Resource use and life history patterns of juvenile Coho and Chinook salmon in an Alaskan estuary

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Abstract

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Estuaries are valuable nursery grounds for anadromous Pacific salmon supplying diverse habitats, quality foraging grounds, and a transition between freshwater and saltwater environments. By providing alternative rearing habitats, estuaries may also bolster the life history diversity expressed in a population, thereby increasing population-level stability. Conversely, the degradation and loss of estuarine habitats has been partially responsible for declines in wild salmon populations. In Alaska, most natural systems are largely intact with minimal anthropogenic alterations. However, the human population and associated land use is increasing. Alaska has the opportunity to learn from the mistakes made in the Pacific Northwest and identify and protect the

critical rearing habitat of these culturally, economically, and ecologically valuable species. To do so, we need an understanding of how juvenile salmon use Alaskan estuaries.

In this thesis, I describe the resource use, residence, and movement patterns of juvenile salmon in the Anchor River estuary in southcentral Alaska. Specifically, I (1) assess the resource partitioning between juvenile Coho and Chinook salmon, (2) determine which age classes use the estuary and for how long, (3) examine the tidal movement of juvenile salmon, and (4) utilize a social network analysis to explore the social structure of juvenile Coho Salmon. Coho and Chinook salmon primarily partitioned resources spatially and to a lesser extent temporally, whereas their prey resources overlapped considerably. Varying abundances of Chinook Salmon provided a natural experiment that I used to determine that Coho Salmon interactively partition habitat resources by primarily occupying tidal marsh channels when Chinook Salmon are present in the main channel. Although juvenile Coho Salmon were present throughout the sampling period (May-Oct), they were most abundant later in the season (Aug) and individuals of all three age classes reared in the estuary for over 100 d. Some Coho Salmon tagged in 2015 were still present in the estuary in 2016. Chinook Salmon were most abundant earlier in the season (Jun-July) and did not remain in the estuary past mid-August. The longest individual residence time for a Chinook Salmon was 42 d.

Channel connectivity influenced the tidal movement patterns of Coho Salmon. I used passive integrated transponder (PIT) tags and in-channel antennas to assess fish movement in two marsh channels. In the marsh channel that remained fully connected to the main channel at low tide, fish movement was mostly independent of the tidal stage or channel depth. In the marsh channel that was only marginally connected to the main channel, fish detections were greatest when the tidal stage was high enough to raise the channel depth. However, contrary to my expectations, fish were detected throughout the tidal cycle and at all channel depths, indicating that they used the marginal connection to move between habitat patches even at low tide.

Juvenile Coho Salmon social relationships varied through time. I constructed static and dynamic social networks from the time-stamped observations of fish detections to explore the social structure of juvenile Coho Salmon. Fish did not preferentially associate with similarly sized fish. Fish did not appear to maintain stable relationships, but instead exhibited fission-fusion dynamics where social relationships were continually formed and dissolved, indicating that the frequent co-occurrence of individuals is likely due to mutual site fidelity and not social preference.

Although the Anchor River is relatively small, the salmon populations it supports are highly important to the culture, economy, and ecology of the region. The results of this thesis demonstrate that the diverse habitats of the estuary support multiple species and life history types for prolonged periods. By appropriately identifying and conserving critical juvenile salmon rearing habitat, we can help maintain healthy salmon populations into the future.

This thesis includes an animated dynamic social network (Video S1) provided as supplementary material.

TABLE OF CONTENTS

LIST OF FIGURES

Chapter 1

Chapter 2

Chapter 3

Appendix

LIST OF TABLES

Chapter 1

Chapter 2

Chapter 3

Appendix

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GENERAL INTRODUCTION

Estuaries are dynamic environments at the juncture of river and sea. The confrontation between river flow and tidal flood creates spatially and temporally complex habitats including beaches, mudflats, off-channel pools, and networks of tributary, distributary, and dendritic channels ranging from tidally influenced but purely freshwater emergent wetlands to deep, open water that is strongly influenced by marine processes (Palaima 2012, Levings 2016). These habitats often experience considerable changes in temperature, depth, salinity, turbidity, and dissolved oxygen across tidal, diel, lunar, and seasonal cycles (Elliott and Whitfield 2011). Not only are physical conditions in continual flux, but habitat availability and connectivity also change with each ebb and flood and are further modified by the spring and neap tidal cycle. These changes in habitat availability necessitate the regular redistribution of nekton species as channels drain with the ebbing tide (Speirs et al. 2002, Gibson 2003) yet simultaneously provide access to terrestrial and avian foragers (Gils et al. 2006).

Salinity is a primary structuring force in estuarine communities. Plant and invertebrate assemblages tend to form vertical zones in predictable sequences according to tidal inundation (Gunter 1961, Crain et al. 2004). Even mobile species such as fish show distinct trends along the salinity gradient (Bottom and Jones 1990, Marshall and Elliott 1998), with some species restricting their use to small portions of the estuary that suit their physiological requirements (Potter et al. 2013). Due to their physically dynamic nature, estuaries are less biodiverse than equivalently productive aquatic ecosystems (e.g. coral reefs), but the tolerant species that are able to reside there reap the benefits of a highly productive system and robust food web (Elliott and Whitfield 2011, Nyitrai et al. 2012).

The same forces that create dynamic and diverse estuarine habitats are also responsible for making them productive. Nutrients are primarily delivered to the estuary from allochthonous (outside the aquatic system) sources in pulses during high flow events (Naiman and Sibert 1979). When nutrient-rich freshwater encounters the ionically-charged saltwater in the estuary, sediment and organic particles flocculate (bind together), and the push and pull of tidal currents enable the particles to accumulate in the estuary (Wolanski and Elliot 2015). The net result of freshwater and tidal influences determines the residence time (and, conversely, the flushing rate) within an estuary, which in turn influences sedimentation and nutrient retention, dispersal of organisms, and connectivity within the estuary (Elliott and Whitfield 2011). Retained nutrients and sediments help nourish emergent and aquatic plants and macroalgae, which in turn contribute organic matter, creating the basis for a productive detritus-based food web (Naiman and Sibert 1979, Sibert 1979, Healey 1982).

The diverse habitats and high productivity within estuaries make them ideal nursery habitats for many species, including anadromous Pacific salmon (*Oncorhynchus* spp) (Healey 1982, Beck et al. 2001). Estuarine habitats provide numerous functions for juvenile salmon. The salinity gradient within estuaries creates an osmoregulatory transition zone, and some juvenile salmon species correspondingly show a progressive movement into more saline waters as they mature (Thorpe 1994). The shallow, spatially complex habitats found in estuaries may provide a refuge from predators (Simenstad et al. 1982), although this likely varies greatly among systems (Thorpe 1994). Where freshwater habitat is limited or degraded, juvenile salmon may use estuaries as alternative rearing habitat (Healey 2009, Simmons et al. 2013). Additionally, salmon fry that get flushed downstream by high flow events may find refuge in estuarine habitats (Tschaplinski 1982).

The presence and diversity of estuarine habitats increases the number of life history types expressed in a population (Bottom et al. 2005, Jones et al. 2014, Craig et al. 2014). Chinook Salmon *O. tshawytscha*, and particularly the "ocean-type" life history, are known to reside in estuaries for extended periods, often inhabiting tidal marsh channels for weeks to months (Bottom et al. 2005, Hering et al. 2010, McNatt et al. 2016). Coho Salmon *O. kisutch* also exhibit plasticity in their juvenile rearing strategies. Juvenile Coho Salmon that migrate downstream shortly after emergence were originally considered surplus individuals (Chapman 1962). However, these "nomads" are now recognized as a distinct life history type that contribute to the adult population and often rear in estuarine habitats as juveniles (Bennett et al. 2011, 2014, Jones et al. 2014) Diversity in life history patterns spreads the risk of mortality for a given population across space and time, thus increasing the stability and persistence of salmon populations (Schindler et al. 2010, Fleming et al. 2014)

Perhaps the most important (or at least most frequently studied) benefit to life in the estuary for juvenile salmon is growth. Fish rearing in estuaries tend to exhibit greater growth rates than their stream-rearing counterparts (Simenstad et al. 1982, Thorpe 1994, Jones et al. 2014). Because larger individuals have a better chance of surviving in the marine environment (Beamish and Mahnken 2001), increased growth in the estuary may confer survival benefits in later life. Correspondingly, a loss of estuarine rearing habitat would result in lower survival of the population (Magnusson and Hilborn 2003).

Human activities have layered numerous stressors on estuarine systems including habitat destruction and alteration, pollution, alteration of flow and tidal regimes, and the introduction of invasive species (Vitousek et al. 1997, Simenstad and Cordell 2000, Bottom et al. 2005, Martinho et al. 2008, Baird and Mehta 2011). More than half of estuarine wetlands in the Pacific Northwest have been lost, likely contributing to the decline of anadromous Pacific salmon and other species (Simenstad and Cordell 2000). Consequently, restoration activities have sought to restore system health and juvenile salmon production, but have met with varying levels of success (Simenstad et al. 2006).

In contrast to the Pacific Northwest, the majority of salmon-bearing systems in Alaska remain intact and largely undisturbed. However, Alaska is experiencing human population growth and urbanization, which places pressure on habitats that support juvenile salmon (Ourso and Frenzel 2003). Furthermore, the economy of Alaska has long been centered around resource extraction. Pacific salmon support multimillion dollar commercial (Knapp et al. 2007) and recreational (Romberg et al. 2008) fisheries, as well as vital subsistence fisheries (Fall et al. 2015). Yet, the environments that support healthy salmon populations also yield profitable resources such as timber and mineral deposits, creating challenges in the co-management of resources. Additionally, climate change is predicted to have a strong impact in Alaska, with substantial increases in temperature and precipitation (Kyle and Barbets 2001). The impact of these changes on juvenile salmon is not fully known and may not be entirely detrimental. For example, increased winter precipitation might decrease egg and fry survival due to scour, while slightly warmer temperatures could increase growth rates thereby increasing the size-dependent survival of juvenile salmon or causing a shift towards early-maturing life histories (Bryant 2009). In the face of this multitude of challenges, it is vital to understand how juvenile salmon rearing habitat relates to key life history traits.

The fieldwork presented in this thesis was conducted in collaboration with scientists from the Kachemak Bay National Estuarine Research Reserve (KBRR). Working with KBRR provided a unique opportunity to study the system from the vantage point of place-based research. This team has partnered with numerous collaborators, each of whom has contributed a unique perspective and skillset leading to a multidisciplinary understanding of a predominantly unstudied region. Previous research has explored stream chemistry and sources of nutrient input in salmon-bearing headwater streams (Dekar et al. 2012, Walker et al. 2012); the relationship among catchment geomorphology, macroinvertebrates, and juvenile salmon distributions (King et al. 2012); and the overwintering habitats of juvenile Coho Salmon (Gutsch 2012). The present study will complement recent work exploring the estuarine environment as rearing habitat for juvenile salmon (Hoem Neher 2013a,b). Additionally, KBRR is actively engaged in community outreach which enabled me to share the results of this thesis research in both formal and informal settings to a broad audience.

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CHAPTER 1: INTERACTIVE RESOURCE PARTITIONING AND DIETARY OVERLAP BETWEEN JUVENILE COHO AND CHINOOK SALMON IN THE ANCHOR RIVER ESTUARY

Abstract

Estuaries provide valuable rearing habitat for juvenile Pacific salmon, and the ways in which species partition estuarine resources has important implications for the management and conservation of these culturally, economically, and ecological valuable species. In the present study, I describe the patterns of spatial, temporal, and dietary resource use between juvenile Coho Salmon *Oncorhynchus kisutch* and Chinook Salmon *O. tshawytscha* in the Anchor River estuary in southcentral Alaska. I found that these species primarily partitioned resources spatially. When both species were present, Coho Salmon were the primary species in tidal marsh channels but Chinook Salmon were almost exclusively captured in the mainstem channel. Coho Salmon were more abundant in the mainstem channel in 2015 when Chinook Salmon were virtually absent, indicating that they may interactively partition habitat resources. There was strong overlap in the diet of these two species. Diet composition varied by site and from summer to fall, but the quantity and energetic value of diet rations did not show evident trends. Coho Salmon were present in the estuary throughout the study (May – October) while Chinook Salmon were primarily captured in June and July. This study demonstrates that the presence of heterogeneous habitats within the estuarine environment promotes the co-existence of these valuable species.

Introduction

The spatial, temporal, and dietary overlap among species has long been of interest to ecologists. When resources are limiting and multiple species occupy the same ecological niche, they must partition resources in order to coexist (Hutchinson 1959, Amarasekare 2003). Animals may divide food, shelter, or other limiting resources to minimize competition. For example, two species that consume the same prey may forage in different habitats (Schoener 1968), or in the same habitat but at different times (Adams and Thibault 2006), or may occupy the same habitat at the same time but specialize in different food resources (Pyke 1982).

Although spatial separation is the most prevalent form of resource partitioning among all animals (Schoener 1974), fish more often partition food resources (Ross 1986). This may be because aquatic habitats are less heterogeneous and resources are more mobile than in terrestrial habitats (Schoener 1974). In estuaries, however, fish often occupy more heterogeneous habitat than in other aquatic systems (Ross 1986), and therefore spatial resource partitioning may be equally as important as trophic partitioning. Furthermore, estuaries are corridors for migratory species such as juvenile Pacific salmon (*Oncorhynchus* spp.*)* that vary in freshwater emergence and migration timing and thus provide an opportunity for evaluating temporal partitioning.

