat diversity in tidal deltas to maximize growth potential for juvenile Chinook salmon that rely on estuaries for growth. Restoration planning that focuses on maintaining diversity while increasing capacity will be important for supporting population recovery and resilience.

Introduction

Habitat use and growth are linked for many fish species and generally reflect balances between environmental, biological, and demographic conditions (Rosenfeld et al. 2005, Railsback and Harvey 2002). Individual growth is ultimately a function of resource availability and environmental conditions (Brett 1979). Growth, and growth opportunity, may change due to the quality and quantity of prey that are available and the conditions under which the prey are consumed. Bioenergetics theory predicts that individuals should utilize habitats that consistently produce more food, produce food with higher energy density, or provide conditions that optimize metabolic demands (Goldberg and Novoplansky 1997, Brown et al. 2004). As the distribution and environmental conditions (e.g. temperatures, prey availability) of available habitats change, individuals may utilize multiple habitats to maximize growth potential (Armstrong et al. 2013). Yet, if competition for available resources also changes in a particular habitat or for a period of time, individual growth may also become limited due to reduced consumption and/or size-structured foraging success (Lorenzen and Enberg 2002). Such density-dependent effects on growth have been observed in systems where prey is limited and local abundances of consumers or prey fluctuate considerably throughout a season (Martino and Houde 2012, David et al. 2016).

Anadromous species encounter and experience several different environments that offer a variety of food resources and shifting environmental conditions as they migrate through freshwater, estuarine, and marine habitats. Pacific salmon (*Oncorhynchus* spp.) utilize each of these habitats to differing degrees, depending on individual species and life history type, during the transition from freshwater to marine environments. The availability and complexity of these environments have been shown to increase productivity and overall survival in many populations (Hall et al. 2018, Magnusson and Hilborn 2003). Though size may not be the sole determinant of survival to adulthood (Claiborne et al. 2014, Nelson et al. 2019), it is generally accepted that, for most species of Pacific salmon, larger juvenile fish survive better to adulthood (Macfarlane 2010, Moss et al. 2005, Sogard 1997). Thus growth, supported by habitats during the early migratory

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phase, may have disproportionate impact on success at later life stages (Beamish and Mahnken 2004, Duffy and Beauchamp 2011).

It is well documented that juvenile Chinook salmon exhibit diverse life history patterns with respect to early migration and habitat use (Reimers 1973, Healey 1980). Specifically, sub-yearling Chinook migrants, which migrate from freshwater during their first spring, rely heavily on estuarine wetlands during their early life history due to their high quality, diverse prey assemblages and optimal rearing conditions (e.g. thermal range, refuge from predators, etc.; Healey 1982, Levings 1986). While the relative benefits of the specific wetland types likely drive growth opportunity, the timing of movement (e.g. gradual or pulsed), residence time, and the abundance or density of conspecifics within the estuary may also influence growth potential for individual migrants. Migration timing and residence time are primarily driven by individual life history type. While yearling fish rear primarily in freshwater, sub-yearling Chinook migrants are generally divided into two primary life histories that use estuaries extensively: fry and parr. Natural origin (NOr) subyearlings typically migrate from freshwater to estuarine wetlands between Feb-Jun. Migrant fry leave freshwater soon after emergence at a smaller size than parr, which remain in freshwater longer, are slightly larger, and migrate somewhat later in the season. Both life history types use tidal deltas for rearing and may reside in these wetlands from weeks to months prior to moving seaward (Reimers 1975, Greene and Beechie 2004). The timing at entry and outmigration abundances for both NOr life history types can fluctuate considerably inter-annually, creating demographic scenarios that are rather flexible year to year. A third group of fish, hatchery origin (HOr) migrants also use estuaries to some degree (Hayes et al. 2019) and generally mimic the strategy of natural origin parr migrants. In contrast to NOr juveniles, both timing at entry and abundance of HOr fish is relatively stable from year to year, though HOr migrants will generally outnumber NOr abundance by an order of magnitude in most systems.

It has been hypothesized that, historically, estuarine wetland diversity has provided opportunity to maximize productivity and resource availability which spread juvenile fish over time and space, reducing the potential for competition for prey (Simenstad et al. 1982). However, over the past 150 years, estuaries have been heavily modified and rearing habitat has been lost or disconnected, potentially reducing capacity for populations that rely on estuaries for growth and rearing (David et al 2016). Managers tasked with restoring habitat generally assume different areas are of equivalent value to different species. Yet prey availability (assemblage and abundance) and thermal conditions can vary at a fine scale between estuarine wetland types (Woo et al. 2019, David et al. 2014), which may influence individual growth potential such that the expected benefit for proposed or potential restoration sites may differ considerably. Furthermore, as hatchery release timing has become less variable (Nelson et al. 2019), competitive interactions may be exacerbated and create density dependent responses in individual growth. Understanding wetland-based bioenergetic differences and potential density dependent interactions could therefore provide additional context to decisions regarding how and where to prioritize restoration efforts (Hafs et al. 2014, Davis et al. 2018).

A prime benefit postulated for estuary residence by juvenile Chinook salmon is rapid growth in productive habitats (Thorpe 1994, Levings 2016). Bioenergetic benefits to individual fish may

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differ among wetland habitats for several reasons including wetland-specific prey quality and variable thermal regimes; each of which could change throughout the rearing season. We evaluated the productivity of various estuarine wetland types for juvenile Chinook salmon by using standard bioenergetics models to estimate growth potential for individual cohorts representing known life history strategies and origins. Modelling growth among individual cohorts allows us to evaluate changes in growth potential through time across the multiple wetland types. Diet composition, prey availability, and temperature data were incorporated into a bioenergetics framework to evaluate wetland-specific growth potential for individual Chinook salmon life history types during estuary residence. We also examined the potential for prey consumption, as estimated by the bioenergetics models, to outpace prey availability. If this occurred, we would expect that density dependence could occur from consumption demand. The consequences would be 1) reduced growth potential at high densities and 2) changes in prey selectivity, such that fish are less selective at higher densities.

Methods

We collected and collated water temperature data, juvenile chinook stomach contents, prey availability samples, and weekly abundance estimates for NOr and HOr fish across four systems (Nooksack, Skagit, Snohomish, Nisqually) to estimate wetland-specific growth rates and consumption for the three main groups of Chinook salmon that use vegetated tidal delta wetlands throughout the out-migration period (Feb-Aug). Vegetated tidal deltas are commonly divided into three wetland types or zones: forested riverine tidal (FRT), estuarine forest transition (EFT), and estuarine emergent marsh (EEM; Cowardin et al. 1979, Collins and Montgomery 2001). The distinct wetland types are determined by their position in tidal deltas relative to riverine and tidal inundation, and thus differ with respect to abiotic and biotic conditions. Our goal was to compare mean and weekly growth rates among wetland types across systems and evaluate whether consumption demand exceeds the energy available as prey in any of the four systems.

Temperature data

We collected temperature data between Feb and Aug of 2014 at sites representing different wetland types, using a combination of iButton, Hobo, Solinst, and CTD Diver temperature loggers either attached to the substrate using existing large woody debris or rebar stakes, or hung in perforated PVC tubes. Loggers provided readings every 15 minutes and were periodically replaced to ensure that they did not max out memory storage capabilities. Data were quality controlled to remove time periods in which loggers were either not submerged (i.e. recorded air temperatures), lay under ice, or became buried in sediment (i.e. recorded hyporheic temperatures). Spot temperature readings obtained during fish sampling were used to supplement temperature logger data, which provided quality control and filled in gaps for periods prior to the earliest dates of deployment. We used linear interpolation to establish trends between spot measurements where data from continuous loggers was not available.

Chinook diets

To evaluate stomach contents of natural- and hatchery-origin fish, we lethally sampled sub-yearling Chinook salmon captured in 2014 from Mar–Jun in the Nooksack, Skagit, and Snohomish systems and from Feb–Aug in the Nisqually to best represent the main rearing period

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for juvenile Chinook salmon in each delta. Upon capture, all fish were checked for coded-wire tags and external marks and measured to the nearest mm fork length prior to inclusion. Contents were identified to the lowest possible taxa, consolidated to one of 21 categories to better represent functional groups (Table A.1), and then recorded as wet weight biomass for each group. A total of 427 individual NOr diets and 105 individual HOr diets were evaluated across system, wetland type and month (Table 4.1).

Table 4.1. 2014 Unmarked (NOr) Chinook diet samples by month for each system and wetland type. Hatchery-origin (HOr) Chinook samples in parentheses for month x wetland groups where paired samples existed within each system.

System	Wetland	Feb	Mar	Apr	May	Jun	Jul	Aug
Nisqually	FRT	-	10	4	7 (1)	7 (9)	1	1
	EFT	1	-	-	-	3 (1)	1	-
	EEM		11	4	4(19)	-	4	7
Nooksack	FRT	-	2	3	3 (7)	-	1(6)	-
	EFT	-	1	2	9 (18)	1 (22)	1(5)	-
	EEM	-	1	-	5(1)	-	-	-
Skagit	FRT	-	10	20	10	7	-	-
	EFT	-	10	20	20	16	-	-
	EEM	-	20	30	42	25	-	-
Snohomish	FRT	-	-	-	-	-	-	-
	EFT	-	-	5	-	-	-	-
	EEM	-	20	33	-	29 (23)	-	-

Prey availability

To quantify and assess prey availability and composition, we sampled the invertebrate community along the surface water (neuston) and near the bottom of the channel (epibenthic) at sites using a standard plankton net (Woo et al. 2018, 0.5m diameter, 80 or 250 µm mesh). Samples were collected monthly in 2014, Apr-Jun in the Nooksack, Skagit, and Snohomish deltas, and Mar-Jul in the Nisqually delta (Table 4.2). Neuston and epibenthic samples were combined into a single sample for each site/date combination to represent prey availability for juvenile salmon throughout the entire water column. A total of 84 combined samples of prey availability were collected in the four systems. While our sampling methodology may not characterize all sources of prey (e.g., benthos, terrestrial fallout) we assume each sample is representative of prey availability at the surface and within the water column where juvenile salmon are actively feeding.

For neuston samples, the net was towed such that the upper 10-12 cm of the net's frame was held above the surface of the water in order to catch the organisms drifting on the surface as well as in the upper water column. Tows occurred against the water current (if present) with the net attached to a telescoping pole (2.4 m to 3.9 m). The net was moved into the current by walking a fixed distance (~10m) along the channel edge with the pole perpendicular to the shore.

Where/when current velocities prevented this method, the sample was taken by holding the net

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stationary against the current for a measured period of time (~60secs). Epibenthic samples followed similar methods for neuston sampling, whereby the net was towed near the bottom (within ~0.5 m) without disturbing the substrate, targeting organisms living on and near the bottom. Where water depth was too shallow to accommodate individual neuston and epibenthic samples, a single sample was collected and assumed to represent the full water column. For each sample collection, the following data were recorded: net type (80- or 250-micron net), tow type (neuston, epibenthic, both), distance the net was towed, length of time the net was towed, water current velocity (measured with a Swoffer 2100 flow meter), and depth.

After each tow, contents were washed into a clean collection jar using either pre-filtered lab water or a garden style pressure sprayer filled with filtered water (250 micron sieve) from the sample location. The samples were ‘fixed’ by adding 95% denatured ethanol in equal amounts to the volume of water used when rinsing the collection jar. Contents of each sample were identified to the lowest possible taxa and wet weight biomass was recorded and divided by the volume of water sieved by the plankton net during sample collection to calculate g/m³ of water for each taxon. Individual taxa were then grouped into the same categories (Appendix 4.1, Table 1) used for diet analysis and volumes summed accordingly.

Table 4.2. Prey availability samples (neuston and epibenthic combined) by system, wetland and month during 2014.

System	Wetland	Mar	Apr	May	Jun	Jul
Nisqually	FRT	2	2	2	2	2
	EFT	2	2	2	2	2
	EEM	2	2	2	2	2
Nooksack	FRT	-	2	2	2	-
	EFT	-	2	2	2	-
	EEM	-	4	4	4	-
Skagit	FRT	-	1	1	1	-
	EFT	-	3	3	3	-
	EEM	-	2	2	3	-
Snohomish	FRT	-	-	1	1	-
	EFT	-	1	4	4	-
	EEM	-	3	4	7	2

Diet and Prey energy density

Diet composition and prey field samples among systems and wetland types were compared based on assemblage differences and energetic densities (J/g for fish diets and J/m³ for prey field). Energy density integrates the quantity and quality of prey or diet composition and is a key input of bioenergetic to estimate individual growth. Individual prey items (from diets or prey sampling) were converted into energy densities (J/g wet biomass) using published values for common prey taxa (Gray 2005, David et al. 2014, Woo et al. 2018). Because of limited fish collections, we examined wetland specific differences by pooling diet data across systems and

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used 14-day running averages to smooth out energy density spikes created by outliers. A similar approach was used for prey field energy densities.

Bioenergetics model

Two questions central to this chapter are 1) whether differences in growth opportunity exist among wetland types, and 2) whether density dependence limits growth opportunities. Because these questions integrate data on individual and population characteristics over large spatial scales and seasonal time periods, we constructed a bioenergetics model to simulate growth and extrapolate consumption to the population of juvenile Chinook salmon. Using this model, we evaluated whether growth conditions varied systematically over time among different vegetated wetland types, by incorporating measurements of wetland-specific temperature and diet, as well as size-at-age data for migrants – including NOr fry and parr as well as HOr migrants – entering the tidal delta at different periods of the rearing season. Secondly, we examined whether consumption demand surpassed food availability in different estuary systems. In this case, we used the bioenergetics model to compound temporally varying estimates of consumption of growing migrants by their abundance over time. We compared this to empirically derived measurements of prey availability over the rearing season to determine whether consumption was likely to surpass demand and cause density-dependent food limitations.

We used the Wisconsin Bioenergetics Model (Hanson et al. 1997) to predict daily changes in consumption, growth, and size across the period of estuarine residence in 2014, a year in which all relevant data sets were consistently collected in three wetland types (FRT, EFT, and EEM) from each of the four large river deltas. Unlike other bioenergetics models that examine snapshots of the population entering at different times in the season (e.g., David et al. 2014, Davis et al. 2019), our modeling framework incorporated temporal dynamics of fish cohorts migrating into deltas. These exhibit seasonal and life-history specific variation in size at delta entry and abundance (Fig. 4.1). This framework matches observed temporal variation in individual growth obtained by analysis of otolith microstructure of juvenile Chinook salmon collected in tidal deltas (see Appendix 4.3).

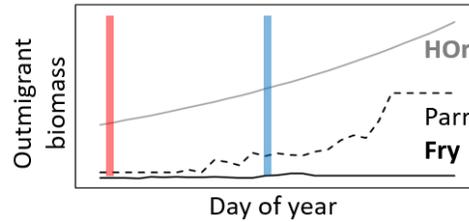
Size at entry into tidal delta wetlands

Individual size at delta entry varies over time for each life history type, reflecting variable degrees of rearing in freshwater. NOr migrants caught at traps were measured either as fry (<45 mm) or parr (>= 45 mm) fish, and we used average size of each life history type measured at the trap each week. Individual biomass is rarely measured for NOr fish at traps, so average lengths were converted to biomass using an allometric function ($\text{biomass} = 0.000004 * \text{length}^{3.2028}$, $R^2 = 0.97$) derived from numerous measurements of fish in the Skagit delta (Table 4.3). For HOr migrants, biomass but not length is routinely measured at time of release, and fish can grow as they migrate downstream. We therefore modeled initial size of hatchery fish entering the delta using biomass data obtained from the RMIS database (rmmpc.org). This database provides observations of biomass at release across the many releases on record. We collected records of size at release in 2000 – 2019 from all four systems. Average biomass at release varied as a function of week of release ($\log_e(\text{biomass}) = 0.0344 * \text{week} + 1.067$, $R^2 = 0.61$), and we used this relationship to model temporal changes in size of HOr migrants for all four systems.