All juvenile anadromous Pacific salmon must pass through estuaries as they migrate from freshwater rearing habitat out to sea, yet each species and life history type differs in "estuarine dependence" or the amount of time it spends rearing in estuarine habitats (Simenstad et al. 1982, Thorpe 1994). Chinook Salmon (*O. tshawytscha*) are usually considered the most estuarine dependent species, as all life history types occupy the estuary and fry migrants rear in the estuary for extended periods (Healey 1982). It was generally thought that Coho Salmon (*O. kisutch*) do not rear in estuaries for prolonged periods; however, recent research indicates that Coho Salmon, particularly the younger age classes, do utilize estuarine habitats for weeks to months and represent distinct life history types (Jones et al. 2014, Craig et al. 2014). Therefore, the co-occurrence of multiple species and life histories of juvenile salmon in estuaries provides a case study for investigating resource partitioning.

Resource partitioning in juvenile salmonids can be selective or interactive (Brian 1956, Nilsson 1967). Interactive partitioning occurs when one species alters its resource use based on the presence or abundance of the other species. Interactive resource partitioning has been observed between juvenile Coho Salmon and other species including steelhead Rainbow Trout *O. mykiss* (Hartman 1965) and Cutthroat Trout *O. clarki* (Glova 1987). In contrast to interactive partitioning, selective partitioning arises from differences in instinctive behavior or body morphology: each species innately selects different resources thereby minimizing interaction between species. Dolloff and Reeves (1990) determined that resource partitioning between Coho Salmon and Dolly Varden *Salvelinus malma* was primarily selective, with each species voluntarily choosing habitat that the other rarely selected. For juvenile salmonids, competition for space and food is tightly linked: fish compete for habitat that maximizes food acquisition (Chapman 1966). Thus, interactive habitat segregation may result in dietary differences between species (Glova 1984).

In this paper, I describe the patterns of spatial, temporal, and dietary resource use between juvenile Coho and Chinook salmon in an estuary in Southcentral Alaska, United States. The Anchor River supports five species of anadromous Pacific salmon. However, the Chum Salmon *O. keta,* Sockeye Salmon *O. nerka,* and Pink Salmon *O. gorbuscha* runs are small and juveniles are not abundant within the estuary. Therefore, I focused on resource use by juvenile Coho and Chinook salmon, which support a popular recreational fishery. Low returns of adult Chinook Salmon in 2014 followed by high returns in 2015 resulted in very few juveniles in 2015 and abundant juveniles in 2016 creating a natural experiment to test for interactive segregation between Coho and Chinook salmon.

Methods

Study area

The Anchor River is located on the southwestern end of the Kenai Peninsula in southcentral Alaska (Figure 1). The watershed hydrology is influenced by snowmelt and groundwater, and the total watershed area is over 580 km^2, 48% of which is wetland (Kerkvliet and Booz 2012). The river provides 266 river kilometers (rkm) accessible to anadromous fishes (Kerkvliet et al. 2013) and supports five species of Pacific salmon in addition to anadromous Dolly Varden and steelhead Rainbow Trout *Oncorhynchus mykiss* (Johnson and Litchfield 2015). The Anchor River is a popular destination for recreational fishermen and supports the largest recreational fishery for Coho and Chinook salmon in the Lower Cook Inlet Management Area (Kerkvliet et al. 2013). There are no hatcheries on the Anchor River, thus all fish in this study are assumed to be of wild origin.

At its confluence with Cook Inlet, the Anchor River forms a bar-built estuary with an approximately 49-ha oligohaline marsh dominated by speargrass *Arctopoa eminems*, American dune grass *Leymus mollis*, and Lyngbye's sedge *Carex lyngbyei*. The lower reach of the marsh vegetation currently ends at approximately rkm 1.2 where the channel flows between an erosional bluff and sand bar before terminating in Cook Inlet. Aerial photographs indicate that the confluence with Cook Inlet was directly below the marsh as recently as the 1950s. Within the marsh, there are several small distributary channels and blind dendritic tidal channels, most of which do not fully drain at low tide. This region experiences substantial tidal influence, with a mean diurnal range of 5.5 m and a maximum high tide over 8 m.

Field methods

We established five sites for repeat sampling: three along a gradient in the main channel ranging from the upper to lower extent of marsh vegetation, and two in tidally influenced blind dendritic channels (Figure 1). In 2015, we sampled approximately weekly from mid-July to early-September. In 2016, we sampled approximately every other week from mid-May to early-September. In both years, we conducted an additional sampling event in early October. Sampling generally took place around low slack tide, except for a few sampling events in 2015 that occurred during incoming tides. During each sampling event, we recorded thalweg depth and took point measurements at the thalweg of temperature, salinity, and dissolved oxygen near the surface, in the middle of the water column, and near the substratum.

Fish were sampled using a pole seine (2.2-m x 6-m, 0.3-cm mesh) or beach seine (2-m x 8-m, 0.5-cm mesh) deployed on foot. In larger channels, we deployed the beach seine parallel to the bank and pulled it in perpendicular to the flow. This method was occasionally altered as need by channel depth and flow constraints. We recorded the distance the net was pulled and the open width of the net (or average width of the channel, if it was less than the width of the net) to calculate sampling effort. In narrow marsh channels, we used block nets (0.3-cm mesh) to enclose a 25-m reach before using a pole seine to capture fish. Fish were identified to species, enumerated, measured (nearest mm), and released. All fish were measured by fork length (FL), or total length (TL) for those species without a forked tail. The number of fish captured per square meter of channel sampled was used as an index of relative density (hereafter, "density") to describe the spatial and temporal trends in fish abundance. A Wilcoxon rank sum test was used to evaluate trends in fish density between species and years at each site.

Fish community and environmental variables

We used nonmetric multidimensional scaling (NMDS; Kruskal 1964) ordination to describe the fish community and environmental variables at each sampling event. Environmental data were summarized by taking the mean and standard deviation of the three water column point measurements (taken at the surface, mid-column, and bottom). The standard deviation represents the degree of stratification in each variable. Environmental data were standardized (by z-score) prior to analysis to adjust for measurements on different scales. Fish that were observed in < 5% of samples were excluded, as they could have undue influence on NMDS ordination. Young of the year fish were sometimes present in considerable densities, yet have different ecological roles than their adult conspecifics. Therefore, I chose to analyze them as separate entities from adults of the same species. Fish density was row standardized (by total) and log-transformed prior to analysis as it was right-skewed and I wished to de-emphasize the importance of occasionally highly abundant species. Euclidean distance was used for environmental data and Bray-Curtis dissimilarity was used for species abundance.

Diet collection and sample analysis

In 2016, we collected diet samples from a subset of juvenile salmon captured during normal sampling events to examine potential differences in foraging opportunities among habitats and diet overlap between species. Diet samples were collected using gastric lavage at all five sites in late-June, early-August, and early-September. A maximum of ten each of Coho and Chinook salmon were haphazardly subsampled across the size distribution of fish present at each sampling event. The fish were anesthetized, measured, and weighed (nearest 0.01g), and then the stomach contents were retrieved by flushing the stomach with water from a syringe and modified catheter tip. Fish were placed in an aerated bucket or in-stream enclosure to fully recover before being released. I assumed that the diets reflected foraging in the habitat where the fish were captured. However, studies on the gut evacuation rates of juvenile salmon indicate that some prey items from the preceding 8+ hours (e.g., over a tidal exchange) may still be present in diet samples (Brodeur and Pearcy 1987, Ruggerone 1989, He and Wurtsbaugh 1993). Observations of tagged individuals indicate fish in marsh channels tend to have strong site fidelity (see next chapter), and thus their diet samples are likely representative of foraging in those marsh channels. However, we do not have data on fish residency in the main channel, and it is possible their diets (collected near low tide) reflect foraging in marsh channels during the preceding high tide.

Diet samples were preserved in 70% isopropanol. In the lab, each sample was rinsed in a 100 µm sieve, gently blotted to remove excess water, and weighed (nearest 0.0001 g). Diet contents were identified and sorted to the lowest practical taxonomic level and life stage (egg, larva, pupa/nymph, adult). Each prey taxon and life stage were enumerated and weighed separately. When analyzing the data, prey taxa were grouped by taxonomic order, except for dipterans which were reduced to finer classifications (Chironomidae, Nematocera, Brachycera, and Other Diptera) because they were highly prevalent in the diet samples. Nematoda and Cestoda were excluded from all analyses as these are generally considered parasites of juvenile salmon, not prey. Non-digestible items (e.g. sand, Trichoptera cases) were also excluded from all analyses.

We used cumulative prey curves (Ferry and Cailliet 1996) to evaluate if the number of samples was sufficient to describe the diet composition of juvenile Coho and Chinook salmon. Curves were computed for each species by plotting the mean number of unique prey items determined from random 100 permutations of the data against the number of diet samples analyzed. Sample size was deemed sufficient for diet characterization if the slope of the linear regression (b) through the last five samples was ≤ 0.05, as this is considered an adequate leveling off of the prey curve (Brown et al. 2012).

Numerical and gravimetric diet composition data were arranged into matrices consisting of diet samples (rows) by prey categories (columns). The data were standardized by row totals so that each cell represented the proportional contribution of a given prey item to each diet. Diet data for each species, site, and sampling event were tabulated by three metrics (Hyslop 1980, Brown et al. 2012):

Frequency of occurrence (FO_i):

$$FO_i = \frac{n_i}{n}$$

where

n_i = the number of diet samples containing prey i,

n = the total number of diet samples, and

Prey-specific average percent abundance by number and weight ($\%PN_i$ and $\%PW_i$, respectively):

$$\%PA_i = \frac{\sum_{j=1}^{n} \%A_{ij}}{n_i}$$

where

$\%A_{ij}$ = the relative abundance (numerical for $\%PN_i$, gravimetric for $\%PW_i$) of prey category i in diet sample j, and

n_i = the number of diet samples containing prey i.

$\%PN_i$ and $\%PW_i$ are computed as the column averages of the numeric and gravimetric matrices, respectively, where empty cells (i.e. when a prey item is absent) are omitted. FO_i is computed as the column averages of the abundance matrix transformed to binary (presence/absence).

Each of these metrics is useful in characterizing diets, yet individually they may provide poor information when evaluating diet overlap because they can be strongly influenced by diet composition and do not necessarily reflect caloric value and therefore fitness. For example, the numerical percentage highly ranks diet items that occur in great numbers, even if they are rarely observed. Frequency of occurrence might highly rank small, low caloric value prey items that are commonly consumed, yet the energy expenditure of acquiring them may make them poor quality prey. Gravimetric percent might be more relevant when considering diet differences among species or habitats because this metric likely relates to growth potential, yet it can be strongly influenced by a few samples that have high weights of a particular prey item. Combining these metrics into a composite index reduces the biases caused by each individual metric (Bigg and Perez 1985). However, the composite Index of Relative Importance proposed by Pinkas and Iverson (1971) and widely used in fish diet analyses introduces biases of its own (Brown et al. 2012). Therefore, I used the Prey-Specific Index of Relative Importance (Brown et al. 2012):

$$\%PSIRI_i = \frac{FO_i(\%PN_i + \%PW_i)}{2}$$

%PSIRI is additive among taxonomic levels, meaning the *%PSIRI* value for a taxonomic class is equal to the sum of the *%PSIRI* values for the observed taxonomic orders within that class.

Resource overlap between juvenile Coho and Chinook salmon

Horn's Index of Similarity (Horn 1966, Krebs 1983) was used to compare resource use between juvenile Coho and Chinook salmon. This index can be used to calculate the spatial, temporal, and trophic overlap between species according to the following equation:

$$\hat{R}_O = \frac{\sum(\hat{p}_{ij} + \hat{p}_{ik})\log(\hat{p}_{ij} + \hat{p}_{ik}) - \sum \hat{p}_{ij} \log \hat{p}_{ij} - \sum \hat{p}_{ik} \log \hat{p}_{ik}}{2\log 2}$$

where

R_O = Horn's index of resource overlap for species *j* and *k,*

p_{ij} = proportion resource *i* is of the total resources utilized by species *j,*

p_{ik} = proportion resource *i* is of the total resources utilized by species *k,* and

any base may be used for the logarithm.

Variables are further explained in Table 1. R_O ranges from 0 (no overlap) to 1 (complete overlap). Index values greater than 0.60 are generally considered to reflect biologically significant overlap (Zaret and Rand 1971, Mathur 1977). Temporal overlap between Coho and Chinook salmon density was calculated for each site and for all sites combined. Spatial overlap was calculated for each sampling period and all periods combined for sampling periods in which both species were present. Diet overlap was only calculated when at least six of each Coho and Chinook salmon were sampled at a given site and sampling period. This reduced the analysis to two sites (Middle Main and Lower Main) during the June 21-26 sampling period (sample sizes are provided in Table 2). Because Chinook Salmon were nearly absent from the Anchor River estuary in 2015, all resource use comparisons use data from 2016 only. Samples where neither species was observed were excluded from analysis. Overlap indices have a long history of use in resource partitioning studies (Horn 1966, Schoener 1970), in part because they are easy to interpret and compare among studies.

However, they are more descriptive than statistically rigorous and are best used in conjunction with statistical analyses.

Multivariate analyses were used to further evaluate diet overlap between Coho and Chinook salmon among sites and sampling events. The gravimetric contribution of each prey category was compared using NMDS ordination based on Bray-Curtis dissimilarity matrices (Kruskal 1964). Because rare species can have a disproportionate influence on NMDS ordinations, prey taxa that were observed in less than 5% of all samples were excluded from these analyses. Prior to analysis, the gravimetric data were log-transformed because they were highly right skewed. Analysis of similarities (ANOSIM) was used to test if the gravimetric composition of the diets significantly differed: 1) between Chinook and Coho salmon; 2) among sampling sites; and 3) among sampling periods. ANOSIM compares the rank-ordering of samples within and between groups defined *a priori.* The test statistic, *R*, ranges between -1 and 1; an *R* close to 1 indicates the within-group dissimilarity is less than the between-group dissimilarity and an *R* close to 0 indicates the dissimilarity is the same within and between groups (Clarke 1993). Significance was determined by permuting the grouping variable 1,000 times to create a null distribution against which to test the observed *R*. Because ANOSIM assumes that the variation is the same within each group, I also conducted a test for multivariate homogeneity of group dispersions using a multivariate analog of Levene's test for homogeneity of variances (Anderson 2006).

Spatial and temporal diet trends

Variation in diet composition between species and through space and time can lend insight into habitat use and resource partitioning, but may not reflect fitness advantages. Therefore, analyzing the amount and caloric value of consumed food provides insight into the value of different habitats and potential competitive advantage between species. The instantaneous ration (I) provides a measure of feeding intensity and is expressed as the mass of the stomach contents relative to the mass of the fish:

$$I = \frac{M_d}{M_f - M_d}$$

where

M_d = the mass of the stomach contents, and

M_f = the mass of the fish.

Likewise, the energy ration (E) reflects the energy intake per gram of fish calculated as:

$$E = \frac{\sum_{i=1}^{n}(M_i E_i)}{M_f - M_d}$$

where

n = the number of prey categories,

M_i = the mass of prey item i, and

E_i = the energy density (kJ•g^{-1}) of prey item i,

M_d = the mass of the stomach contents, and

M_f = the mass of the fish.

Prey energy density values were retrieved from David et al. (2015). To avoid potential bias due to differences in feeding periodicity and digestion, I first tested if the instantaneous and energy rations were influenced by the time of day the sample was collected using linear regression. There was no significant influence due to the time of day, so all samples were pooled and linear regression models were used to evaluate if E and I were influenced by species, sampling site, or date. Both E and I had a lognormal distribution and were therefore log-transformed prior to analysis.

All analyses were performed using R 3.3.2 (R Core Team 2016). The *vegan* package was used for multivariate analyses (Oksansen et al. 2016).

Results

Fish community and environmental variables

The fish assemblage varied by site and by year in the Anchor River estuary. A total of 18 species were sampled, with Staghorn Sculpin *Leptocottus armatus*, juvenile Coho Salmon, juvenile Starry Flounder *Platichthys stellatus*, and Threespine Stickleback *Gasterosteus aculeatus* comprising 98% of the catch in 2015 and 84% of the catch in 2016. The fish community showed distinct trends in relative densities at each site, except for the Middle Main site which had considerable variability in fish assemblage (Figure 2B). Staghorn Sculpin and Starry Flounder were most prevalent in the lower reaches of the estuary (mainstem and marsh channels), young-of-the-year Threespine Stickleback were exclusively found in marsh channels, and Chinook Salmon were predominantly captured in the mainstem sites. Marsh channel sites demonstrated considerable variability in environmental metrics and were typified by stratified conditions and higher salinity, while main channel sites had more consistent environmental conditions and high dissolved oxygen levels (Figure 2A).

Juvenile salmon spatial and temporal habitat use

Coho Salmon were a dominant species in the Anchor River estuary in both 2015 and 2016, with an average density (± SD) of 0.46 (± 0.53) fish•m^{-2} and 0.31 (± 0.46) fish•m^{-2}, respectively (Figure 1). Coho Salmon were present at all sites and were captured throughout the sampling season (Figures 3 and 4). Coho Salmon density did not significantly differ between years at each site (1-tailed Wilcoxon rank sum test, $p > 0.05$ for each site) except for the Upper Mainstem site which had significantly more Coho Salmon in 2015 (1-tailed Wilcoxon rank sum, $p = 0.03$). Conversely, juvenile Chinook Salmon were nearly absent from the estuary in 2015 but were numerous in 2016 with an average density of 0.22 (± 0.70) fish•m^{-2}. Juvenile Chinook Salmon were almost exclusively captured in the main channel (Figure 1). They were most abundant in June and were not captured after August (Figure 3). Fish density was significantly different between species in each of the marsh channels and at the Upper Main channel site (Wilcoxon rank sum, $p < 0.05$), but not at the Middle Main and Lower Main channel sites.

Juvenile Coho and Chinook salmon partitioned resources in space and time. During each sampling period, spatial partitioning in fish density ranged from 4%-27% overlap, with the greatest overlap occurring in late June when Chinook were most abundant (Table 3, Figure 4). Within each site, temporal partitioning ranged from 22-79% overlap, with the greatest overlap occurring in the Middle and Upper main channel sites where Coho Salmon, like Chinook Salmon, were more abundant earlier in the season (Table 4).

Salmon diet composition and overlap

The cumulative prey curve for Coho Salmon diet samples ($n = 90$) reached a terminal slope (last 5 data points) of $b = 0.045$, indicating that the sample size was adequate for describing the prey assemblage (Figure 5A). The cumulative prey curve for Chinook Salmon diet samples ($n = 40$) reached a terminal slope of $b = 0.071$, indicating that the sample size was marginally inadequate for describing diet composition (Figure 5B).

Coho and Chinook salmon diet composition strongly overlapped. Both species consumed a diverse array of prey items including terrestrial arthropods, epibenthic crustaceans, aquatic insects, and larval/juvenile fish. For both species across all sites and sampling periods, dipteran flies (esp. Chironomidae) were the most frequent and important prey item, followed by amphipods (Amphipoda), and springtails (Collembola; Table 5). Horn's Index indicated greater than 84% overlap (Table 6), and NMDS ordination showed minimal separation in the diets of these two species (Figure 6). There was not a significant difference in Coho and Chinook salmon gravimetric diet composition (ANOSIM; $R = 0.003$, $p = 0.43$).

Juvenile salmon diet composition varied by site and sampling period (global ANOSIM; $p < 0.05$ for all). All sites had significantly different diet composition from one another (pairwise ANOSIM; $p < 0.05$ for all), except for Upper Marsh compared to Lower Main ($R = 0.01$, $p = 0.27$) and Upper Marsh compared to Middle Main ($R = 0.03$, $p = 0.24$). The diets from the first two sampling events were not significantly different from each other ($R = 0.02$, $p = 0.26$), but diet composition shifted in the fall such that diets from the sampling event in early-September were significantly different from those in late-June ($R = 0.13$, $p = 0.01$) and from those in early-August ($R = 0.13$, $p = 0.005$). Diet variance was not significantly different for all pairwise comparisons (multivariate test for homogeneity of group dispersions, $p > 0.05$ for each pairwise comparison) except for Upper Main compared to Upper Marsh, Lower Marsh, and Middle Main ($p < 0.01$ for each). This is likely due to the smaller sample size at Upper Main. There was no difference ($p > 0.05$) in variance among sampling events or between species.

Although diet composition varied spatially and temporally, the instantaneous ration (I) and energy ration (E) of the diets only varied by site ($p < 0.001$ for both I and E, Tables 7 and 8). I and E were not significantly different between Coho and Chinook salmon and did not significantly vary based on time of day. Given our sample sizes and a significance level of $\alpha = 0.05$, there was sufficient power ($1 - \beta = 0.80$) to detect differences between Coho and Chinook rations with an effect size of 0.54, which is considered a “moderate” difference (Cohen 1988). We may have observed non-significance because the true effect size was small and we thus lacked statistical power to observe it (mainly due to high variability in rations among individuals), or because there was in fact no difference in diet rations between the two species.

Discussion

Our results indicate the juvenile Coho and Chinook salmon in the Anchor River estuary primarily partition resources spatially, and to a lesser degree temporally. There was a strong overlap in the diets of the two species, indicating that they do not partition food resources within the estuary. These findings are contrary to those of Eaton (2010), who found that juvenile Coho, Chinook, and Chum salmon in the Grays River estuary (Washington, USA) primarily partitioned food resources and were secondarily segregated in time, but spatial partitioning was less important. This indicates that patterns in resource use and overlap among species varies among systems.

The variation in juvenile Chinook density during the present study provided a natural experiment to test interactive resource partitioning. Perturbation experiments are useful (and perhaps necessary) to test interactive resource partitioning (Paine 1971), yet large scale manipulation of the system is generally infeasible. However, Chinook Salmon were nearly absent from the estuary in 2015, but were abundant in the main channel in 2016, which allowed us to capitalize on this natural experiment to test interactive resource partitioning between Coho and Chinook salmon. Coho Salmon were generally less abundant in the main channel in 2016 than in 2015 and more abundant in the tidal marsh channels. This would indicate that they preferentially moved out of the main channel due to the presence of juvenile Chinook salmon thus demonstrating interactive resource partitioning.

Interactive resource partitioning may imply but does not test competition, nor does it reveal the mechanism of potential competition. If we assume that fish select habitat to maximize fitness (Mangel and Clark 1986, Railsback and Harvey 2002), the fact that juvenile Coho Salmon were more prevalent in tidal channels and less prevalent in the main channel in 2016 indicates a fitness cost to co-occurring with Chinook Salmon. Possible mechanisms include depletion of shared prey resources, costs associated with agonistic encounters between the species, or an increase in predation risk. Testing these mechanisms was beyond the scope of the current study, but would be a useful avenue for future research.

Although, juvenile Chinook Salmon were almost exclusively captured in the main channel of the Anchor River estuary, numerous other studies have demonstrated that Chinook Salmon make extensive use of tidal marsh channels (Bottom et al. 2005, Hering et al. 2010, David et al. 2014, McNatt et al. 2016). In the present study, Chinook salmon may have avoided marsh channels because Coho Salmon were present in high densities, or may simply have found suitable habitat in the main channel. The Anchor River is considerably smaller and shallower than many of the estuaries where juvenile salmon have been studied (e.g. the Columbia River estuary; McNatt et al. 2016). With pools, woody debris, and summer flow around 0.5 $m \cdot s^{-1}$ as suitable habitat in the main channel, Chinook Salmon may not need to take refuge in marsh channels. In freshwater habitat, juvenile Chinook Salmon tend occupy larger channels than Coho Salmon (Quinn 2005) which may be an example of selective resource partitioning: the two species have evolved different habitat preferences that minimize competition for resources. Or conversely, either species would occupy all estuarine habitats in the absence of the other, but both participate in interactive resource partitioning to spatially restrict their realized niches when they co-occur. This study was only able to test interactive partitioning in Coho Salmon, but the response of Chinook Salmon to varying densities of Coho Salmon would likewise be informative. Eaton (2010) found that experimentally increasing the density of Coho Salmon caused a decrease in Chum and Chinook salmon densities as fish likely emigrated to neighboring habitats, indicating that fish density influences spatial partitioning of resources.

Despite the fact that diet composition varied between sites and from summer to fall, Coho and Chinook salmon had very similar diet composition. Instantaneous ration and energy ration did not vary between species, but did vary slightly among habitats with rations from the Upper Main site being smaller than those from the marsh channels and lower mainstem sites. Diet composition was similar between the two tidal marsh channels and between the Middle and Upper Main channel sites, while the Lower Main site had the most variable diet composition and more closely resembled the marsh channels. This may reflect the hydrology of estuaries; as receding tides drain from marsh channels, they carry potential prey items with them such as terrestrial and aquatic insects and thus subsidize the diversity of prey resources in the lower portion of the estuary which supports more marine-related prey such as amphipods and crustacean larvae.

Estuaries have suffered a heavy toll from urbanization globally (Kennish 2002). Estuaries in the Pacific Northwest are a testament to human impact, and extensive work has been done to restore ecological function and replace lost rearing habitat for juvenile salmonids (Simenstad and Cordell 2000, Gray et al. 2002, David et al. 2014). While much of Alaska's salmon habitat remains intact, the human population and land use continue to grow and place pressure on natural systems (Ourso and Frenzel 2003). Alaska boasts some of the largest wild salmon populations in the world, which support a multimillion dollar commercial and recreational fishery (Knapp et al. 2007, Romberg et al. 2008) in addition to subsistence fisheries (Fall 2015). Preserving rearing habitat for juvenile salmonids is vital to maintaining sustainable salmon populations (Frissell 1993, Lichatowich et al. 2000). This study demonstrates that the presence of heterogeneous habitats within the estuarine environment promotes the co-existence of two closely related and culturally, economically, and ecologically valuable species.

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Tables

Table 1. Explanation of variables used in Horn's overlap index for evaluating juvenile salmon spatial, temporal, and trophic resource partitioning.

Axis	p_{xi}	p_{yi}	n
Temporal	proportion of total catch of species x in period i	proportion of total catch of species y in period i	number of sampling periods
Spatial	proportion of periodic catch of species x in site i	proportion of periodic catch of species y in site i	number of sites
Trophic	%PSIRI of prey i in the diet of species x	%PSIRI of prey i in the diet of species y	number of prey categories

Table 2. Number of diet samples collected by species, site, and sampling period.

	June 21-26		Aug 8-10		Sept 6-7		*All periods*	
Site	Coho	Chinook	Coho	Chinook	Coho	Chinook	*Coho*	*Chinook*
Upper Marsh	11	1	10	0	10	0	*31*	*1*
Lower Marsh	10	3	10	0	10	0	*30*	*3*
Upper Main	0	8	2	10	0	0	*2*	*18*
Middle Main	10	10	1	0	0	0	*11*	*10*
Lower Main	10	6	6	2	0	0	*16*	*8*
All sites	*41*	*28*	*29*	*12*	*20*	*0*	*90*	*40*

Table 3. Spatial overlap in juvenile Coho and Chinook salmon density during each sampling period.