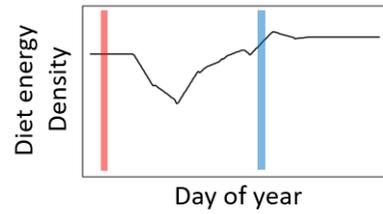
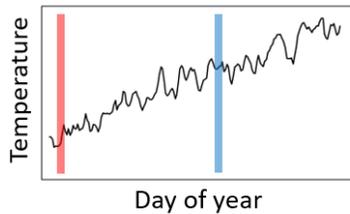
4. Consumption and growth

Weekly variation in outmigrant size

- Fish enter at different sizes
- May determine length of stay
- Influences energetic needs

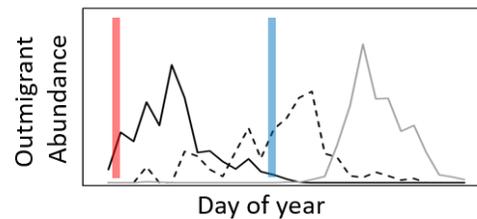


Bioenergetics model of daily growth in delta wetlands



Weekly outmigrant cohort

- Abundance differs by LH type and week
- Affects resource consumption
- Resource consumption limits growth



Daily outputs

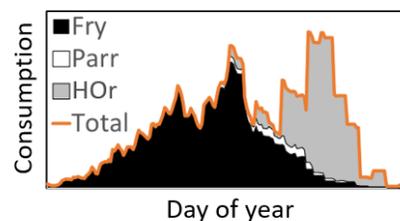
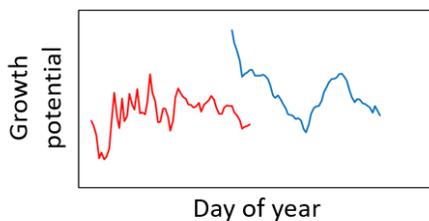


Figure 4.1. Schematic of inputs and outputs of bioenergetics model, including temporally variable size (g) of outmigrants by life history type, standard temperature ($^{\circ}\text{C}$) and energetic density (J/g) inputs into the bioenergetics model, and variable abundance of life history types, through which consumption estimates were expanded. Red and blue bars illustrate two different weeks in which temporally variable characteristics of the population and delta wetlands can influence individual growth for groups of migrants arriving into the delta at different times (left panel of daily outputs). Right bottom panel illustrates outputs of total consumption, once individual consumption estimates are expanded by outmigrant abundance.

4. Consumption and growth

Modeling individual growth within delta wetlands

Bioenergetic models are based on a simple equation describing energy balance in an organism:

$$\text{Eq. 4.1} \quad \text{Consumption} = \text{Metabolism} + \text{Waste} + \text{Growth}$$

Metabolism combines respiration at rest, active metabolism, and digestion, and waste combines egestion and excretion (Hanson et al. 1997). Wetland-specific differences in growth could arise due to differences in the types of prey consumed, as well as from temperature-dependent metabolic processes (a third potential wetland-specific difference, metabolism based on wetland-specific activity differences, could not be evaluated due to lack of data). The Wisconsin Bioenergetics Model uses a standard set of equations to estimate consumption and growth based on user-supplied inputs of 1) temperature patterns over time, 2) energy density of prey, and 3) diets of individuals across time. When applying individual estimates of bioenergetics to populations, the model requires inputs on abundance over time. We followed the wetland-specific bioenergetics model for the Nisqually delta (see Davis et al. 2019 for details on methods), which modeled daily changes in growth and size. This model utilized the key equations, assumptions and parameters specific to Chinook salmon from the Wisconsin Bioenergetics Model (Stewart and Ibarra 1991) and included a minor change in assumptions concerning temperature-dependent thresholds of metabolism in juvenile fish (Plumb and Moffitt 2015).

We used bioenergetics model outputs of growth potential (specific growth rate: $\Delta g/\text{day} / g$ individual biomass) and total consumption to evaluate 1) whether particular wetland types exhibited strong growth benefits over time and 2) whether particular systems exhibited evidence for surpassing consumption of available prey. For our diet inputs we used the two-week running averages of total prey energetic density (J/g wet weight) calculated from fish across all systems. The model required estimates of P, the proportion of maximum consumption. Based on analysis by Davis et al. (2019) which showed that modeled estimates of size were similar to empirical measurements when $P = 0.4$, we held P constant at that value and used the model to predict growth rates, consumption, and change in size. This value of P produced daily growth rates in line with the range in growth observed in otoliths from juveniles collected in two of the four deltas (see Appendix 4.3).

We followed individual growth of each weekly cohort of fish until individuals achieved a fingerling or parr size (70-75 mm or approximately 5 g), after which we assumed these individuals emigrated from the delta (Healey 1980). In order to let the model determine the time course to reach emigration size, we specified the end of the rearing period as the end of July and observed the rate at which fish attained the threshold migrant body size (all fish achieved 5 g by the end of the time period).

Population expansions

To obtain an estimate of total consumption by outmigrants entering the delta, consumption rates of individuals arriving at different times in the season needed to be expanded by temporally changing cohort abundance. The model relied on weekly estimates of abundance of natural-origin (NOr) migrant fry and parr and hatchery-origin (HOr) releases entering the delta during

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different weeks of the rearing season (February-July). Because HOr migrants were not consistently enumerated at outmigrant traps, we estimated weekly abundance differently for NOr and HOr migrants. For NOr migrants, we used data collected from rotary screw traps throughout the migration period in each system to estimate weekly population abundance. Abundances (i.e. counts) were expanded based on capture efficiency tests of marked fish released upstream of the trap to obtain a true estimate of total abundance (see Chapter 3). Information collected from fish captured each week at screw traps included fork length (mm) and origin (NOr or HOr) as well as the proportion of the population that was migrant fry or parr based on length criteria described above. Estimates of NOr outmigrant abundance entering the tidal delta used in population expansions assumed 100% survival from outmigrant traps through growth in the delta.

For HOr outmigrants, we used density estimates of HOr from fish sampling within the delta due to inconsistent sampling of HOr migrants at screw traps in each system. For individual systems and wetland types, captures of HOr fish were often rare, so density estimates were not evenly distributed even after HOr release dates. We therefore compiled HOr density estimates of observations across all years available for each system (see Chapter 3) to obtain a smooth week-dependent curve of expected density. Combining across years assumes hatchery releases follow a similar timing of release each year, which is typically true for a particular river system and was verified via the Regional Mark Processing Center database (RMIS 1977). These curves were transformed into estimates of proportion of total abundance in individual weeks, and then the proportions were applied to the total size of the hatchery release in 2014 for each system to obtain an estimate of HOr juveniles migrating into the delta by week. Similar to NOr migrants, we assumed 100% survival of HOr migrants from release location upriver through delta residence.

We used weekly summaries of abundance from outmigrant trapping efforts as inputs of cohorts into each of the four tidal deltas (Table 4.3). Generally, earlier weekly cohorts are dominated by fry while later cohorts are dominated by parr and HOr migrants. We used the observed starting and ending weeks for each life history type entering the delta to constrain the number of different weekly cohorts run.

Model runs

We ran bioenergetic models for either system or wetland type by varying inputs of outmigrant abundance and size at entry, diet, and temperature. Simulations were run on a daily time step and we summarized growth by week for reporting. Sample sizes of diets were sufficient to characterize running averages for separate wetland types or systems but not both. For wetland-specific runs, we focused on how individual growth potential varied based on different timing of entry into three delta wetland types. We focused on migrating fry, as this life history type stands to benefit the most from delta residence, and varies little in size at delta entry, thereby allowing this aspect of bioenergetics to remain relatively constant. We used NOr migrant numbers from the Skagit, since the focus of the questions concerned growth in wetlands in the context of density-dependent interactions, and the Skagit exhibited the greatest wetland densities and likelihood of density dependence (see Chapter 3). Reflecting the range of variation in migration timing in the Skagit, we modeled delta entry of fry at 5, 10, 15, and 20 weeks.

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Table 4.3. Data inputs into bioenergetics models, and frequency of collection by system (NOr = natural-origin, HOr = hatchery-origin).

Model inputs	Frequency	Systems with data
Size of fish entering delta		
Fry lengths	Weekly	Skagit, Snohomish, Nisqually*
Parr lengths	Weekly	Skagit, Snohomish, Nisqually*
HOr biomass	Annual	All
NOr Length-biomass relationship		Skagit**
Bioenergetic inputs		
Temperature	Daily	All
Energy density in diet	Weekly (predicted)	All
Abundance of life history types		
NOr outmigrants	Weekly	All
Hatchery releases	Annual	All
HOr fish density in delta	Biweekly-monthly	All

* Nooksack lengths were assumed to follow seasonal patterns of the Nisqually, the most similar system.

**Biomass is not routinely measured for individual fish at traps and was therefore based on 3 years of measurements during monitoring in the Skagit.

For system-specific runs, our focus was more empirical – did systems exhibit evidence for consumption outpacing prey availability in 2014? Here, we tracked all life history types entering at multiple weeks at different size. For system-specific runs, we averaged energetic densities and temperatures measured in different wetland to create system-specific daily summaries for model runs. We expanded individual daily consumption by weekly population expansions until individual weekly cohorts reached 5 g and summed total consumption across all life history types arriving and growing in different weeks.

Bioenergetic outputs

We used outputs of body size and growth rate (g/day) to evaluate temporal realism of the model, and specific growth rates (g of growth/g body weight) to compare growth potential of different wetland types. Outputs of consumption were used in conjunction with weekly abundances of each cohort (NOr fry, NOr parr, and HOr) and energetic density of prey to evaluate consumption demand (see Baldwin et al. 2000). We expected consumption to equal prey availability when

$$Eq. 4.2 \quad \sum_{i=1}^n D_i * C_i = 10000 * P$$

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Where D = total Chinook density (fish/ha) and C = consumption (J/fish) for each, i , life history group, P = prey availability energetic density (J/m³), and the constant 10000 converts m³ to ha when depth = 1 m. Hence, the maximum Chinook density that a wetland type could sustain – what we might call energetic capacity – is $10000 * P / C$.

A major assumption of our analysis was that NOr and HOr diets were similar during periods of overlap in each tidal delta. If diets were indeed similar, consumption could be evaluated with a single bioenergetics model to estimate consumption through time to represent both NOr and HOr Chinook salmon. We evaluated diet overlap and found no differences between NOr and HOr composition (PERMANOVA, $p = 0.140$), and therefore proceeded with our analysis. A detailed explanation of our analysis between NOr and HOr diets can be found in Appendix 4.2.

Diet composition, prey availability, and prey selectivity

In addition to the bioenergetics approaches to assess potential competition or density dependence effects on individual growth, we evaluated changes in diet composition and the relationship to prey assemblages with changes in local density, and as a function of individual size. A relationship between either metric and local fish density may indicate potential behavioral changes that may not show up directly in an analysis of consumption demand or growth potential. To analyze overlap between diet and prey we selected a subset of diet and prey assemblage samples from the similarity matrix that were collected from the same site within ≤ 7 days of one another. We assumed individual diets collected within 7 days of prey field samples were likely more representative of one another and ensured we maintain the largest dataset possible for analysis. As such, we reduced the total number of diet (427 to 205) and prey (84 to 38) samples accordingly. Next, because multiple diet samples may have been collected from a particular site/date, we averaged the individual similarity values for particular site x dates where multiple samples existed creating a mean similarity value to compare to the single prey assemblage sample. Prior to analysis, diet and prey field data were square root transformed and standardized to total sample weight to represent relative proportions of individual categories in each sample. Transformed data were then used to create resemblance matrices of Bray-Curtis similarities for use in the model framework. Bray-Curtis similarities are calculated as proportions, and when multiplied by 100 represent the percent of shared species between samples with values ranging between 0 (no overlap) and 100 (complete overlap). All multivariate analyses were performed in Primer-7 (Version 7.0.13, Clarke and Gorley 2015).

We developed two primary hypotheses relating foraging behavior/strategies to changes in local density and individual size:

H1: Density-dependent competition would lead to less selective (more generalist) feeding strategies under higher densities, resulting in a positive relationship between local density and diet/prey similarity.

H2: Larger individuals would have a competitive advantage over smaller individuals, enabling them to be more selective than smaller fish, which would result in a negative relationship between individual size and diet/prey similarity.

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Initial data exploration revealed two important characteristics of our data: 1) variance was not homogenous across the range of the predictor variables (density and fork length, and 2) strong evidence that the relationship between diet/prey similarity and our predictor variables may differ at the extremes of our values. Given the apparent structure of our data we used quantile regression to evaluate how diet/prey similarity changes as a function of local density and individual fork length for Chinook salmon. Quantile regression generally follows linear regression methods but supports evaluation at the user-specified percentile rather than the mean of the response (Koenker 2005). Regression quantiles are especially useful where relationships (slopes) between the response and covariates may differ at the extremes versus the mean of the distribution in particular when interpreting potential limiting factors. We evaluated changes in diet/prey similarity at the 10th, 50th (median) and 90th percentiles. Our model included continuous predictors for total Chinook salmon density (NOr + HOr) and individual fork length as well as a System factor to account for any differences among tidal deltas. Uneven sample sizes among system and wetland types precluded us from including wetland type as an additional factor therefore samples were pooled across wetland types within each systems for analysis. . Quantile regression was performed using the *quantreg* package (Koenker 2020) and plots were created using *ggplot2* (Wickam 2016) and *ggpubr* (Kassambara 2018) in R (R Core Team 2018).

Results

Water temperature patterns

Temperature patterns observed in 2014 across systems and among wetland types were highly variable, though a general warming trend was evident across all groups throughout the rearing period (Fig 4.2). We did not observe any systematic differences in the rank order of water temperatures among any systems or wetland types. Water temperatures did not generally exceed the 15°C mark in any system or wetland type until early June; the exception to this pattern occurred in the Nooksack tidal delta when temperatures in the FRT and EEM both exceeded 15°C prior to June, though each peak was followed with subsequent cooling events. Within wetland types, temperatures were much less variable across systems during the early part of the rearing period (pre-June) with the exception of a spike in FRT wetlands within the Nooksack tidal delta. After June, water temperatures became more variable, particularly in the EEM and EFT wetlands across systems, and reached temperatures that are likely detrimental to individual growth. During this period, temperatures in the Nooksack and Snohomish EEM (and to a lesser degree the EFT) wetlands appeared to increase more rapidly compared to other systems or wetland types. Water temperature in the Skagit and Nisqually EEM and EFT wetlands were generally lower after June than the other systems.

Diet and prey energy density

Diet energy density varied considerably throughout the rearing season, both among wetland types and systems (Fig 4.3). Similar to our observations of water temperatures, no wetland types or systems had systematically higher diet energy density values across the entire period. Diets in FRT and EFT wetlands had higher energy density values at the start of the rearing season, though diet energy converged across all wetlands by week 14. Energy densities of diets collected in EEM wetlands appeared to fluctuate between periods of relatively high and low energy values.

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Diets in EFT wetlands had the highest energy density values in the early rearing season before decreasing in May and again increasing for the remainder of the rearing period. FRT diets were somewhat less variable than the other wetland types and were characterized by two very similar periods of decreasing energy densities; one from Mar – mid-Apr and the other from mid-May through the end of the rearing period.

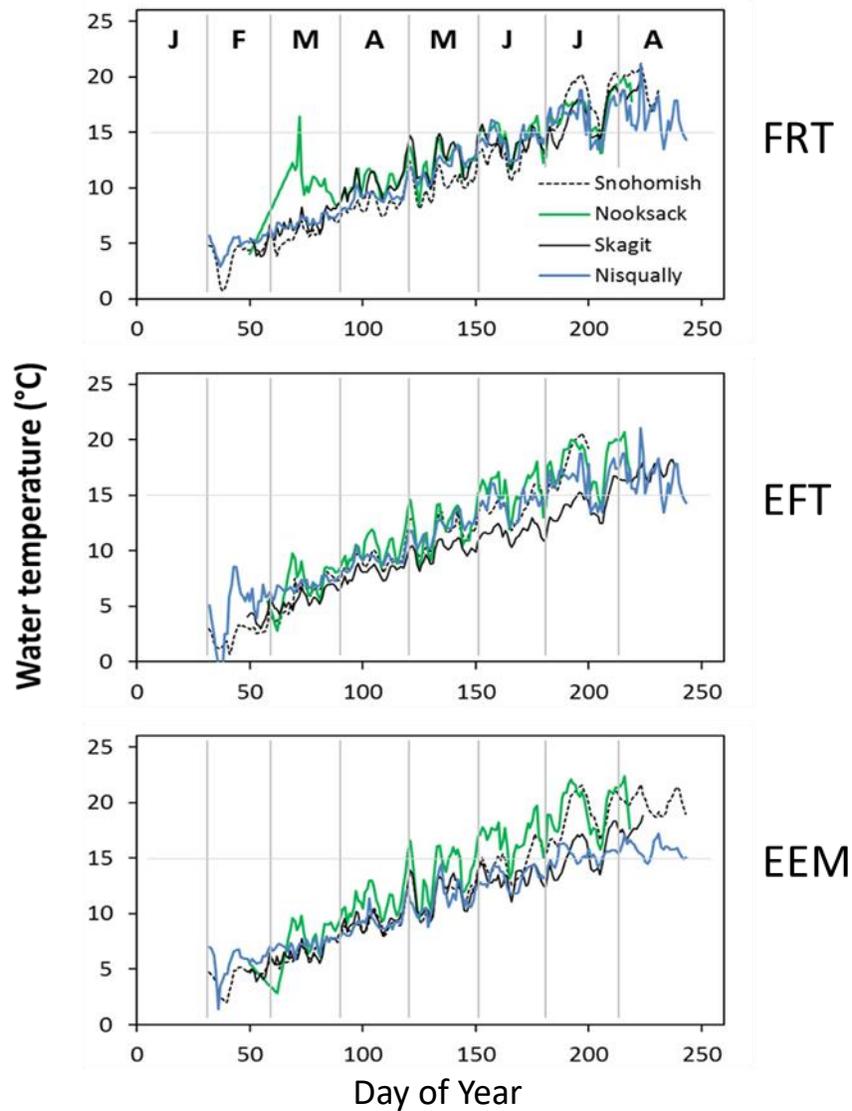


Figure 4.2. Water temperatures recorded between February and August 2014 (months separated by vertical lines in each panel). Data are summarized by wetland type (FRT, EFT, and EEM wetlands in rows) for four estuary systems (colored lines). Horizontal line at 15 degrees facilitates comparison across panels and represents the maximum optimal temperature for juvenile salmon growth at sizes, feeding rates, and dietary energy densities observed in this study (Brett 1979, Beauchamp 2009).