Sampling period	Horn's Index
May 24-25	(Chinook absent)
June 6-10	0.12
June 20-26	0.27
July 6-8	0.26
July 18-20	0.12
Aug 8-10	0.04
Sept 2-7	(Chinook absent)
Oct 3-7	(Chinook absent)
All periods	0.24

Table 4. Temporal overlap in juvenile Coho and Chinook salmon density at each sampling site.

Site	Horn's Index
Lower Marsh	0.22
Upper Marsh	0.59
Upper Mainstem	0.68
Middle Mainstem	0.79
Lower Mainstem	0.35
All sites	0.69

Table 5. Diet composition for juvenile Coho and Chinook salmon by frequency of occurrence (*FO*), prey-specific percent number (*%PN*), prey-specific percent weight (*%PW*), and Prey-Specific Index of Relative Importance (*%PSIRI*).

	Coho Salmon (n = 90)				Chinook Salmon (n = 40)			
Prey Taxa	FO	%PN	%PW	%PSIRI	FO	%PN	%PW	%PSIRI
Arachnida				*2.2*				*1.0*
Acari	6.3	14.0	8.0	0.7	5	30.9	4.8	0.9
Araneae	17.7	5.7	11.1	1.5	5	2.0	3.1	0.1
Clitellata	1.3	100.0	100.0	1.3				
Collembola	31.6	46.2	21.5	10.7	15	16.1	8.6	1.9
Gastropoda	1.3	10.0	96.4	0.7				
Insecta				*54.5*				*87.0*
Coleoptera	15.2	4.3	14.3	1.4	7.5	5.1	11.7	0.6
Diptera				*44.5*				*70.0*
Brachycera	27.8	6.8	24.2	4.3	15	5.1	30.0	2.6
Nematocera				*37.1*				*63.0*
Unidentified Nematocera	11.4	13.8	24.5	2.2	15	7.2	12.8	1.5
Chironomidae, adult/emergent	30.4	10.4	15.4	3.9	25	13.1	14.9	3.5
Chironomidae, larva	60.8	31.7	14.6	14.1	80	44.9	34.9	31.9
Chironomidae, pupa	63.3	29.0	24.3	16.9	90	31.6	26.3	26.0
Unidentified Diptera, larva	15.2	12.1	28.1	3.0	22.5	14.6	24.0	4.3
Ephemeroptera	5.1	25.5	18.9	1.1	35	20.5	24.2	7.8
Hemiptera	8.9	11.1	26.0	1.6	12.5	2.0	3.9	0.4
Hymenoptera	10.1	11.3	14.5	1.3	10	2.6	4.6	0.4
Orthoptera	1.3	5.6	59.0	0.4				
Plecoptera, nymph	12.7	8.4	8.3	1.1	37.5	9.1	12.3	4.0
Thysanoptera, nymph	3.8	5.6	9.9	0.3	7.5	6.2	3.1	0.3
Trichoptera, nymph					2.5	13.0	60.6	0.9
Unidentified Insecta, larva	17.7	12.9	18.5	2.8	17.5	11.0	18.3	2.6
Crustacea				*26.3*				*8.9*
Amphipoda	50.6	37.6	45.2	21.0	22.5	25.1	28.7	6.0
Decapoda, larva	1.3	4.3	8.4	0.1				
Arguloida	3.8	3.4	6.0	0.2	5	1.9	20.5	0.6
Harpacticoida	7.6	69.3	37.3	4.1	2.5	38.7	3.0	0.5
Other Copepoda	13.9	10.4	4.2	1.0	2.5	50.0	91.6	1.8
Ostracoda	1.3	1.4	0.6	<0.1				
Teleostei				*4.4*				*1.2*
Teleostei, egg	3.8	25.8	46.8	1.4				
Teleostei, larva/juvenile	10.1	12.6	47.0	3.0	5	20.0	30.0	1.2

Note: Italicized *%PSIRI* values are sums of the constituent taxa. Data are pooled across all sites and sampling events.

Table 6. Diet overlap between juvenile Coho and Chinook salmon based on the Prey-Specific Index of Relative Importance (*%PSIRI*) for sampling events with adequate representation of both species.

Site	*n* Coho	*n* Chinook	Horn's Index
Middle Main	10	10	0.87
Lower Main	10	6	0.84

Table 7. Analysis of variance table for factors influencing instantaneous ration *I.*

Source	df	SS	MS	F	p-value
Total	129	34.90	0.27		
Species	1	<0.01	<0.01	<0.01	0.99
Error	128	34.90	0.27		
Site|Species	4	5.66	1.41	6.00	<0.001*
Error	124	29.24	0.24		
Date|Species	1	<0.01	<0.01	0.02	0.90
Error	127	34.90	0.27		
Site|Species+ Date	4	5.74	1.44	6.06	<0.001*
Error	123	29.16	0.24		
Time of Day| Species+Date +Site	1	0.05	0.05	0.10	0.75
Error	122	29.13	0.24		

Asterisk (*) denotes significant values.

Table 8. Analysis of variance table for factors influencing energy ration *E*.

Source	df	SS	MS	F	p-value
Total	129	29.41	0.29		
Species	1	0.06	0.06	0.26	0.61
Error	128	29.35	0.23		
Site|Species	4	4.08	1.02	5.00	<0.001*
Error	124	25.28	0.20		
Date|Species	1	<0.01	<0.01	<0.01	0.96
Error	127	39.35	0.23		
Site|Species+ Date	4	4.17	1.04	5.09	<0.001*
Error	123	25.18	0.20		
Time of Day| Species+Date +Site	1	<0.01	<0.01	<0.01	0.99
Error	122	29.13	0.24		

Asterisk (*) denotes significant values.

Figures

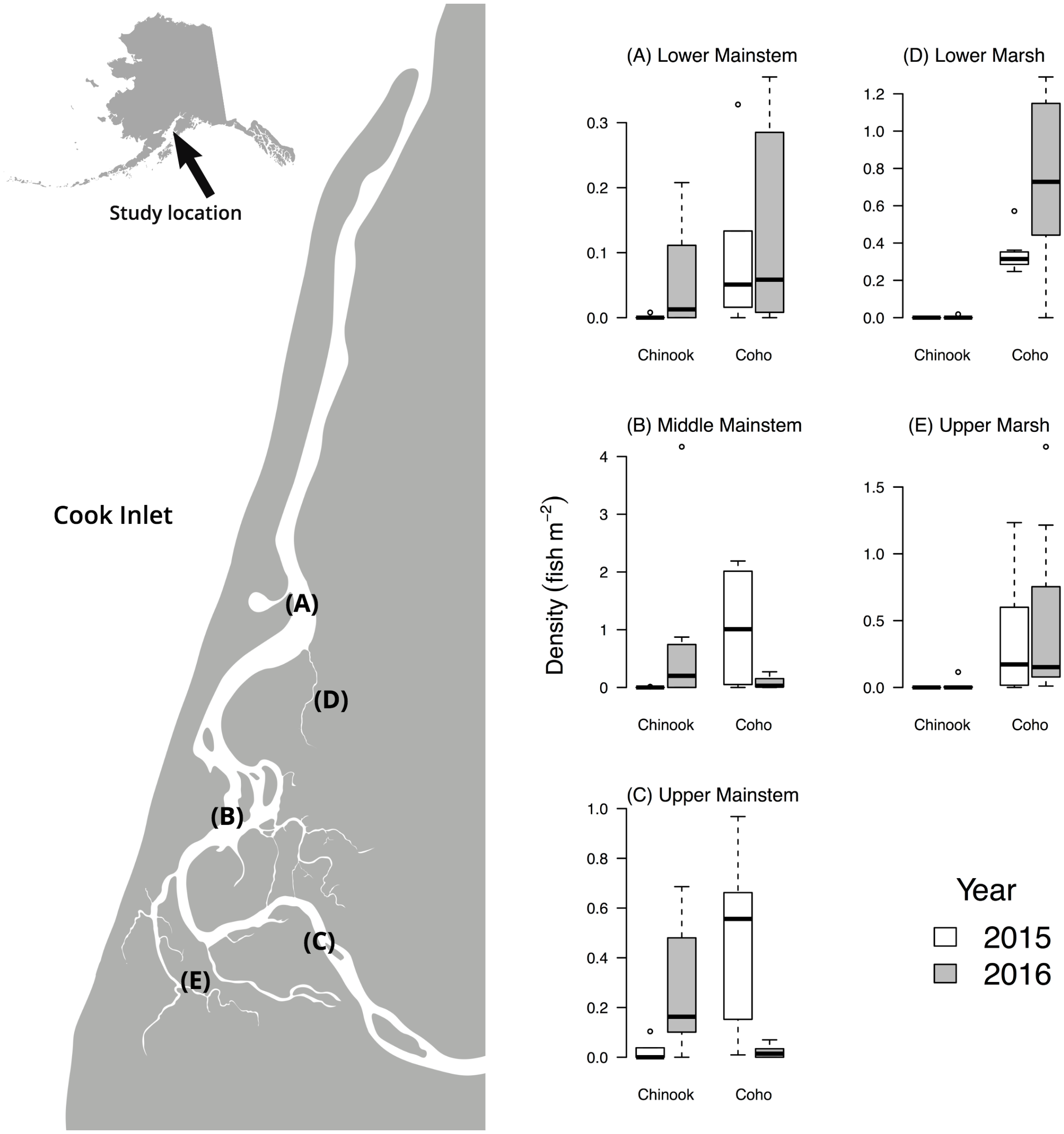
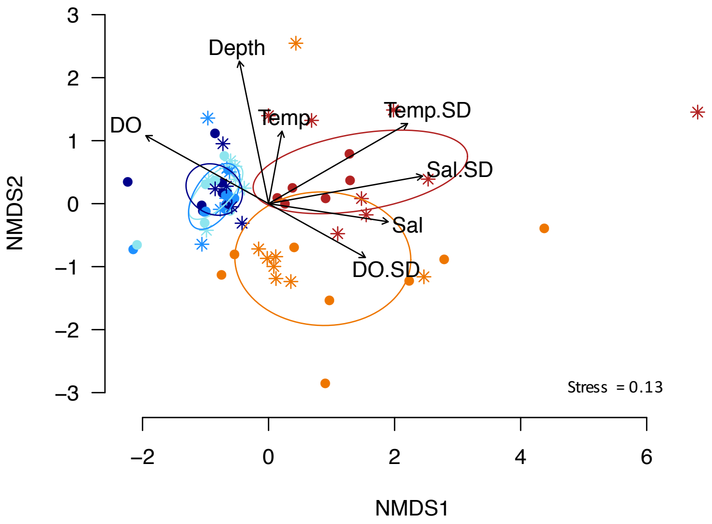


Figure 1. Site map and location of the Anchor River estuary. Sampling occurred along a gradient in the main channel (A – C) and in two dendritic marsh channels (D and E). Boxplots on the right provide the density of juvenile Coho and Chinook salmon captured in 2015 and 2016 at each site (site names correspond to the letters on the map).

(A) Environmental variables



(B) Fish community

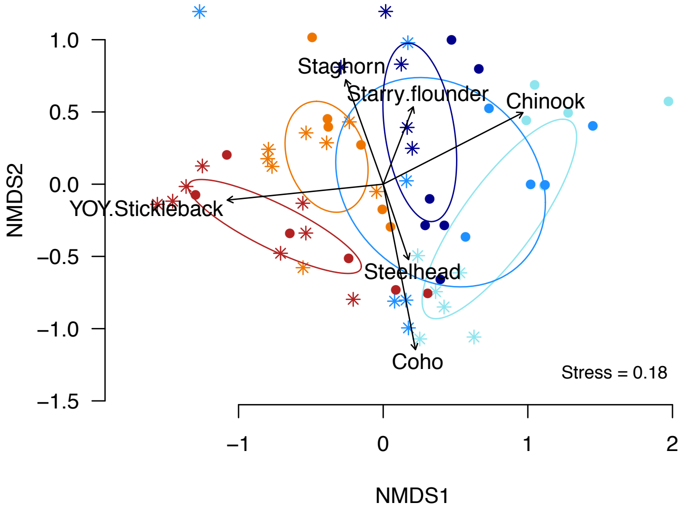


Figure 2. Nonmetric multidimensional scaling plots of environmental metrics (A) and relative fish density (B) in the Anchor River estuary. Points represent samples from 2015 (asterisks) and 2016 (circles) and are colored by site: Red = Upper Marsh, orange = Lower Marsh, light blue = Upper Mainstem, medium blue = Middle Mainstem, dark blue = Lower Mainstem. Ellipses depict the standard deviation from each site centroid. Arrows indicate the magnitude and direction of variable loadings that significantly ($p < 0.05$) contributed to the composite axes. DO = dissolved oxygen, Temp = temperature, Sal = salinity, SD = standard deviation (degree of stratification), YOY = young-of-the-year.