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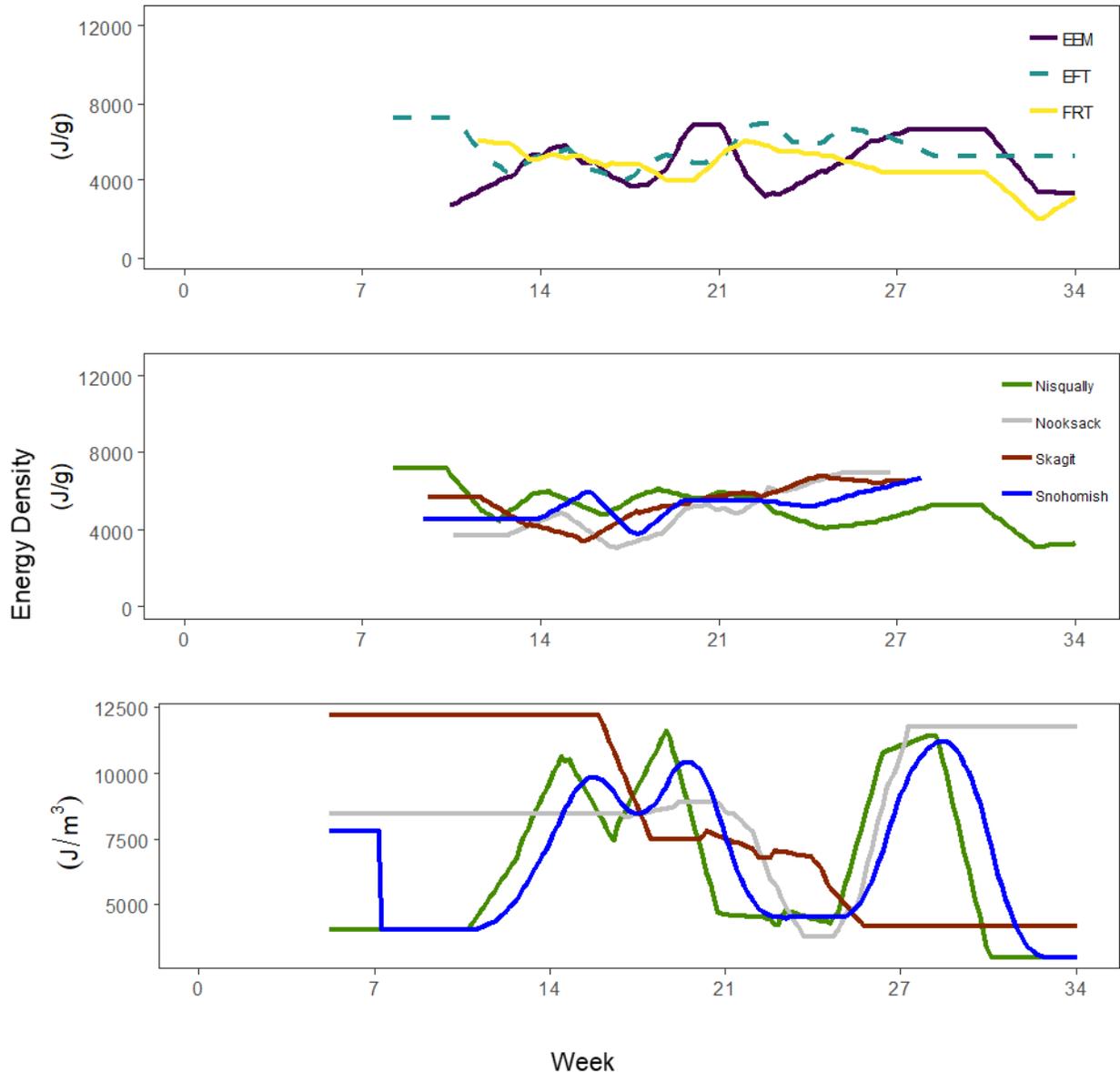


Figure 4.3. Two week running averages of energy density for NOr diet by wetland type across all systems (top), NOr diet by system across all wetland types (middle), and prey field samples by system across all wetland types (bottom).

When diets were combined across wetland types within systems, we observed similar variability through the rearing period (Fig 4.3). However, differences among systems were less dramatic than among wetland types and three of the four systems had relatively similar temporal patterns in diet energy density. While energy densities were extremely different at the beginning of the rearing season among all systems, diets from the Skagit, Nooksack, and Snohomish displayed consistent increases in energy density from mid- to late- April through the end of the rearing season. Interestingly, diets from Nisqually showed nearly the opposite pattern whereby diets had higher energy density at the beginning of the season and displayed a consistent decrease from late-April through the end of the period.

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Energy density of prey availability samples were compiled across wetland types within systems over the rearing season. In three of the four systems (Nooksack, Snohomish, and Nisqually), temporal patterns of prey energy density were remarkably consistent (Fig 4.3). While initial values in these three systems were quite variable, prey energy density began tracking with peaks in early March before decreasing into mid-April and then increasing again at the beginning of June. This drop is co-incident with peaks in Chinook salmon density in deltas (Chapter 2). Prey energy density in the Skagit started out higher than any other system but then consistently decreased throughout the remainder of the rearing period. With the exception of the Nooksack, total prey energy density was the lowest at the end of the rearing period (late-Jul and early- Aug).

Wetland-specific growth

We modeled wetland-specific growth potential for separate weekly cohorts of NOR fry entering the estuary during weeks 5, 10, 15, and 20 of the outmigration period. To facilitate useful comparisons, we summarize and present the results for four specific cohorts that enter the estuary to rear at different times and sizes and theoretically represent conditions across the entire outmigration period (Fig 4.4).

Mean growth potential did not differ significantly among wetland types within the four cohorts we modeled and generally increased from the beginning to end of the outmigration period (Fig 4.4). However, weekly growth estimates among wetland types within each cohort revealed this was largely due to relatively high initial growth potential for the week 15 and 20 cohorts which then dropped rapidly to values that reflected growth potential at the beginning of the outmigration period (Figure 4.4, bottom panel). The rank order of wetland-specific mean growth potential was different for each cohort, suggesting that variable growth benefits in each wetland type depended upon initial size and arrival timing. Comparing the weekly estimates of growth potential strongly supported the variable benefits of wetland types within a given cohort: rank order of growth by wetland type changed frequently over the modeled growth period. However, mean growth potential was highest in FRT wetlands earlier in the outmigration period while mean growth potential in EFT wetlands was higher later in the period. Mean growth potential in EEM wetlands was never highest but consistently increased throughout the season.

Weekly trends in growth potential for each wetland type were rather different within and among cohorts. Growth potential for all wetland type generally decreased from the beginning of the period to the end of the rearing period for each cohort. The exception was growth within EEM wetlands for fish that entered the estuary early in the outmigration period (Weeks 5 and 10). The steepest decreases in growth potential occurred during the latter part of the rearing period and were especially evident for fish that entered the estuary in week 15 or later. Individuals migrating to the delta during these periods experienced relatively rapid decreases in growth potential in all wetland types during estuary residence.

In addition to general trends in wetland-specific growth potential among cohorts and across weeks, variability within wetland types was also quite striking. Wetland-specific growth potential often followed bimodal or cyclic changes in growth throughout the duration of a single cohort growth period. These variable trends were especially evident within EEM and EFT

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wetlands suggesting conditions may fluctuate and influence the growth potential for individuals that reside

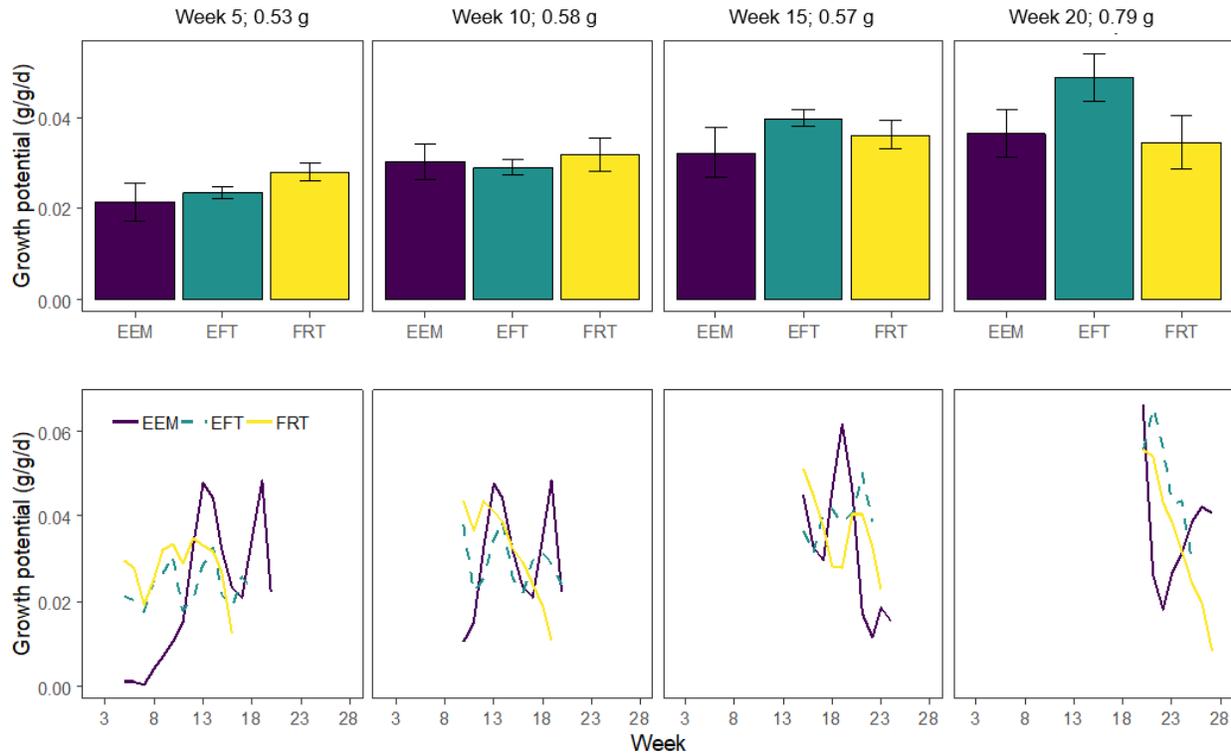


Figure 4.4. Mean growth potential (grams per gram wet weight/day) estimated from the bioenergetics model by wetland type (top panel) and by wetland type and week (bottom panel) for each cohort. Cohorts are labeled with the week size at entry to the estuary.

within those environments. Across all four scenarios, growth potential in EEM wetlands was the most variable on a weekly basis. Growth potential in EEM wetlands showed swings that resulted in 2- to 4-fold increase/decrease in estimated growth potential over a ten week span at the beginning and at the end of the outmigration period.

System-specific consumption demand

We combined the estimates of consumption from the bioenergetics models with known abundances of NOR fry, NOR parr, and HOR migrants by week, as measured by smolt trap operations in each system, to determine whether systems were exceeding energetic capacity at any point during the rearing season. Total consumption, period of peak consumption, and the shape of consumption curves varied substantially among systems (Fig 4.5). Consumption in the Skagit tidal delta was generally 2x higher than the next highest system (Snohomish) and 3.5 to 10x higher than the Nooksack or Nisqually, respectively. Peak consumption in the Skagit and Snohomish deltas also occurred earlier in the season (Mid-April) than either the Nisqually or Nooksack deltas (early May). Consumption in the Skagit and Snohomish deltas gradually increased from the earliest part of the outmigration period through week 18 before beginning to decline whereas consumption in the Nooksack and Nisqually remained relatively low through week 17 or later before peaking and then declining again through the end of the rearing season.

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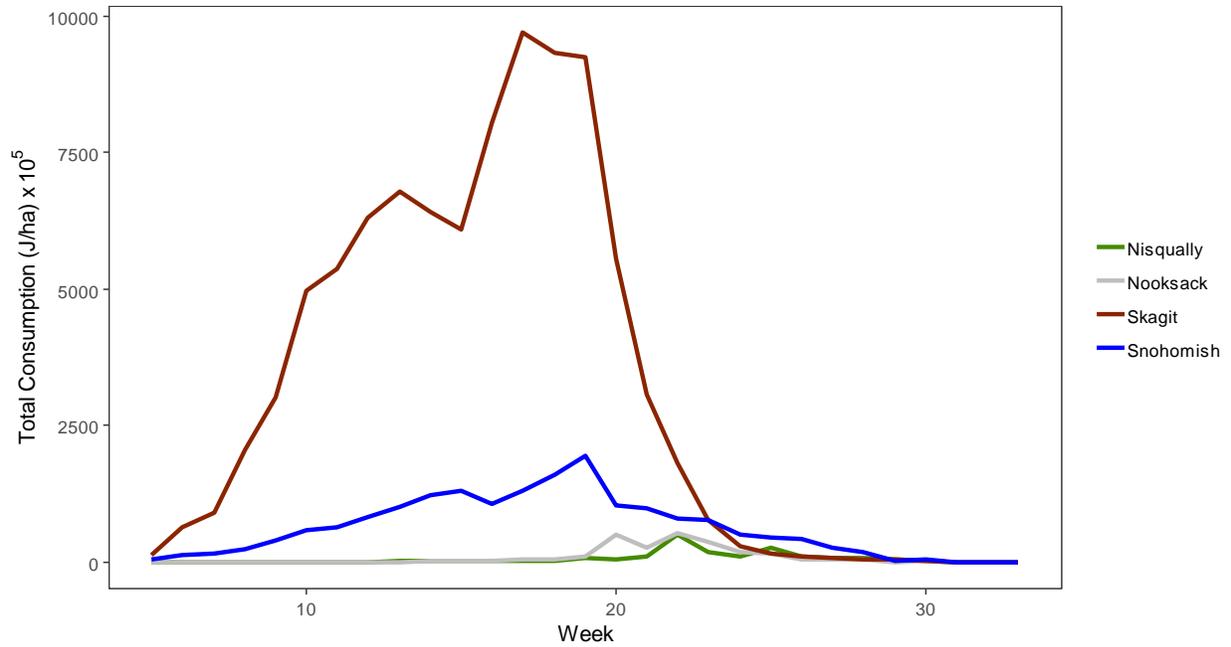


Figure 4.5. Total energy consumption (NOr fry + NOr parr + HOr) by week for each system.

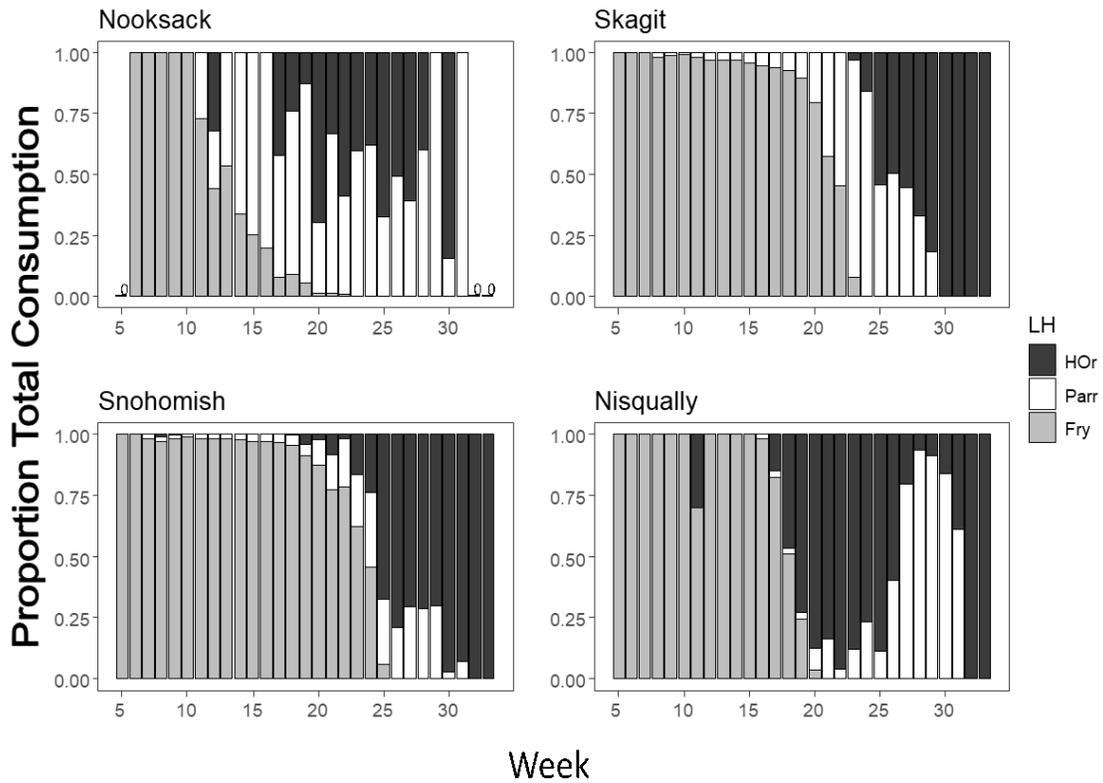


Figure 4.6. Proportion of total consumption demand by week and attributed to each life history type in each system.

4. Consumption and growth

The proportion of total consumption by life history and/or origin type differed considerably by week among the systems (Fig 4.6). Consumption in the Skagit and Snohomish tidal deltas was largely dominated by NOr fry between weeks 5-22 (i.e. Feb- May) before switching to NOr parr and/or HOr migrant consumption throughout the remainder of the season. In contrast, consumption patterns in the Nooksack and Nisqually were dominated for a shorter period of time by NOr fry migrants before becoming largely attributable to NOr parr and HOr migrants around week 14 – 18 (i.e. Mar – Apr). Both Nisqually and Nooksack also had considerable consumption demand by NOr parr in the latter part of the rearing season (after June) which was not present in the Snohomish and Skagit tidal deltas.

Consumption estimates were expanded based on system-specific weekly abundance estimates and compared with the total energy available from prey expanded across the entire tidal delta to assess potential prey limitations or energy deficiencies. Based on 2014 inputs, our model results suggest that consumption was not limited by total prey energy in any system through the rearing season (Fig 4.7). Differences between energy available as prey and consumption demand were highest at the tails of rearing period when consumption demand was the lowest due to low abundances in each system. The ratio between prey availability and consumption demand approached 1 in the Skagit and Snohomish tidal deltas beginning in early April and continued

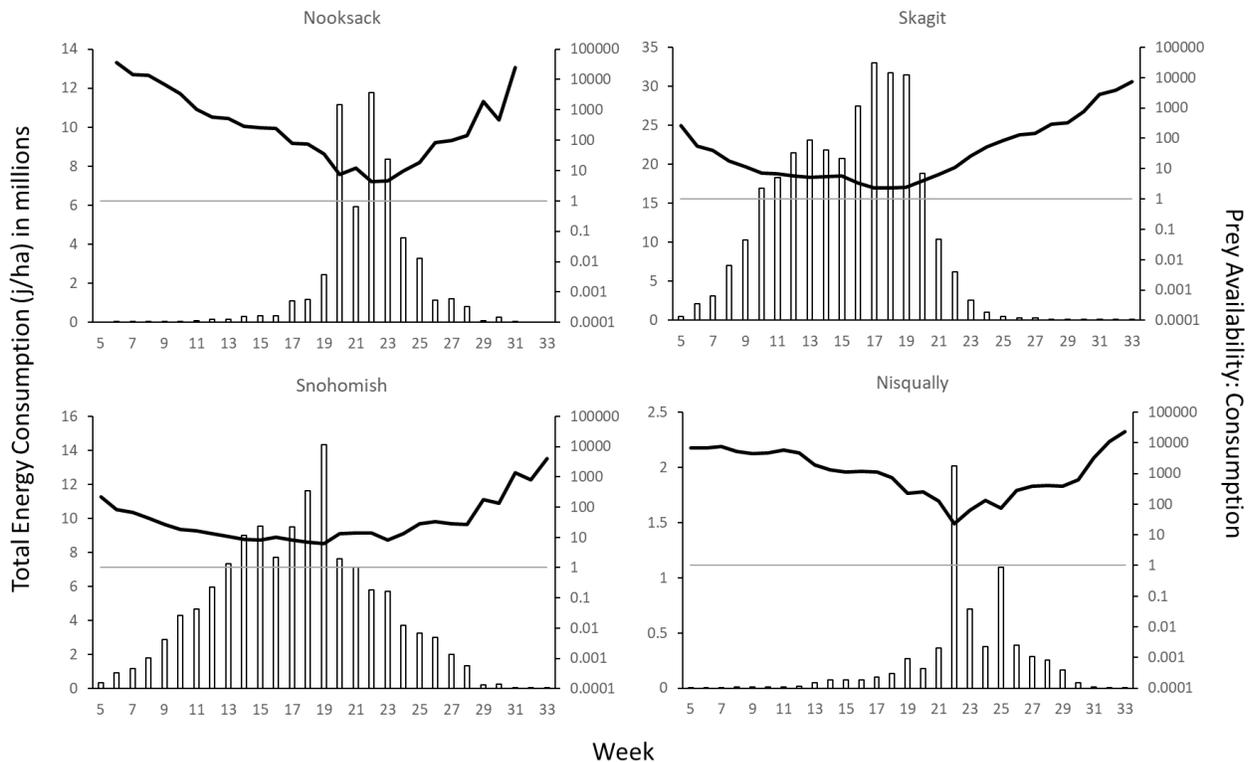


Figure 4.7. Total energy consumption (NOr fry + NOr parr + HOr) by week (bars; primary y-axis) and the ratio of consumption demand to prey energy availability (lines; secondary y-axis) by week for each system. Note the differences in primary y-axis values for each system. Grey line at value of 1 (secondary y-axis) represents where consumption demand and prey energy availability are equal. Values higher than 1 indicate prey energy availability is higher than consumption demand.

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through late May. In contrast, the ratio was lowest in the Nooksack and Nisqually for a much shorter period, and prey availability was never less than 10x that of consumption demand.

Prey-diet overlap and competition/selectivity

We used paired diet and prey samples to quantify the degree of overlap between diet and prey assemblages in each wetland type. In general, diets did not accurately reflect the prey assemblage available to juvenile fish in any wetland type or system. Among systems across all wetland types, prey assemblages and diet composition samples shared between 5.52 and 24.84% of species by WWB; the Nisqually and the Snohomish were the least and most similar, respectively (Table 4.3). Among the wetland types, FRT had the least overlap between prey and diet samples (mean = 8.75%) and the EFT shared the highest percentage (mean =14.35%) of species by WWB. Interestingly, we found no overlap between diets and prey field samples in the Nooksack EEM wetlands. We hypothesize that this pattern may represent fish that fed in adjacent marine waters and not the EEM wetlands where they were captured, given the prevalence of marine derived prey in the stomach contents.

The general and consistent lack of overlap among diet and prey samples among and within wetland types and systems was likely associated with the proportion of insects versus non-insect categories in each sample type (Figure 4.8). Chinook diets, when averaged by system or wetland type, always had higher proportion of insects than the associated prey field samples. The percent of insects in diet ranged between 46.8-94.3% and 70.4-90.1% by system and wetland type, respectively. In contrast, the percentage of insects in prey field samples never surpassed 35% among systems or wetland types.

We also evaluated how prey/diet overlap changed as a function of local Chinook density and individual fork length as a way to assess potential density-dependent effects on growth and/or competition (Fig. 4.9). Across wetland types, similarity between diet composition and prey field assemblage was generally less than 15% at the lowest observed densities and ranged between 0 and 47% at the highest densities. The opposite was true as a function of fork length whereby similarity ranged between 0 and 47% for the smallest fish but decreased with increasing fork length such that similarity for the largest fish was generally less than 10%. Model results indicated a significant positive relationship between diet/prey similarity and total Chinook salmon density at the 90th percentile (0.100, $p = 0.007$), non-significant but positive at the

Table 4.3. Mean Bray-Curtis similarities among prey assemblage and NOr diet composition samples from the four tidal deltas. Bray Curtis scores were based on relative proportions of WWB. Values in italics are marginal means across either system or wetland types.

System	EEM	EFT	FRT	All
Nooksack	0.00	5.28	6.9	6.09
Skagit	7.52	14.38	10.75	10.88
Snohomish	14.91	34.77		24.84
Nisqually	5.03	2.96	8.59	5.53
All	9.15	14.35	8.75	

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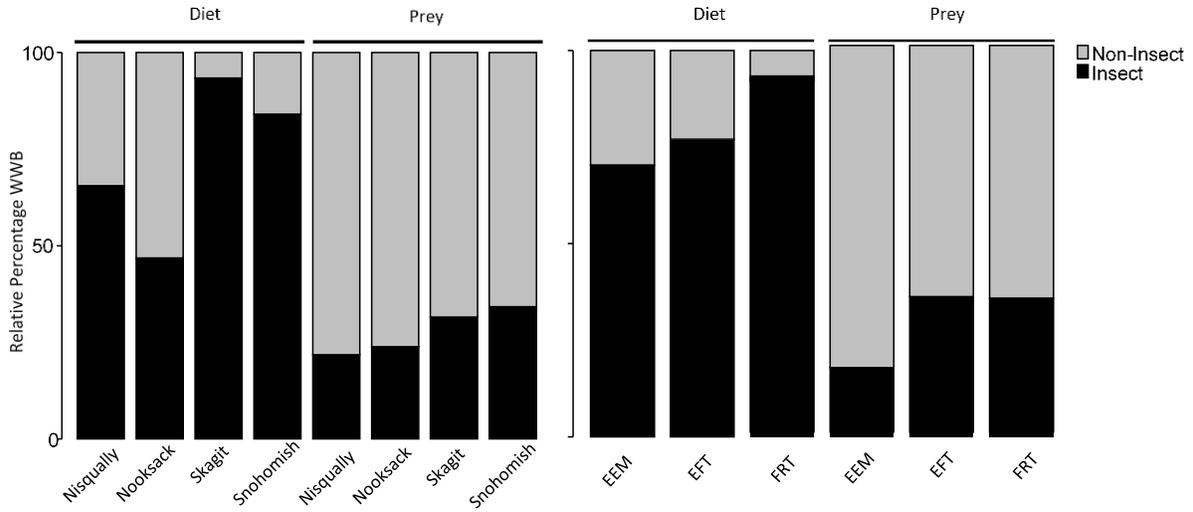


Figure 4.8. Mean relative percentages by WWB for insect and non-insect species/groups from Chinook diet samples and prey field samples by system and wetland type.

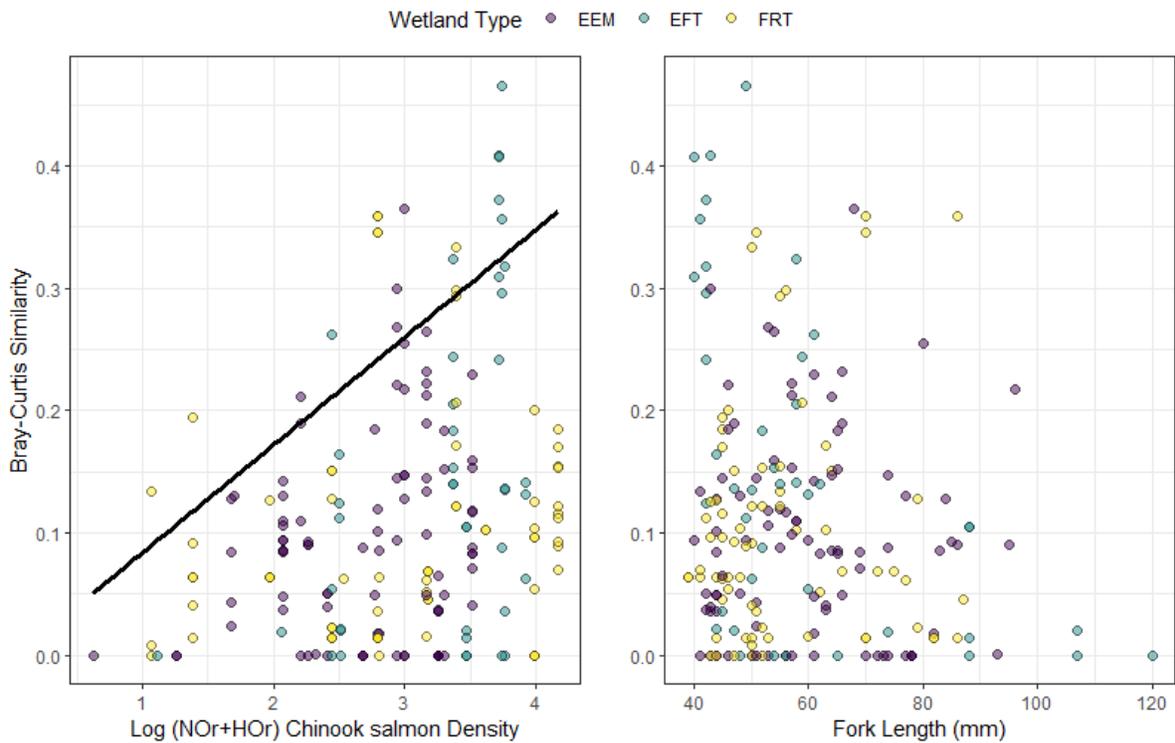


Figure 4.9. Prey/diet similarity (Bray-Curtis similarity as a function of local density (left) and individual fork length (right). Solid line represents significant relationship for 90th percentile.

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median (0.013, $p = 0.060$), and had no relationship at the lower 10th percentile (0.00, $p = 1.000$). Diet/prey similarity increased by 10% for every ten-fold increase in Chinook salmon density for values in the highest 10% of observations. The relationship between fork length and diet/prey similarity was non-significant and slightly negative at the median (-0.001, $p = 0.269$) and 90th percentile (-0.013, $p = 0.137$) and had no relationship at the 10th percentile. Our results indicate that fish diets became more diverse with increasing density and that fork length did not contribute significantly to changes in diet/prey similarity.

Discussion

Analysis of inputs and outputs of bioenergetics models provides rationale for explaining differences in growth and consumption among wetland types relevant to our analyses of distribution and density dependence in previous sections (Sections 2 and 3). Our results strongly support the idea that habitat diversity is important for populations and highlight how timing of estuary residence along with variation in temperature and prey availability, and potential competitive interactions, can influence individual growth experience. These results are also strongly supported by data on individual growth obtained from otolith microstructure (See Appendix 4.3). Bioenergetic projections of individual growth indicates that considerable variation occurs among wetland types and throughout the outmigration period. Changes in growth potential were likely related to the complex interaction and timing between optimal thermal conditions and elevated dietary energy density. The projected variability in growth potential suggests a dynamic range of opportunities for fish that enter the estuary at different times and sizes. Estimated total consumption demand by Chinook salmon also varied widely among the four tidal deltas and depended on not only bioenergetics but also the period and magnitude of peak consumption and the proportion attributable to the various life history types. Although our estimates of consumption demand did not surpass prey energy availability, changes to inputs (i.e. temperature patterns, outmigration abundances) could lead to different outcomes, and otolith microstructure results provide evidence of density-dependent growth (Appendix 4.3). Lastly, we identified a potential competitive disruption to foraging strategy that may also influence growth potential. Within EFT wetlands, diet composition and prey field assemblages became more similar with increased local densities indicative of reduced selectivity.