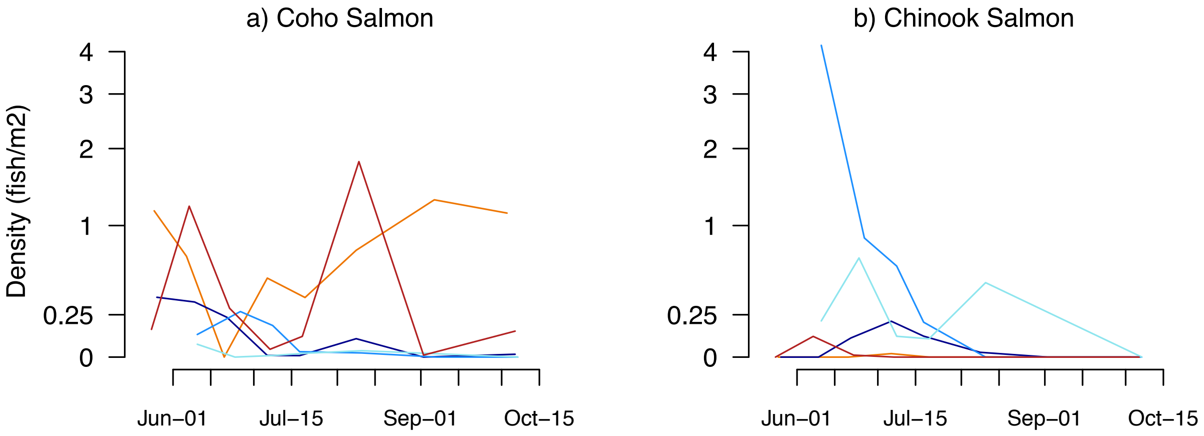


Figure 3. Temporal trends in juvenile Coho (a) and Chinook (b) salmon density at each sampling site in 2016. Lines are colored by site: Red = Upper Marsh, orange = Lower Marsh, light blue = Upper Mainstem, medium blue = Middle Mainstem, dark blue = Lower Mainstem.

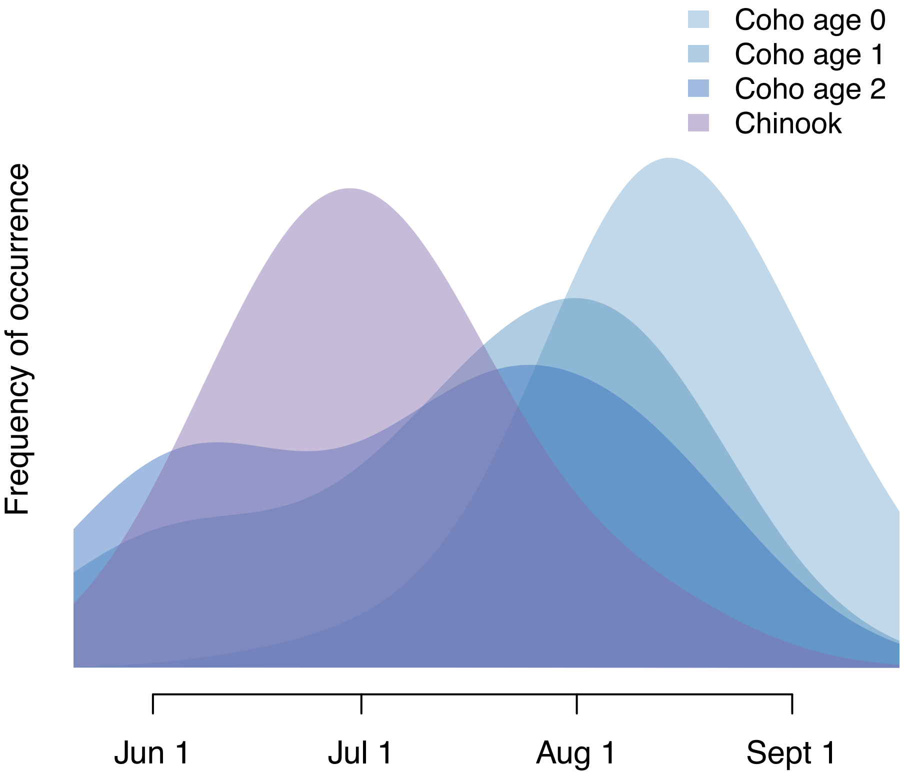


Figure 4. Temporal trends in fish abundance by species and age class.

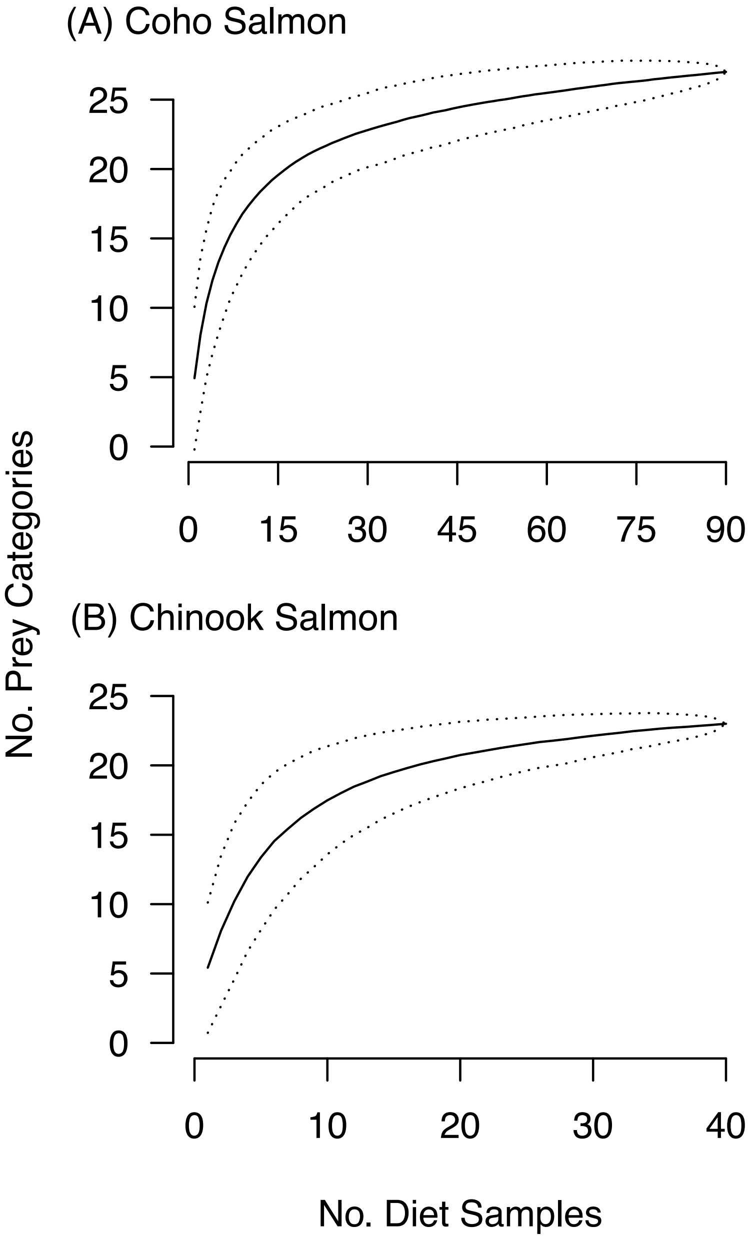


Figure 5. Cumulative average number of prey taxa (solid line) and standard deviation (dashed lines) in relation to the number of diets samples analyzed for juvenile Coho (A) and Chinook (B) salmon.

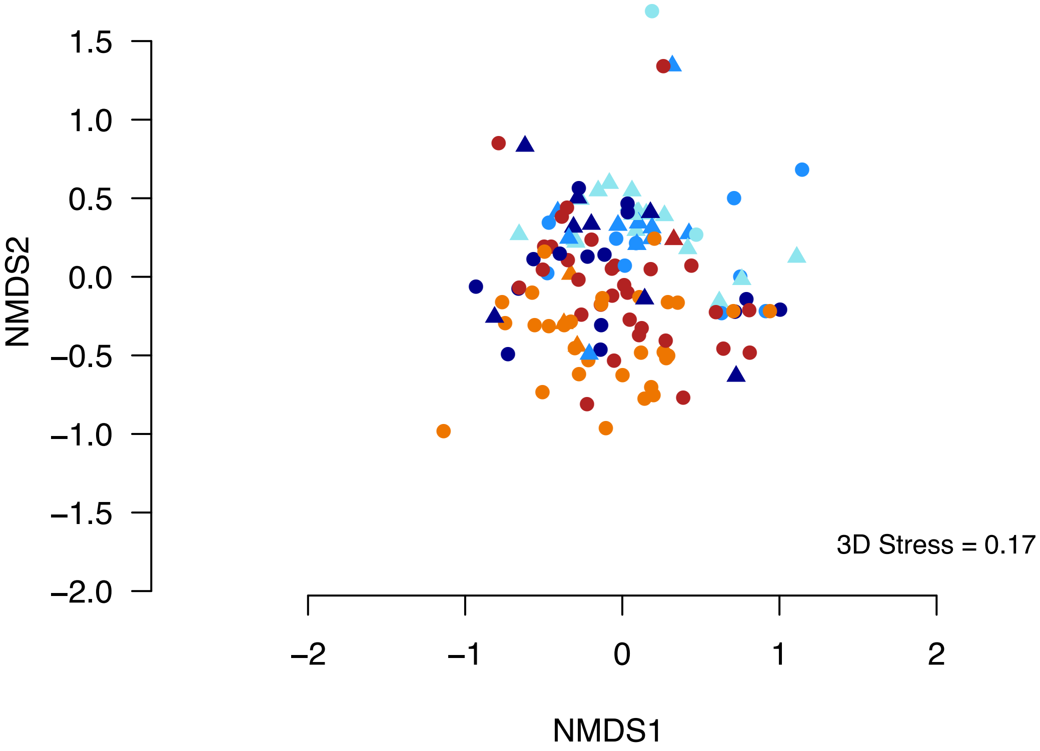


Figure 6. Nonmetric multidimensional scaling (NMDS) ordination plot showing the diet composition of Coho (circles) and Chinook (triangles) salmon based on the gravimetric contribution of prey items. Points are colored by site. Red = Upper Marsh, orange = Lower Marsh, light blue = Upper Main, medium blue = Middle Main, dark blue = Lower Main. Stress is a measure of goodness of fit between rank-ordered observed distances and those predicted by from the dissimilarity matrices.

CHAPTER 2: GROWTH, RESIDENCY, AND MOVEMENT OF JUVENILE COHO AND CHINOOK SALMON IN THE ANCHOR RIVER ESTUARY, SOUTHCENTRAL ALASKA.

Abstract

Estuaries provide diverse rearing habitats for juvenile Pacific salmon, often supporting multiple species and age classes. Tidal inundation creates a dynamic network of routinely variable habitats that may differ in their connectivity and intermittent availability. Few studies have evaluated the tidal movements of individual salmon, and those that have primarily focused on juvenile Chinook Salmon *Oncorhynchus tshawytscha* in channels that fully drain with each tidal cycle. In the present study, I compare the movement of juvenile Coho Salmon *O. kisutch* in two dendritic marsh channels that vary in their connectivity to the mainstem channel yet retain water at low tide. I used tagging, recapture, and remote detection to document the movement, residence time, and growth of juvenile Coho and Chinook salmon in the Anchor River estuary in southcentral Alaska. The average absolute growth rate for Coho Salmon was 0.33 $mm \cdot d^{-1}$. Maximum estuarine residence for all three age classes of Coho Salmon was > 100 d. In contrast, only a single age class of juvenile Chinook Salmon was present in the estuary with a maximum residence time of 42 d. Juvenile salmon entered and exited both marsh channels throughout the tidal cycle, but movement in the marginally connected channel was most strongly influenced by tidal stage. These results demonstrate that tidal marsh channels that retain water at low tide provide habitat that is continually accessed, even when connectivity is intermittently restricted.

Introduction

All juvenile Pacific salmon must pass through estuaries on their journey from freshwater to marine habitats, but some species and life history types rear in estuarine habitats for extended periods. Chinook Salmon are generally considered the most estuarine dependent salmon species as fish from the ocean-type life history often rear in the estuary for weeks or months (Healey 1982, Healey 1991, Thorpe 1994). More recent studies have demonstrated that larger Coho Salmon may reside in the estuary for a couple of weeks before emigrating to marine habitats, while the smaller subyearling (age 0) Coho Salmon rear in the estuary for prolonged periods (Miller and Sadro 2003, Jones et al. 2014, Craig et al. 2014). Subyearling Coho Salmon might enter the estuary because they were displaced from stream-rearing habitat (Chapman 1962) or they might represent an alternative life history type which relies on estuarine habitats (Bennett et al. 2014, Jones et al. 2014). Therefore, the diversity and quality of estuarine habitats may increase the number of life history types expressed in a population (Jones et al. 2014, Craig et al. 2014) thereby contributing to greater population-level stability (Schindler et al. 2010, Fleming et al. 2014).

Within emergent estuarine marshes, networks of distributary and dendritic channels provide beneficial habitat for juvenile salmon. These channels may partially or completely drain with each tidal cycle, necessitating a redistribution of the fish community that occupies them (Gibson 2003). Marking studies have shown that juvenile salmon repeatedly return to tidally drained channels, indicating these habitats are favorable when available (Levy and Northcote 1982, Hering et al. 2010, McNatt et al. 2016). Passive integrated transponder (PIT) technology has been used to evaluate the tidal movements of juvenile Chinook Salmon within marsh channels that drain with each tidal cycle in the Salmon River (Oregon, USA; Hering et al. 2010) and the Columbia River (Oregon, USA; McNatt et al. 2016). Both studies found that juvenile Chinook

Salmon generally entered and exited the channels late in the flood and ebb tides, respectively, although fish also entered and exited against the tide. What is less known is the potential tidal movements of PIT-tagged juvenile Coho Salmon and the movement of juvenile salmon within tidal channels that do not fully drain with each tide. I address both knowledge gaps in the present study.