Bioenergetic projections of growth

The main finding from the bioenergetics model – that wetland-specific differences in growth can vary over time –has important implications for management of tidal delta wetlands and species recovery. Understanding how variation in model inputs can influence projected growth estimates will aid interpretation and applicability across multiple systems. General temporal trends across the entire rearing period suggested freshwater wetlands (FRT) are more beneficial early in the season whereas the more marine-influenced environments (EEM) afford higher estimated growth potential as the season advanced. Given the structure of the standard bioenergetics model, variations in model projections might be expected based on empirical differences in water temperature and/or diet and prey data across wetland types. Davis et al. (2019) found evidence for similar seasonal shifts in wetland-specific growth opportunity and attributed the observed

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differences to prey energy density and consumption rates related to changes in individual size. We found diet energy density among the wetland types throughout the rearing period was clearly variable (Fig 4.3), and each wetland type offered high quality prey at some point in time. Temperatures increased linearly throughout the rearing period, though the slope of the increase was slightly different among wetland types (Fig 4.2). Although changes in either of these inputs could directly impact individual growth, it is likely that the covariation among temperature and dietary energy density is useful for explaining projected differences (Fig 4.10). For example, peak growth potential in all wetland types was generally associated with periods of high dietary energy density. Yet for EFT and to a lesser degree FRT wetlands, periods of high energy density coincided with relatively low water temperatures which muted the potential benefit and estimated growth potential. Conversely, the relatively high dietary energy densities observed in these wetland types during cool periods (i.e. early in the season) provide a considerable growth benefit relative to EEM wetlands where energy densities are at a minimum during similar periods. In contrast, during periods of elevated water temperatures energy densities in the FRT and EEM wetlands were relatively low and high, respectively, creating higher estimated growth potential in EEM wetlands later in the season. If fish are sensitive to growth opportunities in their environment and

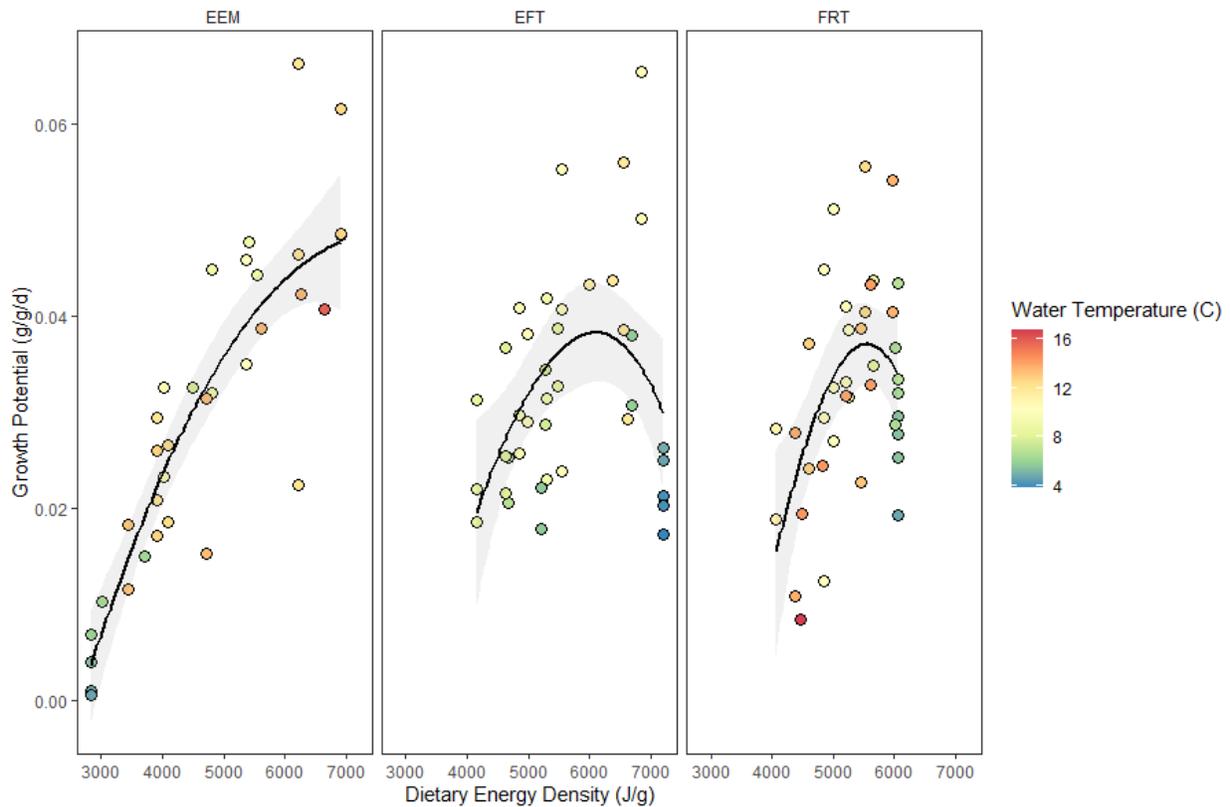


Fig 4.10. Estimated weekly mean growth potential from bioenergetics model as a function of dietary energy density and water temperature across all three wetland types for all simulated cohorts. Line represents conditional mean from loess fit to aid visualization.

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select areas based on their productivity (Railsback and Harvey 2002, Rosenfeld et al. 2005), these patterns might be expected to facilitate downstream migration. Such covariation in temperature and energy density and the resulting influence on estimated individual growth potential emphasizes the importance of wetland diversity in tidal deltas to maximize growth opportunity for juvenile Chinook salmon.

While intra-annual variability in temperature and prey availability are important to understanding difference in potential growth, it is also worth considering how inter-annual variability may change interpretations or expectations for juvenile salmon in tidal delta habitats. Temperature mediates growth opportunity via thermal impacts on metabolic processes (Brett 1971, Richter and Kolmes 2005, Davis et al. 2018). We modeled growth using temperature data from 2014, a rather cool year throughout the region (PSEMP Marine Waters Workgroup 2015). Inter-annual variability in temperatures can have dramatic effects on estuary thermal conditions. For example, differences between 2014 and 2015 temperatures, among wetland types within the four tidal deltas we examined for this study, revealed temperatures increased considerably faster in 2015 (Fig 4.11) resulting in higher overall temperatures and warmer conditions earlier in the outmigration period. Increasing temperatures would either require increased consumption in order for individuals to maintain similar growth potential or result in decreased growth potential, assuming consumption remained unchanged. The impacts from increased consumption are discussed below. Alternatively, increasing temperature during estuary residency may contract the suitable rearing period, thereby reducing residence time (Chamberlin et al. in review). If residence time is indeed

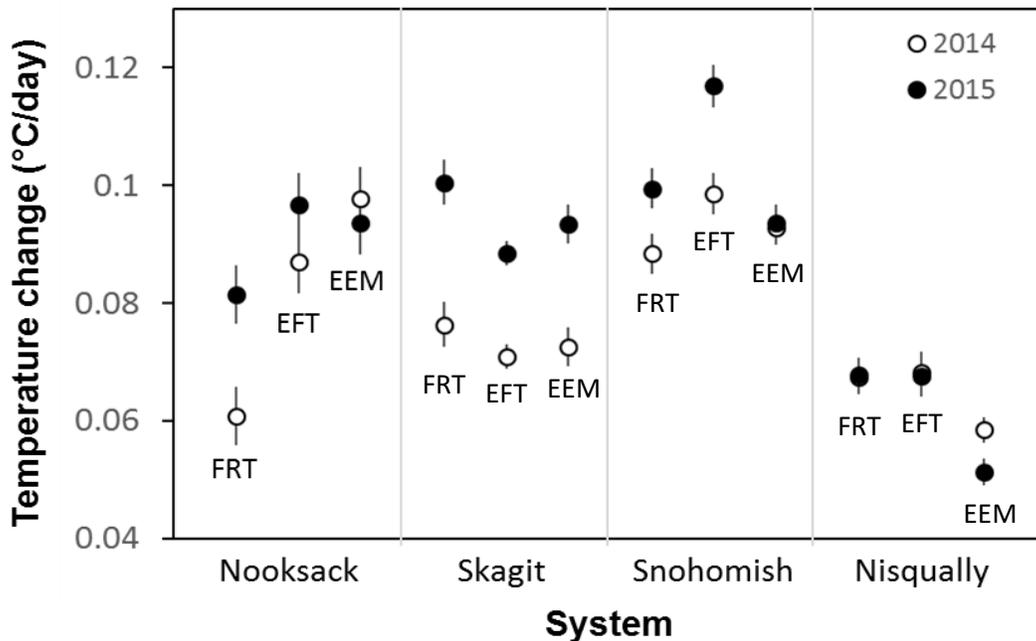


Figure 4.11. System-, wetland- and year-specific variation in seasonal temperature changes (°C/day). Points represent the slope ($\pm 95\%$ confidence interval) of the linear relationship between average daily temperature and day of year.

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correlated with temperature patterns, systems and/or wetland types with buffering potential (i.e. cooling mechanisms) via tidal inundation or vegetative shading may provide prolonged periods of optimal rearing temperatures, potentially influencing residence times and growth potential for juvenile Chinook salmon. Given that warm temperatures are expected to be increasingly common (Scavia et al. 2002, Roessig et al. 2004), it will be important to consider the bioenergetics implications of long-term temperature change for estuarine-dependent juvenile Chinook salmon.

Uncertainties

Like most bioenergetics models, our measurement of water temperature occurred at much better temporal resolution than diet data. Hence, our conclusions about differences in diet composition and prey availability could be strengthened by additional data. Modeled temporal dynamics are more likely to be driven by temperature swings, or variance in diets among individuals. While it may be difficult to accumulate sufficient observations annually to run high-resolution bioenergetics models, additional monitoring will benefit by pairing local density measurements with diet and prey sampling, and can add to diet and prey composition results presented here so that better conclusions about habitat-specific variation and diet selectivity can be revised in an adaptive management context.

Some elements of the bioenergetics model deserve greater complexity to match the ecology of juvenile Chinook salmon. Real fish in estuaries are capable of extensive movements (Hering et al. 2010, McNatt et al. 2016), facilitated by tidal inundation and river flow that allow movements both up and downstream in the estuary (e.g., Bennett and Burau 2015). More dynamic movement scenarios likely invoke differing metabolic costs on individuals. It is plausible that the metabolic cost of remaining in less dynamic, slower-moving wetlands could be lower than remaining in another wetland with higher velocity or greater tidal dynamics. Any potential differences in metabolic demands among wetland types would certainly influence the estimate of growth potential for individuals in those particular environments. Our model did not incorporate any such variation in the metabolic constants used to estimate growth. Future efforts should attempt to estimate variable metabolic demands and include them in the bioenergetics framework to address these uncertainties.

While we modelled wetland-specific growth potential within a given wetland type for each cohort, fish naturally use a mix of wetland types during outmigration. In this context, the model results point to some time-specific differences in growth opportunity among wetland types, yet true growth potential for an individual fish will likely differ somewhat. Fish rearing in the estuary will likely use different wetland types by 1) moving dynamically based on tidal and current dynamics that may be partially out of their control, and 2) making choices between staying in a particular wetland with its growth opportunities and moving when those growth opportunities decline to a particular level. Based on the sizes of fish during the rearing period, the first response is likely more important during early phases of immigration, when fish are small and cannot overcome certain current dynamics, while the second response is likely to occur after individuals have grown for several weeks within the estuary. Both responses will likely involve habitat switching to varying degrees. We expect that dynamic movements of fish

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within estuaries is one major reason for sometimes muted (Fig 4.9, David et al. 2014, Lott 2004) or conflicting wetland-specific results. Nevertheless, empirical analysis of individual growth suggests that in certain years, wetland-specific growth differences may emerge (see Appendix 4.3). Refining model-based approaches for projecting the influence of wetland-specific bioenergetics will likely involve individual-based simulation approaches (e.g., Railsback and Harvey 2002) that incorporate spatial variation and bioenergetics-based movement decisions.

Lastly, our bioenergetics model incorporated a fixed value for the proportion of maximum consumption ($P_{max} = 0.4$) to estimate growth opportunity. Using a fixed value for P_{max} allowed us to compare growth opportunity among wetland types throughout the outmigration period as a function of dietary energy and thermal conditions. Short term changes, or variability, in individual P_{max} could certainly influence estimates of growth opportunity. Obtaining observed P_{max} requires empirical information on the growth of an individual over a given time period (i.e. scale morphometric, mark/recapture techniques) which was not possible with the data in this study. Where these data have been available, studies have shown that variability does indeed occur (Davis et al. 2019, Gamble 2016). Davis et al. (2019) found observed P_{max} values ranged between 0.24 and 0.47 among FRT, EFT, and EEM wetlands in the Nisqually delta. However, the authors concluded that the observed changes in the proportion of maximum consumption were strongly correlated with fish size and that differences in growth were more likely due to thermal conditions and prey availability/prey energy among wetland types.

Consumption demand in estuaries

Consumption demand has been used as a tool to assess competitive interactions and habitat capacity among piscivores in a variety of environments (Moss et al. 2009, Hartman and Margraf 1992). We evaluated population level consumption demand (total energy consumed) for juvenile Chinook salmon throughout the outmigration period and compared values to estimated prey energy production as a way to assess plausible density dependent processes that may regulate growth potential. If total estimated energy consumption by Chinook salmon equaled, or surpassed, the total estimated prey energy availability we may expect a negative growth response (e.g. reduced growth potential). Our comparisons of energy consumption and energy density of available prey indicated consumption did not outpace energy availability under our selected model conditions in any of the four tidal deltas. Yet consumption did increase considerably during peak outmigration periods in all systems and the periods when consumption approached prey energy limits coincided with periods during which observed densities exceeded capacity in each system (Fig 4.8; see also Fig 3.4). It is important to note that our analysis was based on temperatures and outmigrations from 2014, which was both a relatively cool year and an average outmigration size. We might expect that our interpretations of consumption demand may change during a warm year or with above average outmigration abundances. In both situations, the total consumption at any given point in the rearing period would likely be higher. In our analysis of 2014, consumption demand by juvenile Chinook salmon in the Skagit delta during periods of peak consumption accounted for up to one-half of the total energy production (Fig 4.8). Therefore, if outmigration abundances doubled, a situation well within the range of inter-annual variability (see Chapter 3), we may expect prey limitations within the delta, assuming thermal and prey field conditions remained similar. Indeed, analyses of individual growth rates observed

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from otolith microstructure indicated lower estuarine growth in years of high outmigration abundance (Beamer et al. 2005 Appendix D), as well as density-dependent growth within seasons (see Appendix 4.3) at local densities that occur within all four systems (Fig. 3.3) in some years.

In addition, dismissing the impact of potential density dependent interactions solely on consumption demand ignores the role of other consumers and prey preferences. In bioenergetics studies of systems with a few key predators (e.g., Baldwin et al. 2000, Martino and Houde 2012), estimates of consumption demand have been used to evaluate conditions under in which demand becomes greater than prey availability. This is not the case for the four Puget Sound estuaries we examined, where a host of predators besides Chinook salmon may consume available invertebrate prey. Chinook salmon represent only a part, and in some cases a relatively minor part, of the total community assemblage in each of the tidal deltas (Fig 4.12). While it is not likely that each of the species present in the delta feed on exactly the same resources at the same time, it is plausible that overlap in foraging does occur, especially for other salmonids, and thus cannot be excluded from consideration. In this context, the notion of competition over energetic resources needs to be examined in a community ecological context. In addition, it may also be prudent to evaluate prey energy availability solely with respect to the items that occur most frequently in Chinook salmon diets. Our analysis, as well as other studies of prey and diet overlap (Table 4.3; Gray et al. 2002), indicates a high degree of selectivity in diets of Chinook salmon from estuarine habitats. While incorporating the entire prey field in an assessment of consumption demand and energy availability accounts for potential dietary shifts and provides the context for Chinook as a component of a larger assemblage, it may be warranted to evaluate consumption as a function of energy available from preferred prey as a means to bound interpretation or expectations.

Lastly, as noted above, inter-annual changes in thermal conditions can have direct impacts on metabolic costs associated with growth and consumption. Presumably, metabolic demands would increase with warming temperatures and thus increase the amount of food consumed per individual to maintain growth. From a population standpoint, increased metabolic demands would increase weekly and total consumption demand should growth potential remain similar to our estimates. In freshwater systems, temperature increases of 1° C have been associated with a 27% increase in consumption for some species (Pease and Paukert 2014). Yet in systems where prey may be limited, any increase in consumption due to elevated temperatures could lead to reduced growth, though the magnitude of effect could also be influenced by conspecific density (Robinson et al. 2010) via changes in outmigration abundance as noted previously. We therefore recommend evaluating the relationship between consumption demand and prey availability over a wider range of outmigration abundances and thermal conditions to understand the interplay of these factors on growth during the estuary rearing period.