Most of the current knowledge about the estuarine life history of juvenile salmon originates from the Pacific Northwest, yet some of the largest salmon populations are in Alaska where hydrology, temperature, light, and other environmental regimes can be dramatically different. Information is particularly lacking on the residency and growth of juvenile salmon in Alaskan estuaries (Hillgruber and Zimmerman 2009). At increasingly northern latitudes, there is a progressive shift to later emigration timing and longer freshwater residence resulting in three age classes of juvenile Coho Salmon (Groot and Margolis 1991). All three age classes are present in estuaries in southcentral Alaska, although age 0 and age 1 fish are more abundant (Hoem Neher et al. 2013). Estuarine residence determined by otolith microchemistry for age 0 and age 1 fish was at least a month, and residence for age 2 fish was 1-2 weeks (Hoem Neher et al. 2013). Several otoliths also showed evidence of overwintering in estuarine or nearshore waters. Information is still lacking on the estuarine residence of Chinook Salmon in Alaska, as well as the growth of juvenile Coho Salmon in Alaskan estuaries.

In the present study, I used tagging, recapture, and remote detection to document the movement, residence duration, and growth of juvenile Coho and Chinook salmon in the Anchor River estuary in southcentral Alaska. I particularly focused on the movement of juvenile salmon in marsh channels that retained water at low tide; one channel remained fully connected to the main channel at low tide while the other was relatively disconnected. I hypothesized that fish movement into and out of the disconnected channel would resemble the tidal patterns observed in channels that drain with each tide (Hering et al. 2012, McNatt et al. 2016), while movement in the continually connected channel would show consistent habitat use regardless of tidal stage. My specific objectives were to (1) evaluate fish growth rates; (2) document the age classes of juvenile Coho and Chinook salmon present in the estuary; (3) determine estuarine residency of each species and age class based on recapture and remote detection; and (4) examine how movement in and out of tidal marsh channels is influenced by channel connectivity, depth, tidal stage, and time of day.

Methods

Study area

The Anchor River is located on the southwestern end of the Kenai Peninsula in southcentral Alaska (Figure 1). The watershed hydrology is influenced by snowmelt and groundwater, and the total watershed area is over 580 km^2, 48% of which is wetland (Kerkvliet and Booz 2012). The river provides 266 river kilometers (rkm) accessible to anadromous fishes (Kerkvliet et al. 2013) and supports five species of Pacific salmon in addition to anadromous Dolly Varden and steelhead Rainbow Trout *Oncorhynchus mykiss* (Johnson and Litchfield 2015). The Anchor River is a popular destination for recreational fishermen and supports the largest recreational fishery for Coho and Chinook salmon in the Lower Cook Inlet Management Area (Kerkvliet et al. 2013). There are no hatcheries on the Anchor River, thus all fish in this study are assumed to be of wild origin.

At its confluence with Cook Inlet, the Anchor River forms a bar-built estuary with an approximately 49-ha oligohaline marsh dominated by speargrass *Arctopoa eminems*, American dune grass *Leymus mollis*, and Lyngbye's sedge *Carex lyngbyei*. The lower reach of the marsh vegetation currently ends at approximately rkm 1.2, where the channel flows between an erosional bluff and sand bar before terminating in Cook Inlet. Aerial photographs indicate the confluence with Cook Inlet was directly downstream of the marsh as recently as the 1950s. Within the marsh, there are several small distributary and dendritic channels, most of which do not fully drain at low tide. This region experiences substantial tidal influence, with a mean diurnal range of 5.5 m and a maximum high tide over 8 m.

Passive integrated transponder (PIT) technology was applied in two tidally influenced dendritic channels to study the residency and movement of juvenile salmon (Figure 1). The Upper Marsh channel is a 5th order channel system that remains fully connected to the main channel at low tide with an approximate average depth of 0.5 m. Two arrays of paired antennas were placed just upstream of the 3rd and 4th order confluence. The Lower Marsh channel is a 2nd order channel. During low summer flows, it is relatively disconnected from the main channel when the tide is below approximately 4 m. At low tide, approximately the first 75 m of the channel consists of shallow (<10 cm) riffle habitat; beyond this point a sill creates a continuous channel pool of approximately 0.3 m depth for the rest of the channel length. Both channels are deeply entrenched in the marsh with bankfull depths generally greater than 1 m above baseline channel depth. Table 1 provides further comparison of the two channels. Appendix A provides more detailed information on the configuration of the PIT antennas and receivers which were custom designed for this project. Depth, temperature, and salinity were recorded at 15 min intervals by stationary level loggers (Solinst Canada Ltd. and HOBO Onset Computer Corp.) anchored in each channel near the PIT antennas. Channel level data was corrected for barometric pressure using data from two baro loggers (Solinst Canada Ltd.) placed above the marsh surface.

Fish sampling, marking, and detection

Fish were sampled at five sites: one site in each of the marsh channels upstream of the PIT antennas and three along a gradient in the main channel ranging from the upper to lower reaches of the marsh (Figure 1). In 2015, we sampled approximately weekly from mid-July to early-September. In 2016, we sampled approximately every other week from mid-May to early-September. We performed one additional sampling event in October of each year. Sampling generally took place during low slack tide, except for a few sampling events in 2015 that occurred during incoming tides. Fish were captured using a pole seine (2.2 m x 6 m, 0.3 cm mesh) or beach seine (2 m x 8 m, 0.5 cm mesh) deployed on foot. Fish were identified to species, enumerated, and measured (nearest mm). All fish were measured by fork length (FL), or total length (TL) for those species without a forked tail. To evaluate fish growth, residency, and movement patterns, all Coho and Chinook salmon ≥ 60 mm FL were anesthetized with buffered tricaine methanesulfonate (MS-222), weighed (nearest 0.01g), and implanted with a PIT tag (Biomark Model HPT8, 8.4mm 134.2 kHz FDXB) in the peritoneal cavity (Prentice et al. 1990). I did not attempt to quantify tagging-related mortality or tag loss because previous work in this region concluded that the large tidal range makes enclosure studies infeasible (Walker et al. 2013). However, studies using similarly sized juvenile salmon reported no adverse effects on behavior or growth, low delayed mortality, and little to no tag loss (Prentice et al. 1990, Dare 2003). A small number of Staghorn Sculpin *Leptocottus armatus* ≥ 80 mm TL were also implanted with PIT tags as these fish are potential predators of juvenile salmon, but their estuarine residence and movement remain unknown. All fish were placed in an aerated bucket or in-stream enclosure to recover before being released.

PIT tags enable unique identification of individuals during recapture or detection at PIT antenna arrays. When a tagged fish passed within range of an antenna, its tag identification number was transmitted to the antenna receiver and recorded along with the time of the detection and the identity of the antenna. Sequential detections at the paired antennas were used to determine the direction the fish was moving. Antenna operation was sporadic in 2015, but more consistent in 2016 with all antennas operating from May 27 to October 22 (the first antennas were operational on March 29 and the last on November 11). Antenna detection efficiency was calculated for each antenna in 2016 in approximately two-week segments (between sampling events) as the number of detections at a given antenna divided by the number of tagged fish known to have passed by that antenna.

Growth and age-class determination

Growth was calculated from the recapture of PIT-tagged fish. To eliminate erroneous growth rates due to imprecision in weight or length measurements or resultant from tagging-related stress, fish that were recaptured within 5 days of tagging were excluded from growth analyses. For fish that were recaptured more than once, only data from the final recapture were used. Two of the most common ways to report fish growth are the absolute growth rate and the specific growth rate (Hopkins 1992). Here, I report both growth rate measurements to facilitate comparisons with other studies. The absolute growth rate (expressed in mm•d^{-1}) is the change in length over the number of days between tagging and recapture:

$$GR_{abs} = \frac{L_t - L_0}{t}$$

where

L_t = fish fork length t days after tagging,

L_0 = fish fork length on the day of tagging, and

t = the number of days between tagging and recapture.

The specific growth rate assumes an exponential increase in fish mass and is calculated as,

$$SGR = \frac{\ln W_t - \ln W_0}{t} 100$$

where

W_t = the mass of the fish t days after tagging,

W_0 = the mass of the fish on the day of tagging, and

t = the number of days between tagging and recapture.

The specific growth rate is expressed as % biomass•d^{-1}. Linear regression was used to evaluate the influence of tagging date, recapture date, location, year, and fish size on the absolute growth rate. Tagging and recapture dates were evaluated as the numeric day of the year (1-365). Using the best fitting multiple regression model for predicted growth rate, fish length at time t was then estimated as:

$$L_t = L_0 + \hat{g}t$$

where

L_t = fish fork length (mm) at time t,

L_0 = initial fish fork length,

g = the estimated absolute growth rate (mm•d^{-1}), and

t = the number of days after initial fish capture.

I did not estimate fish length for any fish sampled after September 10th because I assumed growth rate would decrease with falling temperatures. I was unsuccessful in recapturing any tagged Chinook salmon and was therefore unable to explore potential differences in growth rate between Coho and Chinook salmon. I was also unsuccessful in recapturing fish in 2016 that had been tagged the previous year. Thus, growth rates only represent June through early September of each year.

Juvenile salmon age classes were distinguished by fish length. Many studies use fixed thresholds to identify cohorts (e.g. Hoem Neher et al. 2013). However, because sampling took place over multiple months, a moving threshold would be necessary to keep pace with fish growth, yet sample sizes were insufficient to estimate cohort thresholds for each sampling event. Therefore, I used the best fitting model for fish growth from the recapture of tagged individuals to estimate the size of all captured juvenile Coho Salmon on a fixed date (August 1st of each year). I then fit a three-component Gaussian finite mixture model to the estimated length frequency distributions to estimate the age-discriminating thresholds between age 0, age 1, and age 2+ cohorts following a procedure modified from Sethi et al. (2017). This method assumes that the length frequency of each cohort is normally distributed and underlies the observed multimodal distribution of the population. After fitting a three-component Gaussian finite mixture model to the estimated length frequency distribution, a simulated dataset with known group membership was then derived from the fitted mixture model. The unconstrained optimization method of Nelder and Mead (1965) was used to find the threshold lengths between each cohort that minimized the misclassification rate in the simulated data. Finally, I used a bootstrapping procedure to resample the observed data and fit the mixture model to establish confidence intervals for the distribution means and variances, thresholds, and misclassification rate. Cohort length thresholds were determined separately for juvenile Coho Salmon in 2015 and 2016. Because no juvenile Chinook Salmon were recaptured, I applied the growth rates determined for juvenile Coho Salmon to estimate the length of Chinook Salmon. Diet analysis indicated that diet energy ration between the two species was not significantly different (previous chapter) and thus they likely had comparable growth rates within the estuary.

To validate this age classification approach, I used juvenile Coho Salmon length and otolith-determined age data obtained from a 2011 study in the Anchor River estuary (Hoem Neher et al. 2013). Sethi et al. (2017) demonstrated that their method enables discrimination of two juvenile salmon age classes from length data with greater than 95% accuracy. Here, I extend the method to three age classes using length data estimated on a fixed day instead of pooled across sampling events. For the validation dataset, I followed the same procedure as outlined above, using the model for fish growth derived in the present study to estimate the size of all fish on August 1st; age classes were then determined from the estimated length distribution. Predicted age class assignments were compared to the age determined by otolith analysis to calculate the overall accuracy.

Estuarine residence and movement

Estuarine residence time was evaluated by the recapture and detection of PIT-tagged fish. Only those fish that were recaptured or detected >1 day after tagging were evaluated in order to minimize bias due to tag loss, which (if it occurs) is most likely to occur in the first 24 h following tagging (Dare 2003). Because we do not know the residence of fish before tagging and after final detection, the reported estuarine residence times are minimum estimates. I assumed that fish remained within the estuary between tagging and subsequent detection events. This assumption is likely valid for small time scales, but may not hold true for longer time scales (particularly over winter) as juvenile salmon may move back to freshwater or nearshore habitats before returning to the estuary (Miller and Sadro 2003, Hoem Neher et al. 2013, Jones et al. 2014). I generated decay curves for the number of fish at large each day after tagging for all fish detected at a PIT antenna to compare estuarine residence between years and species. A Wilcoxon signed rank test was used to test if the proportion of fish remaining at large each day after release was significantly different between years and between Coho and Chinook salmon in 2016. Analysis of variance was used to evaluate residence duration among Coho Salmon age classes, and student's *t*-tests were used to test the influence of fish size and tagging date on residence duration.

The movement of juvenile Coho and Chinook salmon within marsh channels was evaluated in relation to the tidal stage and time of day. In the Upper Marsh channel, the PIT antennas were located in a channel pool that maintained a depth > 0.5 m at low tide. The antennas in the Lower Marsh channel were located in the shallow (< 0.1 m) reach between the main channel and a sill behind which the channel maintained a pool of approximately 0.3 m depth at low tide. I expected that movement through this portion of the channel would be minimal when the tidal height was insufficient to influence the channel depth. To examine patterns of fish movement by tidal stage, channel depth was normalized around high tide and associated to PIT tag detections by interpolating depth readings recorded immediately before and after each detection. Direction of fish movement was determined by sequential detections at the paired antennas. To minimize errors in direction assignment resulting from fish passing undetected, I established the criteria that the sequential detections must occur within 15 min (median time to pass both antennas in the Lower Marsh channel was 7.7 min for entrance and 2.7 min for exit). For the majority of detections, direction could not be determined because antenna efficiency was low (Table 2). Occasionally, one fish would stay near an antenna for an extended period resulting in inflated detection data for that time and tidal period. To reduce this issue, I restricted the data to include only the first detection per fish per 10 min period at each antenna. Chi-square tests were used to evaluate the number of detections by tidal stage and time of day. A student's *t*-test was used to compare the water depth and tidal stage during entry and exit detections.

Analyses were performed using R 3.3.2 (R Core Team 2016). The *mclust* package (Fraley and Raftery 2002, Fraley et al. 2012) was used to determine age class size distributions.