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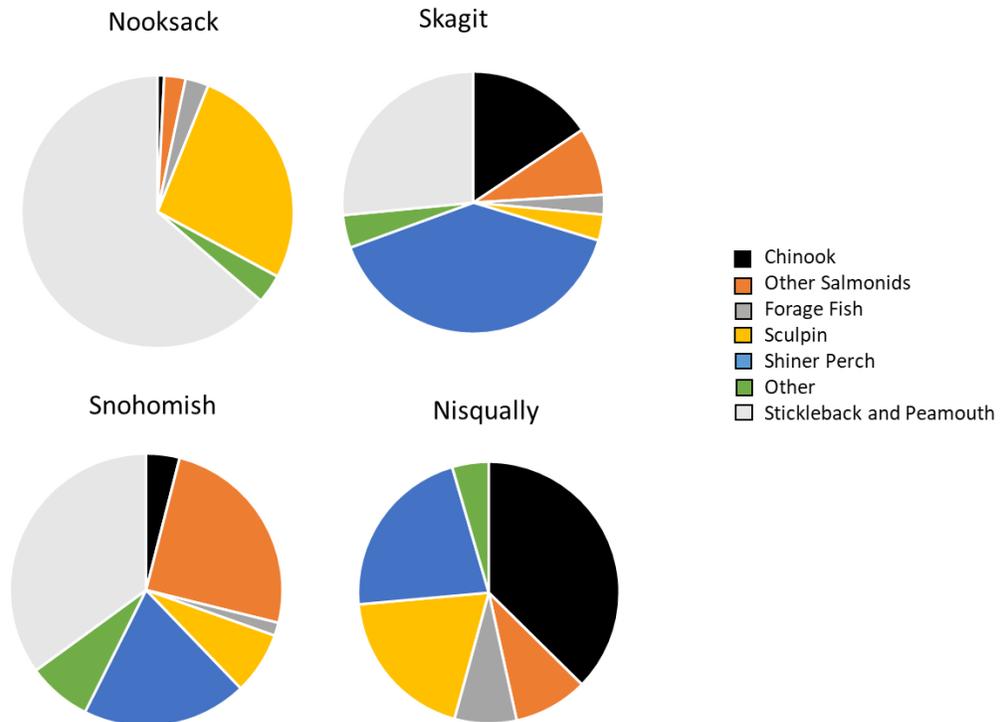


Figure 4.12. Relative proportion of abundance of major assemblage groups in each of the four tidal deltas included in this analysis. Data provided by Lummi Nation, Skagit River System Cooperative, Tulalip Tribes, and Nisqually Tribe.

Prey-diet overlap and selectivity

Demographic variability may also alter or influence growth opportunity directly via competition for resources or changes in foraging strategy (Lorenzen 1996, Lorenzen and Enberg 2002, Guénard et al. 2012). We described changes in diet and prey overlap with respect to change in local density and individual size as a proxy for evaluating potential impacts of competition on individual growth. We predicted that selectivity should change with changes in local density or with differences in individual fork length, reflecting the idea that when competing for food, fish are forced to be less selective, but that size influences how “choosy” an individual may be. Local density had a positive relationship with overlap between diet composition and prey assemblage, especially for individuals already experiencing reduced selectivity (90th percentile). This finding suggests that as density increased, fish became less selective and incorporated more of the available prey in a given area (Fig. 4.9). Positive associations between diet/prey similarity and Chinook salmon density are consistent with the idea that as demand for food resources increases, fish may need to incorporate prey beyond preferred taxa so that diets more closely represent the available prey assemblage. While expanding resource use may be advantageous during periods of high demand, potential consequences include reduced prey quality and overall diet energy density as well as increased activity costs associated with greater foraging needs, which may negatively impact growth or growth opportunity (Martinussen et al. 2011).

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The influence of body size on foraging behavior and success has been documented before for juvenile salmon (Chittenden et al. 2018, Schabetsberger et al. 2003, Keeley and Grant 1997). Differences in diets among small and large individuals may reflect both morphological constraints (i.e. gape limitations; Armstrong et al. 2010) as well as hierarchical feeding structure due to body size (Keeley and Grant 1997). The former may limit “what” can be eaten while the latter is related to competitive interactions including territory size, swimming speed, etc. Model results did not indicate that fork length influenced changes in prey/diet similarity. Visual inspection of the data does suggest that the largest fish had consistently low prey/diet similarities indicating a higher degree of selectivity. In contrast the smallest individuals had much more variable similarity values and included the highest measured similarities in the dataset. If such selectivity allowed larger individuals to consistently select for and eat the highest quality prey, then we would assume this may result in a growth advantage for larger fish. However, the high degree of variability in prey/diet similarity across all but the largest individuals challenges that specific interpretation.

The lack of relationship, or the high degree of variability, between local density/fork length and diet/prey overlap may reflect prey assemblage and abundance dynamics or nuances of fish behavior, especially during periods of high density. Invertebrate assemblages and abundance can fluctuate dramatically among wetland types and seasonally in estuarine environments (Woo et al. 2019, Beamer et al. 2016, Gewant and Bollens 2005). While we were unable to evaluate selectivity within each wetland type due to sample sizes it is worth noting the potential differences. Prey assemblages in FRT and EEM wetlands can often be dominated by relatively few taxa (Woo et al. 2019, Beamer et al. 2016), likely reflective of their position at the freshwater and marine extremes, respectively, within the delta (Fig 4.9). Pairwise comparisons between diets and prey field corroborate the idea of dominance whereby overlap was lowest (i.e. selectivity highest) in FRT and EEM wetlands (Table 4.3). Thus, when prey resources become dominated by a single or relatively few taxa, the potential for increasing or changing diet diversity may be limited. Such dynamics may be insensitive to increases in local density, especially should decreased prey diversity (or single species dominance of prey field) coincide with periods of high density.

Fish behavior, specifically fish movement, could also influence our interpretations and/or variability in our dataset. Our analysis is built upon the assumption that individual diets collected within a week of prey sampling within a particular wetland type were representative of the sampled prey field assemblage. Because fish may move freely among wetland types, it is possible that a fish captured in one wetland type may have fed in a different wetland type prior to capture and therefore may result in lower values for diet/prey similarity. Estimates of digestion and evacuation rates in salmonids suggest complete turnover of stomach contents within ~28 hours at temperatures observed in tidal deltas during the outmigration period (He and Wurtsbaugh 1993, Brodeur and Percy 1987). Using these estimates for digestion, fish that moved among wetland types within a single day could produce uncertainty in our evaluation of diet/prey overlap and could mute, or exacerbate, any potential relationship with local fish density or individual fork length.

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Density dependence and individual growth

Tidal delta habitats provide juvenile salmon with productive rearing environments during early life stages. Several landscape and habitat characteristics drive juvenile salmon distribution and abundance throughout tidal delta environments (Chapter 2). A main goal this chapter was to evaluate and describe how individual growth opportunity differed among wetland types and change throughout the season, affording individuals that migrate at different sizes and times a range of growth potential. Our results support the idea that greater wetland diversity is likely important for maintaining the greatest individual growth benefits for juvenile fish. However, the four tidal deltas compared in this study also experience periods during the outmigration season when estimated capacity within the estuary is exceeded to varying degrees (Chapter 3). As such, we also sought to evaluate the ability of these tidal delta habitats to support individual growth during periods of high density within the outmigration period.

Density-dependent impacts on growth are often hard to isolate outside the lab environment. However, behavioral changes assumed to be related to density-dependent processes which may in turn impact growth can be more readily estimated. Resource limitation is a primary mechanism by which density dependence may influence individual behavior. When habitat capacity (and thus resources) is limited, individuals may have several “options” including, 1) reduce consumption, 2) increase diet diversity/reduce selectivity, 3) move to other habitats, or 4) migrate out of tidal delta (Chapter 3). While we were not able to assess density-dependent movement, we were able to evaluate the other potential pathways by which density dependence may limit, or impact, growth opportunities via consumption or feeding strategy. Our analysis of consumption demand and energy availability was designed to inform whether situations that would require reduced consumption occur with the four tidal deltas. If consumption demand exceeded our estimate of energy availability, we could conclude that individuals would either reduce consumption or migrate. Analysis of consumption revealed that demand indeed approaches the prey energy limitations for some systems, especially during periods when densities are observed to exceed capacity (Chapter 3). While our results do not definitively suggest density-dependent limitations on consumption, it presents a plausible pathway for growth limitations that through some refinement (as noted above) may present a different interpretation. Similarly, our analysis of foraging behavior was not definitive but certainly suggestive of potential changes due to increased local density. Considering the high degree of variability when comparing diet and prey samples not collected at exactly the same time, we still saw evidence that increased density induced changes in diet composition for a particular wetland type. Future efforts designed to reduce the considerable variability in sample comparisons may lead to more definitive conclusions. Nevertheless, these results coupled with density-dependence in average size in the Skagit delta (Beamer et al. in prep) and empirical analyses of otolith microstructure (Appendix 4.3), support the conclusion that density-dependent limitations to growth do exist under certain conditions in all four systems.

Implications for science-based restoration

While the results in Section 4 largely are consistent with the previous section, the focus on bioenergetics offers some additional perspectives on improving habitat restoration.

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Promote habitat restoration portfolios

Adding “capacity” through habitat restoration can potentially alleviate impacts from density-dependent processes for Chinook salmon (Greene and Beechie 2004). Given the evidence for dynamic changes in temperature and productivity and the highly variable and dynamic growth potential among different habitats, promoting restoration across all wetland types may help improve rearing opportunities for fish capable of movements among environments that are seasonally and spatially variable. The portfolio effect has been shown to be capable of spreading risk to Chinook salmon populations via preservation of life history diversity, which may buffer periods of lower productivity (Schindler et al. 2010, Greene et al. 2010). Habitat mosaics invoke similar portfolio effects for populations that use coastal ecosystems including estuaries (Sheaves 2009, Davis et al. 2019, Gray et al. 2002). Our results suggest that restoration or recovery planning that maximizes habitat diversity will likely impart greater benefits to fish populations with respect to conditions that favor increased growth opportunity. Increased habitat diversity may also provide greater habitat connectivity. In light of incipient climate impacts of increasing temperature and sea level rise, maintaining habitat diversity will provide the greatest range of opportunity to maximize growth potential for individual fish and also alleviate potential impacts on growth due to density-dependent processes.

Implications for hatchery release strategies

We used consumption demand to assess how well individual systems are able to support estimated consumption with available prey resources. Hatchery produced Chinook salmon were present in all of the systems we evaluated and are the majority of the systems that produce Chinook salmon in Puget Sound. Consumption by HOr fish accounted for 50-100% of total consumption in each system soon after they are initially encountered in the estuary (Fig 4.6). In two of the systems we evaluated (Nooksack and Nisqually), these periods of intense hatchery consumption coincided with the peaks in total consumption as well as declines in energy density of available prey, suggesting hatchery fish may be the largest consumers among the groups of juvenile chinook salmon we modelled (Fig 4.7). Changes to both abundance and timing of release for hatchery Chinook salmon production has been suggested as a tool to support of the Southern Resident Killer Whale population in the Salish Sea (SRKW Task Force 2019). Increased abundance of hatchery production under current timing of release strategies, would certainly increase the estimated consumption in tidal deltas where this occurred. Should consumption increase enough to surpass available energy, hatchery releases could negatively impact both NOr and HOr groups and would be counterproductive to the recovery strategies of natural origin Chinook populations as well as the SRKW populations for which the increased production was intended to support. While our model results suggest there is no limitation on food resources under the conditions we evaluated, otolith microstructure analyses clearly provide evidence of density-dependent growth and reduced growth later in the rearing season. It is therefore prudent to consider scenarios where both temperature and abundance (NOr and HOr) vary, as mentioned above, to develop a more holistic expectation for consumption demand. Conversely, evaluating release strategies that minimize competition between NOr and HOr individuals in large river deltas may offer solutions for maintaining functional estuarine habitats for both NOr and HOr migrants.

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Appendix 4.1. Tables of compositional differences in diet and availability

Table 1. Categories for diet and prey assemblage samples. Specific species and life stage notes added for reference where necessary.

Categories	Notes (species, lifestages, etc.)
aquatic flatworm	
Barnacle, Ostracod	Cirripedia nauplii
benthic bivalvia	
benthic nematode	
benthic/epi oligochaetes	
Collembola, Arachnida	
Copepoda	Harpacticoida, Calanoid, cyclopoidia
Echinodermata	
emergent diptera	Chironomidae, epibenthic dipteran, ceroptegonidae
Ephem_Plecopt_Odonata	aquatic/epibenthic
epi/pelagic decapoda	change to epi/pelagic decapod in diets
epiben/pelagic mysid	Euphausiidae, Mysidae
epiben/plank Cladoceran	
epibenthic cumacea	
epibenthic gastropod	
Hemiptera	
Indigestible_Material	
Insecta_Other	Coleoptera, Psocoptera, Trichoptera, Isoptera, Lepidoptera
isopod	
Other Amphipod	Americorophium, Corophium, Eogammarus, Monocorophium, Amphithodae
pelagic cnidaria	gelatinous zooplankton
pelagic fish	
pelagic tunicate	
planktonic amphipod	Hyperiidae
Plant material	
Polychaeta	benthic/planktonic
Rotifera	
Tanaidaceae	
terrestrial diptera	Brachycera, Nematocera
terrestrial hymenoptera	
UnID Digested	
UnID larvae	

Appendix 4.2. Evaluating diet overlap among NOr and HOr Chinook salmon in tidal delta habitats

Introduction

Changing growth opportunity is a primary mechanism by which density dependence may impact individual fish within the tidal delta. During periods where capacity is exceeded and densities remain high, increased consumption of available prey may result in lower growth opportunity for individual fish residing with the delta. A primary goal of Chapter 4 was to quantify and compare consumption demand with estimates of total available prey throughout the outmigration period. Our evaluation of consumption demand directly incorporates changes in density among life history types (fry, parr, HOr) allowing for consumption to be attributed to specific groups of fish that enter at, and rear for, various periods of time. Such a framework allows us to make relevant inferences specific to changes in density and thus consumption among groups. However, a major assumption of our bioenergetics and consumption analysis was that NOr and HOr diets were similar during periods of overlap in each tidal delta and thus both groups likely competed for similar prey. If diets are similar we assume a single bioenergetics model can be used to estimate consumption for all life history types.

Methods

We used a subset of Chinook salmon diets where NOr ($n = 70$) and HOr ($n = 108$) samples were collected within the same wetland type in the same month in each system to evaluate potential overlap in diet composition among fish of different origins (see Table 4.1). To test diet similarity among NOr and HOr fish we used permutational multivariate analysis of variance (PERMANOVA, Anderson 2001, Anderson et al. 2008) on paired samples of NOr and HOr diets by wetland type and month within each system (Table 4.1). In order to make reasonable comparisons between samples we used a fully nested design whereby origin (NOr v. HOr) was nested within wetland type and month, each nested within a particular system. Prior to analysis, stomach content data were standardized to total wet weight biomass (WWB) within each sample (i.e. relative proportions). Relative proportions of WWB were then square root transformed to reduce the influence dominant taxa and all empty samples were removed along with digested and indigestible content categories. Bray-Curtis similarities were then calculated for each pair of samples whereby samples that shared exactly the same proportions of all species be scored as 100 (complete overlap) and those that shared no common species were given a score of 0 (complete separation). The model was run on a Bray-Curtis similarity matrix calculated for all pairs of transformed diet composition data and results were evaluated after 10,000 permutations using Type III (partial) sum of squares. In addition to the PERMANOVA procedures, permutational analysis of multivariate dispersion (PERMDISP) was conducted within and among all groups of the nested effect for Origin (i.e. Origin within wetland type, month and system). PERMANOVA is sensitive to differences in multivariate dispersions and thus a significant effect may indicate differences in location (e.g. assemblage differences) or dispersion (i.e. variability) among groups. PERMDISP provides a useful compliment to PERMANOVA procedures especially when interpreting significant model results. To visualize model results and similarity

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diet composition among NOr and HOr Chinook salmon we used non-metric multidimensional scaling (NMDS) plots. Vectors representing taxa with Pearson correlations ≥ 0.5 with the two primary axes were superimposed upon each plot to which diet categories were influencing differences among samples or groups. All analyses were done using PRIMER v6 software (Clarke and Gorley 2006).

Results and discussion

Our model explained more than half the variability ($R^2 = 0.54$) in diet composition among NOr and HOr Chinook salmon within each wetland type, month, and system (Table 1). NOr and HOr diets were not significantly different ($p = 0.140$) in any of the four systems for each wetland type by month group. Differences in diet were instead attributed to differences among wetland types within each month and system (Table 1).

Table 1. PERMANOVA results comparing diet composition of natural- and hatchery-origin juvenile Chinook by month and wetland type in each system. Parentheses denote the nested structure for each term such that the most interior term represents the highest level of nesting (i.e. System). Italics indicate significance at $\alpha = 0.05$.

Source	df	SS	MS	Pseudo-F	P(perm)
System	2	34555	17277	1.1575	0.284
Month(System)	3	19912	6637.2	1.3253	0.269
<i>Hab(Month(System))</i>	5	<i>30340</i>	<i>6068</i>	<i>2.3768</i>	<i>0.022</i>
Origin(Hab(Month(System)))	11	30761	2796.4	1.2293	0.14
Res	156	3.55E+05	2274.9		
Total	177	5.36E+05			

There was considerable overlap in diet composition when NOr and HOr individuals co-occurred in space and time. Average similarities ranged from 15.4 to 71.9% depending on the Month and Wetland type where individuals were captured (Table 2). Mean similarities increased from May to July and were generally highest in EFT wetlands. Diet similarity between NOr and HOr also varied substantially within and among wetland types and months suggesting some sample shared considerably more or less than indicated by the average similarity within the group. Lastly, it is important to note that similarities were calculated based on the presence *and* abundance of each prey species/taxa in each individual diet. Similarities based only on presence/absence of species/taxa in diets of NOr and HOr would likely yield a higher degree of overlap.