Results

During the two years of the study, we tagged a total of 2,145 Coho Salmon, Chinook Salmon, and Staghorn Sculpin. Tagged juvenile Coho Salmon were successfully detected at stationary PIT antennas and physically recaptured each year. Juvenile Chinook Salmon were scarce in 2015, and although they were abundant in the main channel in 2016, we were unable to recapture any tagged Chinook Salmon and only approximately 5% were detected at PIT antennas in marsh channels. PIT antennas were successfully used to determine residency and movement of individuals, despite the challenging environment of the estuary that resulted in low detection efficiencies (Table 2).

Growth and age-class determination

Fish growth varied by species and was influenced by date and fish size. Growth rates were calculated from the recapture of 67 Coho Salmon and 4 Staghorn Sculpin (Table 3). Coho Salmon had an average absolute growth rate of 0.33 $mm•d^{-1}$ (SE = 0.002). The mean growth rate for Staghorn Sculpin was 0.95 $mm•d^{-1}$, nearly three times that of Coho Salmon, although the sample size was small. Coho Salmon absolute growth rate ($mm•d^{-1}$) was significantly influenced by tagging date and fish size (multiple linear regression, $F_{2,64} = 18.65$, $p < 0.01$, $r^2 = 0.35$). In general, smaller fish and those tagged earlier in the season had higher growth rates. Year, recapture date, tagging location, and recapture location did not have a significant influence on absolute growth rate. The best fitting equation to predict Coho Salmon absolute growth rate was:

$$\hat{g} = 1.152 - 0.00278t_0 - 0.0353L_0$$

where

g = absolute growth rate (mm•d^{-1})

t_0 = the day of the year (1-365) the fish was tagged, and

L_0 = the initial length of the fish (FL in mm).

Three age classes of juvenile Coho Salmon were successfully distinguished in the Anchor River estuary (Table 4, Figure 2a). Age 1 fish were the dominant size class accounting for nearly half of all Coho Salmon captured. The age 0 and age 2+ cohorts were approximately equal in abundance. This method for determining age classes was successful with an accuracy of 91.4% (32/35 fish correctly assigned to the age determined by otolith analysis from the 2011 validation dataset). This is a substantial improvement over the fixed thresholds proposed by Hoem Neher et al. (2013) which had an accuracy of 68.6% for the same dataset.

Estuarine residence time

Coho Salmon were present in the estuary throughout the sampling period and PIT-tagged individuals showed prolonged rearing in these habitats. Median residence for the three Coho Salmon age classes ranged from 12 - 64 days (Tables 5 and 6). All three age classes resided in the estuary for an extended time with maximum residence > 100 d for all age classes in both years. The longest residence observed for Coho Salmon within one calendar year was 133 days. However, 24 fish that were tagged in 2015 were detected at antennas in the spring of 2016 yielding a maximum of 415 days at large. Nearly all of these fish were last detected in early- to mid-May 2016, at which point they presumably out-migrated to marine habitats as smolts. Although we tagged over 300 Chinook Salmon in 2016, only 5% were detected by PIT antennas and none were recaptured. Observed residence times varied by sampling method (physical recapture or PIT detection; Table 5). This was particularly notable for Coho Salmon, where residence determined by PIT detections was substantially greater than residence determined by recaptures.

In both years, detection rates steadily decreased from the day of tagging (Figure 3). There was a significant difference in the observed estuarine residence (proportion remaining each day following tagging) between Coho and Chinook Salmon in 2016 (Wilcoxon signed rank test: W = 507, df = 132, $p < 0.01$). There was also a significant difference in Coho Salmon residence time between years (Wilcoxon signed rank test: W = 8770, df = 132, $p < 0.01$); however, this difference may be due to a variation in sample timing and antenna operation between years. There was no relationship between fish size and residence time for Coho Salmon (t = -0.90, df = 654, p = 0.37) or Staghorn Sculpin (t = 1.78, df = 17, p = 0.09). However, there was a significant relationship between fish size and residence time for Chinook Salmon (t = -2.69, df = 13, p = 0.02), with smaller fish residing in the estuary for a longer period. For Coho Salmon, there was a significant difference in residence among age classes ($F_{2,624}$ = 10.97, $p < 0.01$), with residence of age 0 fish less than that of age 1 fish (Tukey HSD: $p < 0.01$) and age 2 fish (Tukey HSD: $p < 0.01$), but no difference in residence between age 1 and age 2 fish (Tukey HSD: p = 0.25). There was a significant negative relationship between tagging date and residence time for Coho Salmon (t = -5.56, df = 653, $p < 0.01$), but not for Chinook Salmon (t = -0.78, df = 13, p = 0.45) or Staghorn Sculpin (t = 0.045, df = 16, p = 0.64). It is possible the negative relationship for Coho Salmon between tagging date and residence time is due to PIT antenna sampling constraints: Coho Salmon were still present in the estuary in November of each year when the antennas were decommissioned, thus we were unable to observe longer residence times for fish tagged later in the season.

Fish movement

Juvenile salmon were detected entering and exiting both marsh channels at a range of depths throughout the tidal cycle (Figures 4 and 5). A total of 26,747 detections were recorded for 321 Coho Salmon and 10 Chinook Salmon in the Upper Marsh channel between 25 May and 2 September 2016. In the Lower Marsh channel, a total of 8,477 detections were recorded for 117 Coho Salmon and 7 Chinook Salmon between 25 May and 1 September 2016. Detection trends for the few Chinook Salmon were not discernably different from that of Coho Salmon, so both species were combined for all analyses relating to movement within marsh channels.

Juvenile salmon movement within the two marsh channels reflected the extent of channel connectivity to the mainstem. In the marginally connected Lower Marsh channel, direction of fish movement was discernable for 97 incursions and 112 excursions. Fish were most frequently detected during the outgoing tide (Figure 4C), but there was no difference in tidal stage between entry and exit detections (t = -0.006, df = 125, p > 0.99), nor was there a difference in channel depth between entry and exit detections (t = 0.58, df = 125, p = 0.56). Overall, the number of detections was significantly influenced by tidal stage (x^2 = 605.1, df = 11, p < 0.01). There was also a significant influence by time of day (x^2 = 262.9, df = 23, p < 0.01) with the majority of detections occurring in the morning and evening. However, the tides were confounded with time of day (Figure 4B). In comparison, fish in the continually connected Upper Marsh channel were detected moving upstream 3,349 times and moving downstream 3,361 times. There was no difference in tidal stage between upstream and downstream detections (t = 0.66, df = 2912, p =

0.51). There was a marginal relationship between channel depth and movement direction (t = -1.78, df = 2912, p = 0.076) with movement into the channel occurring at slightly greater depths than movement out of the channel. Although not as dramatic as in the Lower Marsh channel, there was a spike in the number of detections on the outgoing tide (Figure 5C) resulting in a significant relationship between the number of detections and tidal stage ($x^2 = 750.1$, df = 11, $p < 0.01$). There was also a significant influence of time of day on the number of detections ($x^2 = 2073.8$, df = 23, $p < 0.01$), but tides were confounded with time of day (Figure 5B).

Discussion

Information on habitat use is necessary to make informed conservation and management decisions and preparedness strategies for culturally, economically, and ecologically valuable species such as Pacific salmon. Specific information on the growth, residency, and movement of individuals in certain habitats can help prioritize decisions and monitor change. In the present study, I demonstrated that juvenile Coho Salmon, and to a lesser extent Chinook Salmon, make extensive use of estuarine marsh habitat in an Alaskan estuary. Our study is the first to use PIT tag technology to quantify the estuarine residency and growth of juvenile Coho and Chinook salmon in an Alaskan estuary and document the movements of juvenile Coho Salmon within a tidal marsh channel.

Estuarine habitats are generally considered favorable for juvenile salmon growth (Healey 1982, Jones et al. 2014). In the Anchor River estuary, juvenile Coho Salmon had an average absolute growth rate of 0.33 $\text{mm}\bullet\text{d}^{-1}$. This is similar to the 0.32 $\text{mm}\bullet\text{d}^{-1}$ growth rate reported for juvenile Coho Salmon in August and September in a wetland stream in the Susitna River drainage in southcentral Alaska (Davis and Davis 2010). However, these growth rates are generally lower than other studies have reported for estuaries in the Pacific Northwest. Jones et al. (2014) reported average growth rates ranging from 0.29 - 0.7 mm•d^{-1} for age 0 and age 1 Coho Salmon in the Salmon River estuary (Oregon, USA), and McNatt et al. (2016) reported an average growth rate of 0.53 mm•d^{-1} for Chinook Salmon during the summer in the Columbia River estuary (Oregon, USA). Fish growth is a function of food availability and temperature. The energetic value of diet rations we observed in the Anchor River (previous chapter) were comparable to those found in other studies (David et al. 2015), indicating the cooler temperatures in Alaska likely account for the lower growth rates we observed. Optimum rearing temperature for juvenile Coho Salmon is 12° - 15°C (Richter and Kolmes 2005), yet our sampling sites were generally cooler with an average temperature of 11°C. To compensate for reduced growth rates, juvenile Coho Salmon in northern latitudes may remain in freshwater for an additional year to attain a larger size critical for marine survival (Beamish and Mahnken 2001).

We observed three age classes of juvenile Coho Salmon in the Anchor River estuary. Age 0 fish entered later in the summer and showed prolonged residence times. Similarly, studies in the Pacific Northwest have generally found that subyearling (age 0) Coho Salmon tend to enter the estuary later in the summer and rear for extended periods, while yearling (age 1) Coho Salmon enter the estuary in the spring and rear for a few weeks before emigrating to marine habitats, while (Miller and Sadro 2003, Jones et al. 2014, Craig et al. 2014). However, because Coho Salmon in the Anchor River generally do not emigrate until they have completed two full years in freshwater (or estuarine) habitats (Kerkvliet and Booz 2012), age 1 and age 2 fish also showed prolonged estuarine residence. Age 1 fish, in particular, were present in the estuary when we began sampling in the spring and persisted in the estuary through fall when sampling ceased.

The estuary may provide overwintering habitat given that some of the fish tagged in 2015 were detected again in 2016. These fish may have returned to freshwater habitats to overwinter (Miller and Sadro 2003, Koski 2009). However, Hoem Neher et al. (2013) found that around one-quarter of otoliths they examined from Coho Salmon in the Anchor River estuary showed evidence of overwintering in estuarine or nearshore habitats. In freshwater habitats of the Anchor River, juvenile Coho Salmon tend to seek groundwater seeps as refugia that offer warmer temperatures (0.7-2.4°C) and higher oxygen than other freshwater habitats, yet fish in these groundwater habitats either maintain or lose mass through the winter (Gutsch 2012). Estuarine or nearshore habitats may offer warmer temperatures with potential foraging opportunities. Jones et al. (2014) reported substantially higher winter growth rates for juvenile Coho Salmon that reared in the Salmon River estuary than those that were sampled in the upper basin before moving to the estuary. Therefore, the estuary may play an important role in supporting Alaskan juvenile Coho Salmon during the critical winter months, but this has not yet been explored.

The present study was the first to document the movements of PIT-tagged juvenile Coho Salmon within tidal marsh channels. Tidal stage had a strong influence on the number of detections, with most detections occurring shortly after high tide. However, unlike similar studies on Chinook Salmon movement (Hering et al. 2010, McNatt et al. 2016), fish were detected across all tidal stages including very low channel depths. The channels studied by Hering et al. (2010) and McNatt et al (2016) generally emptied with each tide. By contrast, the Lower Marsh channel in our study had a sill near the channel mouth which allowed it to retain water at approximately 0.3 m depth, and the Upper Marsh channel was continuously connected with the main channel with an average depth of approximately 0.5 m. In the Lower Marsh channel, our PIT antennas were positioned in the shallow pool and riffle habitat between the sill and the channel mouth. I had initially hypothesized that fish would not pass through this stretch of the channel until the tide rose enough to fill the channel, similar to the patterns observed in channels that empty with each tide (Hering et al. 2010, McNatt et al. 2016). Contrary to our expectations, fish were frequently detected at the antennas when the channel depth was not influenced by the tide. The observed detection pattern in the Upper Marsh channel was closer to what I anticipated: fish freely utilized the habitat throughout the tidal cycle with a peak of detection activity following high tides.

Although our antenna detection efficiencies were not high enough to permit us to determine residence times within specific channels, the combination of antenna detections, recaptures, and detection with a portable PIT reader indicate that some juvenile salmon likely inhabited the Lower Marsh channel for several days. The number of detections generally decreased during the neap tidal cycle, such that there would be several days where no fish would be detected passing the antennas, yet we would recapture tagged fish within the channel during this period. This indicates that tidal channels that retain water at low tide provide more consistent habitat than those that fully drain with each tide, yet full channel connectivity allows continual access to marsh channel habitat, potentially an important consideration when planning marsh restoration or prioritizing habitats for conservation.

Alaskan resources face challenges on multiple fronts. The economy of Alaska has long been centered around resource extraction. Pacific salmon support multimillion dollar commercial (Knapp et al. 2007) and recreational (Romberg et al. 2008) fisheries, as well as vital subsistence fisheries (Fall et al. 2015). Yet, the environments that support healthy salmon populations also yield profitable resources such as timber and mineral deposits, creating challenges in the co-management of resources. Additionally, Alaska is experiencing an increase in human population and urbanization, which places further pressure on habitats that support juvenile salmon (Ourso and Frenzel 2003). Because human populations tend to concentrate around waterways and near coasts, estuaries receive a disproportionate impact (Vitousek et al. 1997). Furthermore, climate change is predicted to have a strong impact in Alaska, with substantial increases in temperature and precipitation predicted for the Cook Inlet Basin (Kyle and Barbets 2001). The impact of these changes on juvenile salmon is not fully known and may not be entirely detrimental. For example, increased winter precipitation might decrease egg and fry survival due to scour, while slightly warmer temperatures could increase growth rates thereby increasing survival of juvenile salmon. Warming temperatures could also result in a shift towards early-maturing life histories (Bryant 2009). In the face of this multitude of challenges, it is vital to understand how juvenile salmon rearing habitat relates to key life history traits. Our results demonstrate that estuarine habitats support multiple age classes of juvenile Coho and Chinook salmon for prolonged periods, potentially contributing to the life history diversity and resiliency of their populations.