Table 2. Mean and standard deviations (parentheses) of Bray Curtis similarities calculated for NOr and HOr diets by wetland type and Month.

	May	June	July
FRT	27.4 (27.9)	44.2 (23.9)	61.5 (18.1)
EFT	33.1 (28.9)	51.1 (28.4)	71.9 (3.6)
EEM	15.4 (23.9)	45.7 (26.6)	

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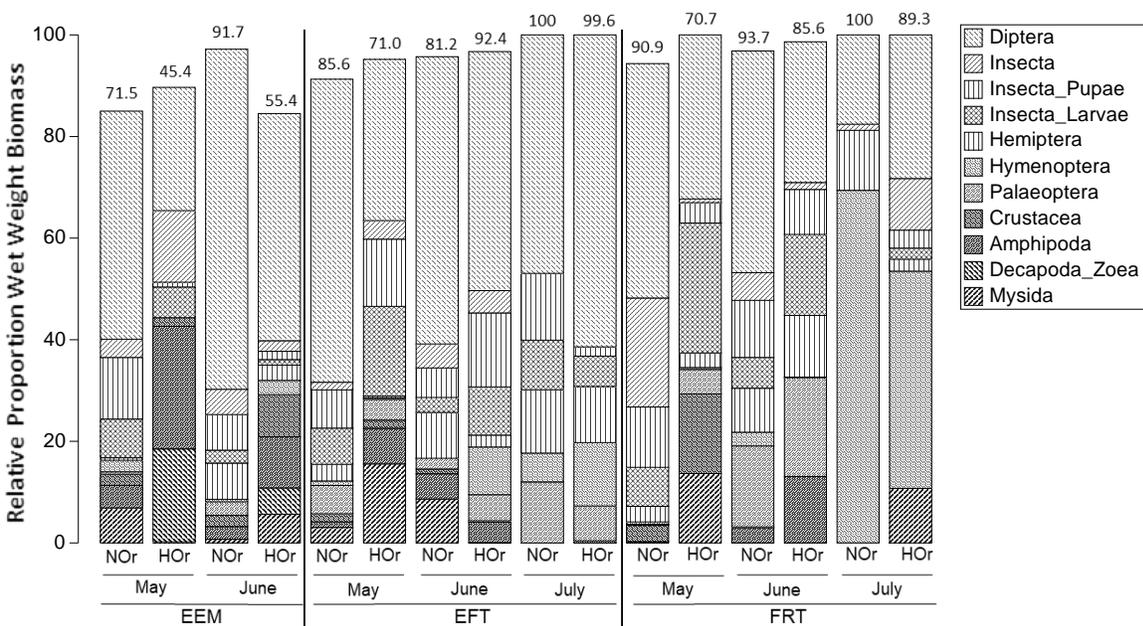


Figure 1. Mean relative proportion WWB for NOr and HOr Chinook salmon within each wetland type and month group. Diet categories represent taxa that accounted for >5% in any individual diet. Percentages above bars represent the total contribution of Insect taxa to diets within each group.

Comparisons among mean relative proportions of WWB suggested insects generally dominated diets for both NOr and HOr fish in each of the wetland types in most months (Figure 1). Relatively small differences between the total proportion of insects in diets were observed between NOr and HOr fish with the largest differences occurring in EEM wetlands. The differences in EEM wetlands may be associated with the greater majority of marine prey (i.e. amphipods, mysids, decapods, etc.) and potential size-related partitioning among NOr and HOr fish whereby HOr fish, due to their larger size, may be able to more readily incorporate larger prey items into their diet. Davis et al. (2018) drew similar conclusions based on differences in stable isotopes signatures among NOr and HOr Chinook salmon in the Nisqually delta. Across all wetland types, Dipterans represented a considerable portion of most diets (Figure 2). Marine prey were present in higher proportions in EEM wetlands and in HOr diets.

We also tested dispersion among diets samples by origin within the nested design. Tests for differences in variability among NOr and HOr fish did not reveal any significant differences among groups with the exception of fish collected in the Snohomish EEM wetlands in June (PERMDISP, $p=0.044$), where HOr diets were significantly more variable than NOr diets (Figure 2). While differences in variability between NOr and HOr fish that co-occurred were not detected, the within group variability was also considerable (Figure 2). Both NOr and HOr fish appeared to consume a wide range of individual prey species/taxa

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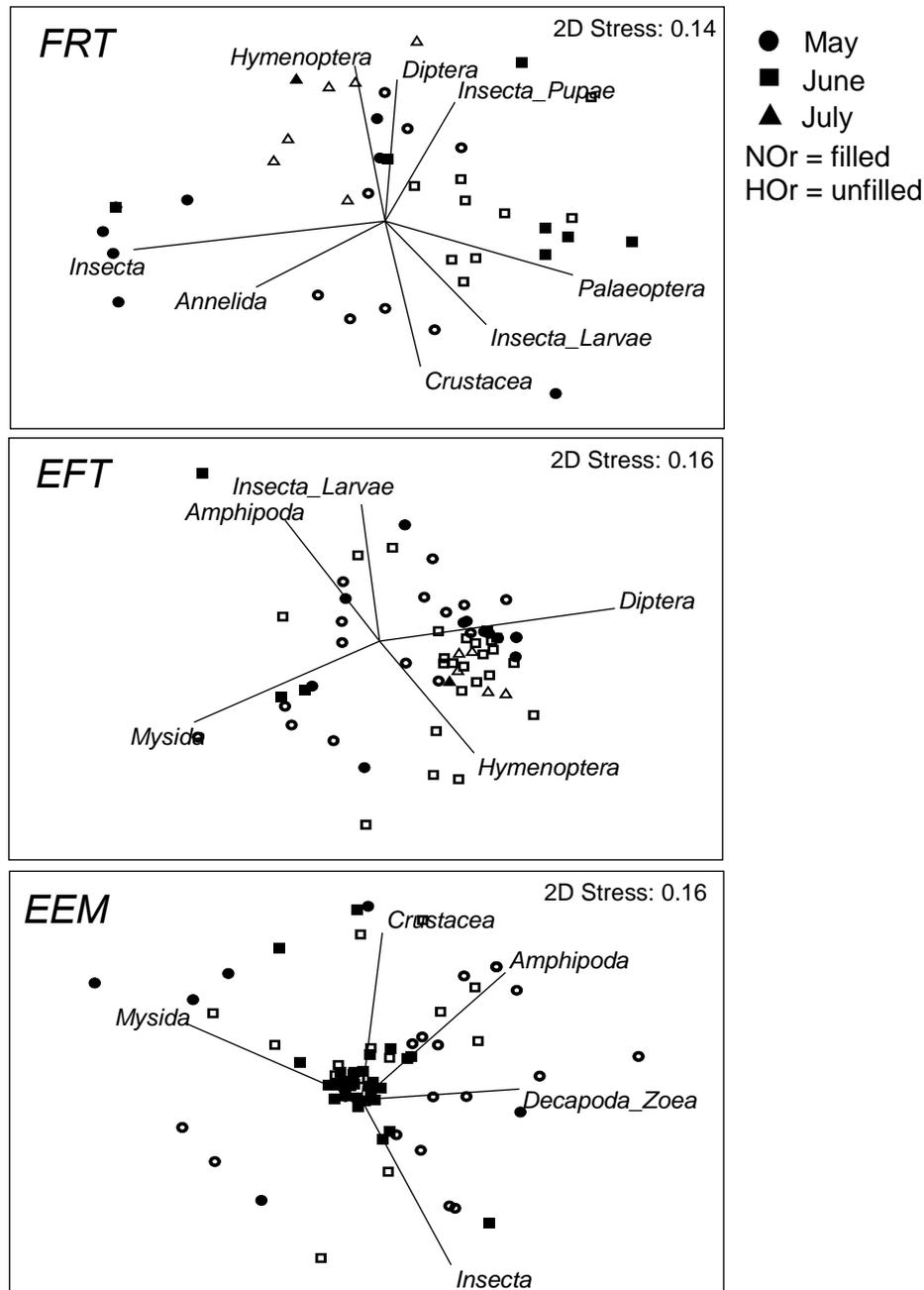


Figure 2. Non-metric multidimensional scaling plots of NOr and HOr diet composition by wetland type and month. Vectors represent prey categories with Pearson correlations > 0.5 with at least one of the primary axes.

The considerable overlap in diets was driven by both the predominance of insects and the high degree of variability within each NOr and HOr diets. Insects are clearly an important component of both NOr and HOr diets, representing greater than 70% of all stomach contents in EFT and FRT wetlands and roughly half of all contents in EEM wetlands. The high degree of variability among individual diets suggests fish are feeding somewhat opportunistically within wetland types depending on what is immediately available in a given place and time. Absent any strong morphometric advantages or competitive interactions, we should expect considerable overlap in

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diet composition between NOr and HOr fish (Figure 2). Our results are similar to those from other studies evaluating diet composition among juvenile HOr and NOr Chinook salmon have found similar results (Cordell et al. 2011, Chittenden et al. 2018) but opposite from the general conclusions drawn from recent work in the Nisqually delta (Davis et al. 2018). However, Davis et al. (2018) also found considerable overlap between individual NOr and HOr diets in FRT, EFT, EEM wetlands. Only long-term assimilation of stable isotopes indicated HOr relied more heavily than NOr on EEM wetlands. While our results suggest NOr and HOr diets are not different, it does not suggest they are exactly the same either. Yet the substantial overlap in diet composition indicates that for consumption purposes NOr and HOr Chinook salmon should likely be managed/evaluated under the same pretenses for analyses of consumption and growth in the tidal delta.

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Appendix 4.3. Validation of bioenergetics model and density dependence using otolith microstructure

Introduction

Otoliths, or fish ear bones, are an effective tool for determining fish growth because additional proteinaceous matrices, consisting of calcium carbonate layers, are incrementally added on a daily basis in species such as salmon (Pannella 1971, Wilson and Larkin 1980, Chittaro et al. 2015, Claiborne and Campbell 2016). Dendrochronological techniques have confirmed that fast growing fish have larger daily increment widths (Nielson and Geen 1982, Volk et al. 1984, Nielson and Geen 1985, Zhang et al. 1995), and otolith microchemistry techniques (elemental or stable isotopes) combined with analyses of otolith microstructure have revealed that they also record timing of habitat transitions (Campana and Thorrold 2001, Volk et al. 2010, Claiborne and Campbell 2016).

Starting in 1995, juvenile Chinook collected in the Skagit River estuary and nearshore were analyzed for life history types and patterns of growth and residence (Beamer and Larsen 2004, Beamer et al. 2005). Otolith microstructure analyses were completed on Skagit Chinook juveniles from three different years with varying levels of outmigration sizes. The results suggest that juveniles reside in estuary habitats a maximum of ~ 10 weeks, while most juveniles reside in estuary habitats for less than eight weeks (Beamer and Larsen 2004). Furthermore, shorter estuary residence occurred in the year with the largest outmigration.

In the current investigation, we used growth data extracted from otolith microstructure for two purposes: 1) to determine whether density-dependent growth was detectable at the local scales related to wetland types where fish were collected, and 2) to assess whether the range in growth rates obtained from bioenergetics model runs from different wetland types were within the range of true growth.

Methods

Preparation and microstructure analysis

Otolith microstructure processing and analysis followed the methods of Stevenson and Campana (1992). Otoliths were mounted in clear epoxy resin and then polished on both sides of the otolith to produce a thin section. Polishing wheels were used with progressively finer polishing cloths and slurries of silicon carbide and aluminum oxide to achieve optimal visual resolution. In some instances, otolith samples were either lost, broken or destroyed during processing and supplemented with the complementary otolith from the original pair. Before supplementing, the potential substitutes were measured for verification of equal length to the original sample to account for any growth differences.

Polished otoliths were then digitally imaged and analyzed using Image-Pro software (Media Cybernetics, Inc.). The microstructure was examined for changes in individual increments (width and spacing between) and microstructure patterns, and the presence of “checks”, prominent marks interrupting a pattern sequence. “Checks” can be indicative of early life history events such as hatch, emergence and first feed, or rearing events such as change of habitat (Marshall and Parker 1982, Campana 1983, and Volk et al. 1995). A radial axis selected for measurements

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was standardized for each river system; a set amount of degrees (river system dependent) dorsal to a longitudinal axis that passes through a consistently identified nuclei (Wilson and Larkin 1982 and Volk et al. 1995). Individual growth increments, interpreted as one day's growth, and "checks" in the otolith microstructure were marked (Stevenson and Campana 1992, Campana 1983, and Chittaro et al. 2015). Distances, individual increment widths, and increment counts between checks/habitats were measured and determined along the radial axis from the otolith core to the edge (time of capture). Check presence combined with increases in growth were assumed to represent change in habitat and recorded as such for each fish along the radial axis.

Average mean increment widths in microns (μm), growth rates (mm/day) and residence times (increment counts) within habitat zones, were determined. The otoliths of fish collected from freshwater provided a recognizable microstructure pattern used as a reference point for all otoliths of fish collected downstream of freshwater habitat. The freshwater pattern had no "checks" other than those associated with early development (hatch etc.). Otoliths of fish collected in the tidal delta habitats were visually analyzed for additional patterns, "checks", or increased growth (change in increment width and spacing) beyond the identifiers observed on the freshwater residence portion of their otoliths. Check presence, combined with increases in growth, were assumed to represent change in habitat.

Individual growth rates were estimated from back-calculated otolith lengths at tidal delta entry using the biological intercept method (Campana 1990). The intercept at time zero was estimated by using a local Puget Sound stock of newly emerged Chinook fry (Skagit River fall Chinook, collected in 1998 & 2000 by Skagit River System Cooperative). The minimum observed values for fork length at time of emergence (L_0) and otolith radius to the emergence check (point of emergence from the otoliths) (R_0) were used (33 mm and 191.62 μm , respectively). We used the Biological Intercept Method for back-calculation:

$$\text{Eq. 1} \quad L_i = L_c + (R_i - R_c)(L_c - L_0)(R_c - R_0)^{-1}$$

where

L_i is the back-calculated length (mm) of the fish at the beginning of a habitat transition,

L_c is the length (mm) of the fish at capture,

L_0 is the length (mm) of the fish at emergence,

R_c is the radius (μm) of the otolith at capture,

R_i is the radius (μm) of the otolith at the beginning of a habitat transition,

R_0 is the radius (μm) of the otolith at emergence.

From back-calculated lengths and increment counts, average growth rates for fish in each habitat were calculated in terms of both length (millimeters per day (mm/day)) and biomass (grams per day (g/day)). Biomass (g) was estimated from length (mm) by an equation developed from the sample fish length and weight data: $y=2\text{E-}06x^{3.3822}$, $r^2=0.9594$. Growth rates (g/d) were estimated

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by dividing total estimated growth by the length of residence. Specific growth rates (g/g/d) were estimated by dividing growth rates by initial biomass.

Using the above equations, we calculated two measures of growth and residency: 1) overall growth across the entire period of delta residence until collection and 2) recent growth over the previous seven days. The first measure is integrative, while the second is more restricted to recent growth. We used the first measure to examine density-dependent and -independent factors influencing growth. We used the second measure to examine range of growth rates, as a means of independent validation of the range of growth predicted by bioenergetics models. For this qualitative comparison, we assumed that growth in the previous seven days was more likely to reflect wetland-specific experience than overall estuary growth.

Statistical analysis

Otolith microstructure data of juvenile Chinook salmon collected at different stages was recorded in a database. The total number of samples analyzed from Skagit River habitats in 1995 was 417; of these samples, overall growth rates were available from 205 individual fish and recent growth rates (7 days prior to collection) from 99 individuals. As part of the ESRP research project, an additional 72 otolith samples collected in 2010 and 2012 from the Snohomish River estuary were added to the database. Of these, 37 samples could be used for estimating overall growth rates, but we opted not to calculate recent growth for the Snohomish samples.

We hypothesized that several factors would describe variation in growth rates within the delta. At the largest spatial scale, we expected possible differences between Skagit and Snohomish deltas. At smaller spatial scales, local differences might exist among wetland vegetation types and fish densities at location of capture, although movements among rearing sites over the course of rearing could wash out these effects. In addition, we expected growth rates to vary with respect to size at entry into the delta (larger sizes have a wider range of prey available), and timing of entry (temperature and prey differ later in the season). We used general linear models to examine these factors in a multi-model assessment framework and determined, using AIC scores (Burnham and Anderson 2002), which of these variables parsimoniously explained the greatest amount of variation in growth rates. Because fish density, biomass, and growth rates were non-normally distributed, we used log-transformations of these metrics in the statistical models.

Analysis of recent growth was more qualitative. We calculated growth rates (g/day) and specific growth rates (g/g wet weight/day), based on biomass estimated seven days before collection. Ranges of these values were compared to estimates of growth from bioenergetics wetland-specific model runs during week 20, approximately when these samples were collected in 1995. We also examined for wetland-specific differences in growth rates, assuming a strong covariance between growth rate and initial size seven days prior to collection.

Results and Discussion

Factors influencing overall growth rates

Overall growth rates varied between 0.02 and 7.38 g/day and averaged 1 g/day. However, the distribution of growth was highly skewed, with nearly 70% of individuals experiencing < 1 g/day growth. Hence, log-transformed growth rates were used in the analysis. We found that the most

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complex model included in the AIC analysis was best supported by the data (Table 1). This model explained over 60% of the variation in log-transformed overall delta growth rates. Models with fewer parameters explained much less variation, and each reduction in the number of parameters increased AIC by 20-30 points. For reference, a change of 3-7 points generally indicates a much poorer model fit (Burnham and Anderson 2002), so a difference of 26 points from the best to the next best model indicates overwhelming support for the best model.

The simplest models included variables directly related to characteristics of individuals (biomass and timing at delta entrance), which exhibited moderate covariance ($r = -0.45$), but nevertheless were both important in explaining variation in overall growth rates. The importance of these parameters highlights the role of prior residence in freshwater and supports the bioenergetic modeling framework of different population cohorts that differ in arrival timing and initial biomass (Chapter 4).

More intriguingly, the best model also included local fish density and wetland type, two variables that might be expected to vary over the course of delta residence. The best model indicated a strong negative effect of density (Table 2, Fig. 1) on growth, and higher growth in EEM and EFT wetland types compared to FRT. That both local density and wetland type at point of capture were important in the model suggests that mobility of fish within the delta may be somewhat restricted if individuals find productive rearing habitat. In this dataset, the period of residence before capture varied between 1 and 42 days, but over 60% of fish in the analysis had resided less than 10 days when captured. Hence, local density and wetland type at point of capture may have also been indicative of the entire period of delta rearing for the majority of fish in this analysis.

We also found differences between Skagit and Snohomish systems, which indicated lower growth in the Snohomish after controlling for other factors (Fig. 1). These results may reflect habitat quality differences – extant wetland habitats in the Snohomish are more modified than in the Skagit (e.g., lower blind channel area, less forest and shrub cover, Beechie et al. 2017). However, the system-specific data also corresponded to strong differences in the years analyzed – 1995 in the Skagit versus 2010-12 in the Snohomish. Hence, observed system differences may reflect large-scale temporal changes, such as region-wide fresh or marine water temperature among years or interannual hydrographic differences.

The overall model results are displayed in Table 2, and relationships of independent variables with growth rates are illustrated as partial regression plots in Figure 1. Comparison of model results (Table 1) illustrate that all variables included in the model strongly differed from 0, except for the contrast between EEM and EFT wetland types. Partial correlations revealed several important results relevant to Chapter 4. First, few individuals we collected had surpassed 5 g initial body weight, and further analysis of the data indicated that criterion was met for biomass at time of capture for nearly 90% of the fish. This provides good support for the assumption that most fish migrate from the delta after attaining 5 g biomass. Second, earlier arrival at larger size correlates with higher growth, corroborating other studies documenting at earlier life stages the importance of size-dependent growth (Chamberlin et al. 2015, Davis et al. 2018a, Davis et al. 2018b, Davis et al. 2019, and Gamble et al. 2018) and carryover effects (Gosselin et al. 2018) in Chinook salmon. In addition, these results may also indicate that like

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other species of salmon (Grand 1997, Keeley & McPhail 1998, Keeley 2000), dominance in feeding by juvenile Chinook salmon is related to size and priority of arrival. Third, the strongly non-linear relationship of growth with density suggests strong density dependence intensifies at relatively low densities, and levels off at densities greater than 1,000 fish/ha. These findings correspond well with findings of density dependence by David et al. (2016), as well as other findings in this report.

Recent growth

Growth data determined from otolith samples also served as an independent check on whether growth rates determined from bioenergetics models were realistic projections. Note that this is not a perfect comparison, due to different temperature ranges, prey availability, and densities in 1995 (otolith data) compared to 2014 (bioenergetics predictions). In addition, otolith-based wetland-specific growth rates average over the previous week and assign individuals to site of collection. The bioenergetics model calculates growth on a daily time step, and assumes individuals remained in a particular wetland type. Nevertheless, specific growth rates predicted by the model runs were close to the average specific growth rates exhibited in otoliths (Table 3) and were within the natural range of variation (Fig. 2).

In 1995, we observed fairly strong wetland-specific differences, at least during the limited time period of the analysis. Estimated initial size at the beginning of the week strongly explained resultant growth rates (g/d) of fish collected from each wetland type, with higher growth rates found in EEM compared to EFT and FRT sites. This was true even for fry size classes, although differences in growth were smaller among wetland types compared to when estimated at larger

Table 1. AIC analysis of five models of increasing complexity describing variation in \log_e -transformed overall growth rates (g/d) in the Snohomish and Skagit tidal deltas. Letter abbreviations of parameters correspond to B = \log_e (biomass at delta entry), T= timing of delta entry (day of year), D = \log_e (density (fish/ha)) of juvenile Chinook salmon, W = wetland type (FRT, EFT, EEM), and S = system (Snohomish or Skagit). All models also include an intercept.

Model	Δ AIC	R ²
B	91.785	0.436
B + T	71.440	0.511
B + T + D	42.820	0.569
B + T + D + W	26.371	0.604
B + T + D + W + S	0	0.648

Table 2. Parameter estimates and statistical analysis of the best model

Parameter	Estimate	Std. Error	t-value	Pr(> t)
(Intercept)	2.572	0.689	3.731	< 0.001
System (Skagit - Snohomish)	-0.889	0.164	-5.407	< 0.001
Wetland (EEM - EFT)	-0.057	0.174	-0.328	0.743
Wetland (EEM - FRT)	-0.948	0.176	-5.397	< 0.001
\log_e (total density)	-0.414	0.064	-6.448	< 0.001

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Day of delta entry	-0.011	0.004	-2.705	0.007
$\log_e(\text{delta initial biomass})$	1.621	0.099	16.363	< 0.001

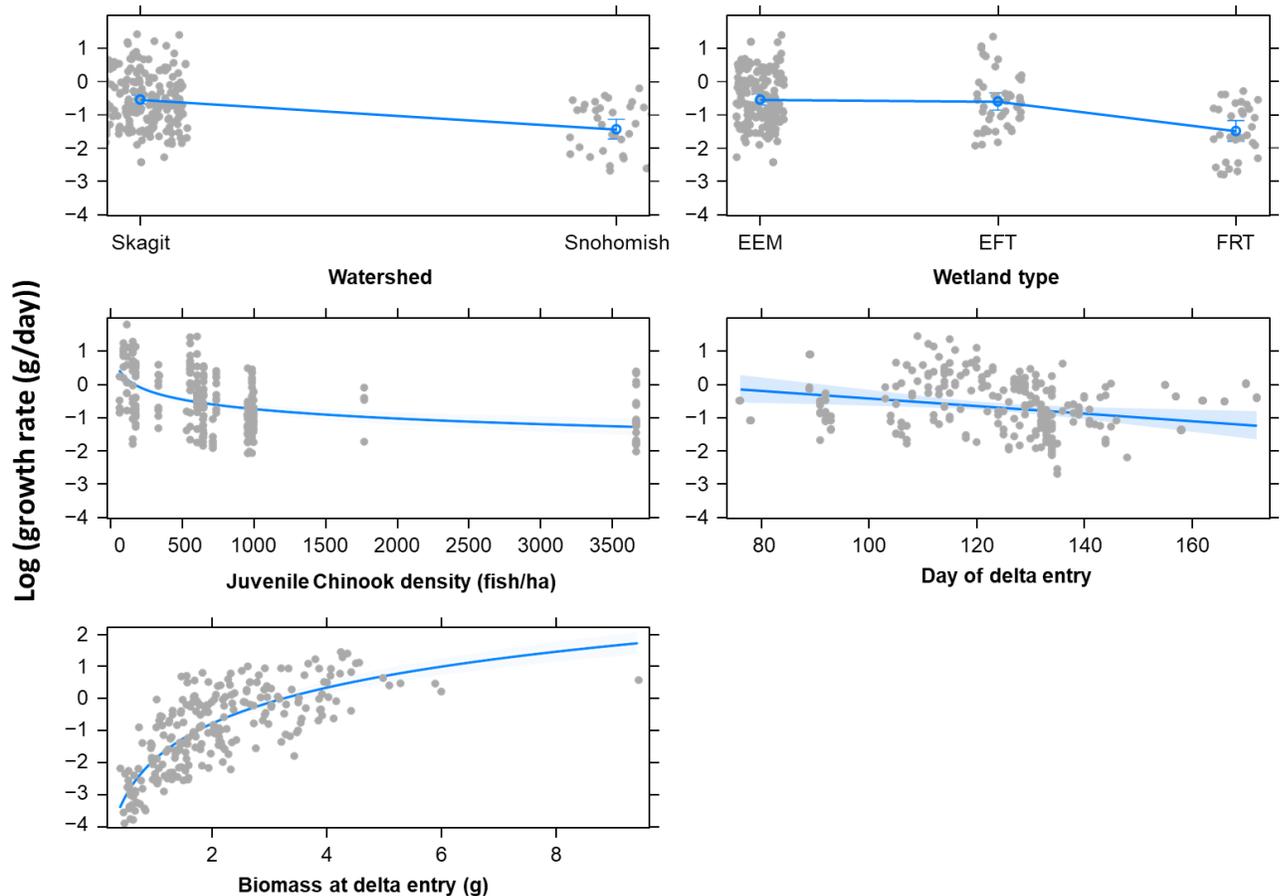


Figure 1. Partial regressions of the best model of \log_e -transformed growth rates, illustrating independent effects of watershed, wetland type, local density (fish/ha), day of delta entry (day of year), and estimated biomass at delta entry. Gray points represent individual samples (jittered in first two panels), and blue lines (\pm standard error as shown by error bars or light-blue shaded areas) are the partial regression relationships.

initial sizes. Note that fish were captured during the later period of delta residence (Table 3, Fig. 3), corresponding to weeks 18-22 in bioenergetics model runs. Different patterns might be expected during earlier weeks of residence, and there may be an “integrative” aspect to wetland-specific results, as fish collected in EEM have naturally passed through FRT and EFT wetlands. Furthermore, the analysis of overall growth rates revealed that growth in EFT wetlands was more similar to EEM compared to FRT over the entire residence period, although individuals (especially fish that were larger or had resided in the delta longer) likely used additional wetland sites compared to site of capture. Nevertheless, these results corroborate growth rate variation exhibited in our bioenergetics model results and reveal wetland-specific differences could differ among years (compare these results to bioenergetics model results in 2014).

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Table 3. Summary of average growth and specific growth rates from 1995 Skagit delta otolith samples assessed for recent (previous seven days) growth by wetland type, and summary of specific growth rate (growth potential) from wetland-specific runs of the bioenergetics model from week 20 in 2014 (see Chapter 4).

Wetland type	Samples (n)	Day of capture (range)	Week of capture	Biomass range (g) at capture	Avg. growth rate (g/d)	Avg. specific growth rate (g/g/d)	Bioenergetics model prediction of avg. specific growth rate*
FRT	12	135-150	20,22	1.1-3.3	0.05	0.03	0.04
EFT	25	136-151	20,22	1.2-7.3	0.10	0.03	0.05
EEM	62	124-151	18,20,22	0.8-12.0	0.16	0.04	0.04

* Not directly comparable to otolith-based estimate due to differences in years analyzed and different estimation techniques.

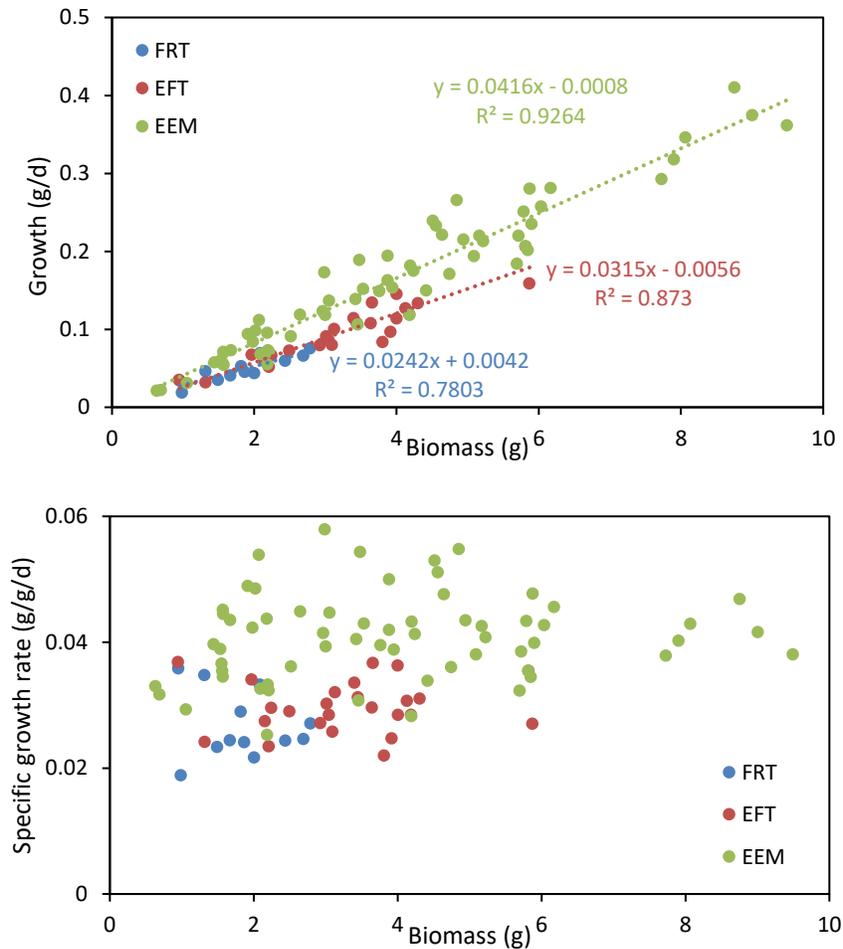


Figure 2. Recent growth rates (g/day) and specific growth rates (g/g wet weight/day) of 99 Skagit juvenile Chinook salmon as estimated from analysis of otolith microstructure in the last seven days before capture in three wetland

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types: forested riverine tidal (FRT, blue), estuarine forest transition (EFT, red), and estuarine emergent marsh (EEM, green). The x-axis in these graphs refers to estimated biomass (g) seven days before capture.

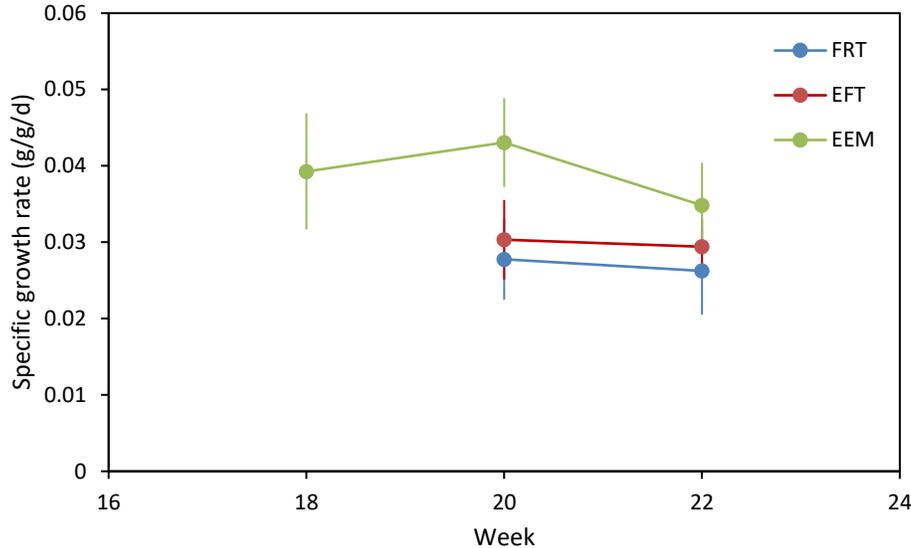


Figure 3. Average recent growth rates (g/g/day) from otolith microstructure of juvenile Skagit Chinook salmon collected in different weeks during delta residence in 1995, from three wetland types: forested riverine tidal (FRT, blue), estuarine forest transition (EFT, red), and estuarine emergent marsh (EEM, green).

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