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Tables

Table 1. Characteristics of the tidal marsh channels sampled in the Anchor River estuary.

	Marsh Channel A	Marsh Channel B
Total channel network length	1,104 m	497 m
Distance from sampling location to main channel	322 m	143 m
Distance from lower PIT antenna to main channel	Array 1: 318 m Array 2: 311 m	68 m
Substrate composition	80% silt, 20% coarse gravel	100% silt
Mean temperature	9.2 °C	11.8 °C
Mean salinity	5.0 psu	5.8 psu
Mean dissolved oxygen	5.3 mg•L^{-1}	6.8 mg•L^{-1}
Mean turbidity	2.5 ntu	5.3 ntu

Note: Temperature, salinity, dissolved oxygen, and turbidity values are averaged across all point measurements taken at each sampling event between 25 May – 10 September 2016.

Table 2. PIT antenna detection efficiencies for 2016.

	Upper Marsh, Array 1		**Upper Marsh, Array 2**		**Lower Marsh**	
Date range	**Upstream antenna**	**Downstream antenna**	**Upstream antenna**	**Downstream antenna**	**Upstream antenna**	**Downstream antenna**
May 24 – June 7	–	0.28	0.38	0.53	0.57	0.57
June 7 – June 22	–	0.35	0.10	0.42	0.53	0.00
June 22 – July 7	–	0.30	0.65	0.44	–	0.50
July 7 – July 19	–	0.00	0.71	0.00	0.50	0.00
July 19 – Aug 9	0.27	0.22	0.67	0.41	0.78	0.00
Aug 9 – Sept 2	0.65	0.50	0.42	0.53	0.40	0.40
Overall	*0.56*	*0.35*	*0.44*	*0.47*	*0.54*	*0.39*

Note: Dashes indicate that no tagged fish were released upstream of the antenna during that sampling period and thus detection efficiency could not be calculated.

Table 3. Absolute and specific growth rates obtained from the recapture of tagged juvenile Coho Salmon and juvenile Staghorn Sculpin. Absolute growth rate is given for both length and mass to facilitate comparison with other studies.

			Average Growth Rate (SE)		
	Year	n	mm•d^{-1}	g•d^{-1}	%mass•d^{-1}
Coho Salmon					
	2015	31/21*	0.29 (0.027)	0.08 (0.0072)	1.21 (0.13)
	2016	36	0.36 (0.022)	0.08 (0.0059)	1.43 (0.12)
Staghorn Sculpin					
	2016	4	0.95 (0.082)	0.36 (0.13)	2.92 (0.24)

*In 2015, length measurements of 31 fish were used to calculate absolute growth (mm•d^{-1}); however, for growth rates based on fish mass, imprecise or missing weight measurements reduced the sample size to 21.

Table 4. Age class length (mm FL) distributions and age discriminating thresholds for Coho Salmon determined by a Gaussian 3-component mixture model using estimated fish fork length on August 1st of each year. Values are given as estimates with 95% confidence intervals in parentheses.

	Age-0	Age-1	Age-2
2016 (n=890)			
Proportion	0.26	0.49	0.25
Mean	53.2 (52.2-54.1)	86.9 (85.8-88.3)	104.5 (102.7-106.6)
Variance	55.1 (47.7-61.8)	55.1 (47.7-61.8)	55.1 (47.7-61.8)
Upper threshold	69 (68-70)	97 (96-100)	--
		Misclassification rate: 0.09 (0.07-0.11)	
2015 (n=1240)			
Proportion	0.28	0.41	0.32
Mean	55.5 (52.4-58.1)	77.3 (72.6-80.1)	92.9 (91.0-94.5)
Variance	110.7 (89.1-129.9)	110.7 (89.1-129.9)	110.7 (89.1-129.9)
Upper threshold	64 (60-68)	87 (81-91)	--
		Misclassification rate: 0.26 (0.20-0.32)	
2011 validation data (n=35)			
Proportion	0.24	0.36	0.40
Mean	41.8 (34.6-52.0)	85.1 (77.5-95.6)	122.1 (114.7-129.6)
Variance	122.2 (55.3-175.3)	122.2 (55.3-175.3)	122.2 (55.3-175.3)
Upper threshold	62 (56-71)	103 (96-113)	--
		Misclassification rate: 0.04 (0.01-0.13)	

Table 5. Estuarine residence times and number of fish tagged, recaptured, and detected at stationary PIT arrays by species and year.

	Number Tagged	Number Recaptured	Number Detected	Residence (days), by PIT detection Mean ± SD	Median	Maximum	Residence (days), by recapture Mean ± SD	Median	Maximum
Chinook Salmon									
2015	5	0 (0%)	0 (0%)	–	–	–	–	–	–
2016	305	0 (0%)	15 (5%)	19.0 ± 10.3	15	42	–	–	–
Coho Salmon									
2015	1016	45 (4%)	300 (30%)	66.0 ± 76.6	42	415	18.6 ± 14.5	16	70
2016	708	36 (5%)	379 (54%)	35.6 ± 30.4	23	133	33.3 ± 19.5	33	77
Staghorn Sculpin									
2015	44	0 (0%)	3 (7%)	70 ± 104	13	190	–	–	–
2016	67	5 (8%)	16 (24%)	18.1 ± 14.8	14	60	28.5 ± 25.3	17	62

Table 6. Estuarine residence times for each age class of juvenile Coho Salmon.

	Number Tagged	Number Recaptured	Number Detected	Residence (days), by PIT detection Mean ± SD	Median	Maximum
2015						
Age 0	100	1 (1%)	31 (31%)	27.0 ± 33.4	12	115
Age 1	468	16 (3%)	71 (15%)	76.7 ± 73.5	64	318
Age 2	349	28 (8%)	167 (48%)	70.5 ± 79.3	45	415
2016						
Age 0	89	6 (7%)	55 (62%)	26.2 ± 24.3	15	108
Age 1	283	21 (7%)	186 (66%)	34.3 ± 26.7	27.5	112
Age 2	235	9 (4%)	138 (59%)	41.2 ± 35.9	25.5	133

Figures

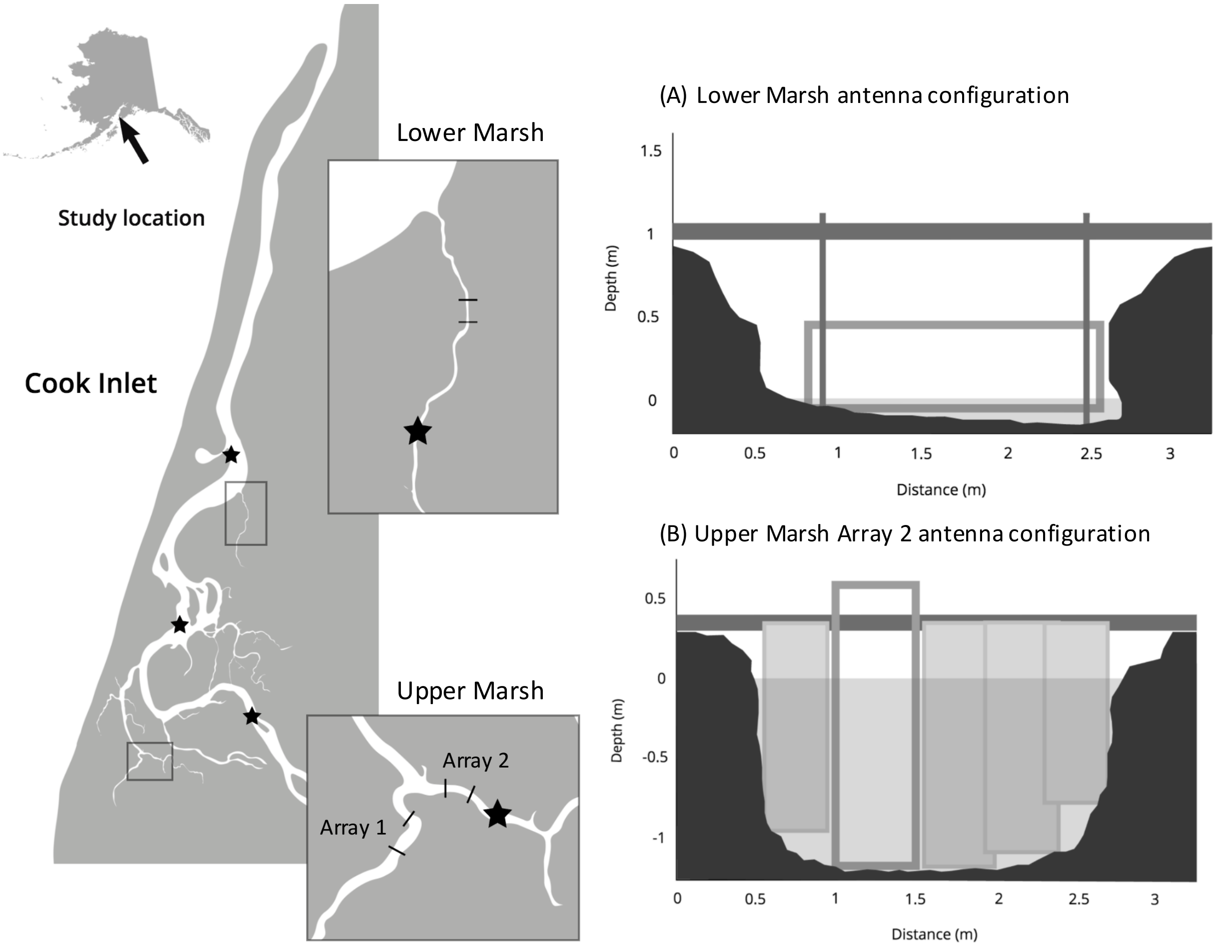

Figure 1. Sampling locations (stars) within the Anchor River estuary, southcentral Alaska. Insets show a close-up view of the marsh channels fitted with PIT antennas (black lines). Panels on the right provide cross-sectional schematics of PIT antennas used in the Lower Marsh (A) and Upper Marsh Array 2 (B). Black polygons represent approximate channel cross-sectional profiles, shading within the channel represents average water depth at low tide, open grey rectangles represent PIT antennas, solid light grey rectangles represent rubber mats used to direct fish through the antenna.

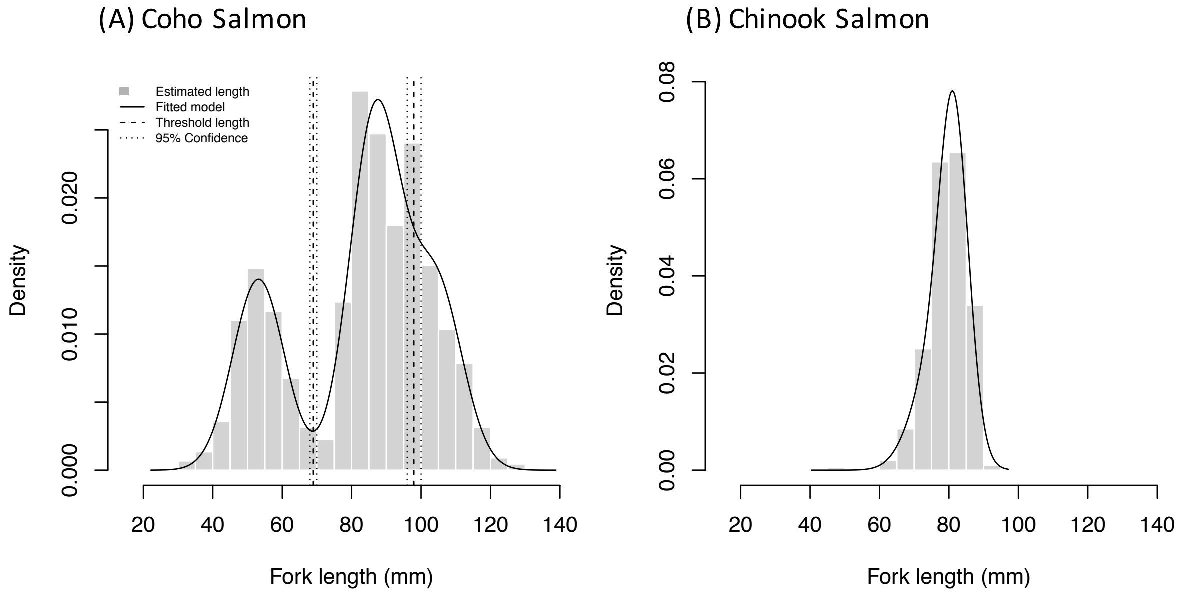

Figure 2. Length frequency distributions and fitted Gaussian mixture models for (A) Coho Salmon (n = 890) and (B) Chinook Salmon (n = 400) in the Anchor River estuary in 2016. Growth rates obtained from the recapture of marked fish were used to estimate the length on August 1st of all fish sampled from May 24 - Sept 10. Dashed vertical lines give the age-discriminating thresholds (with 95% confidence intervals) between the three age classes of Coho Salmon.

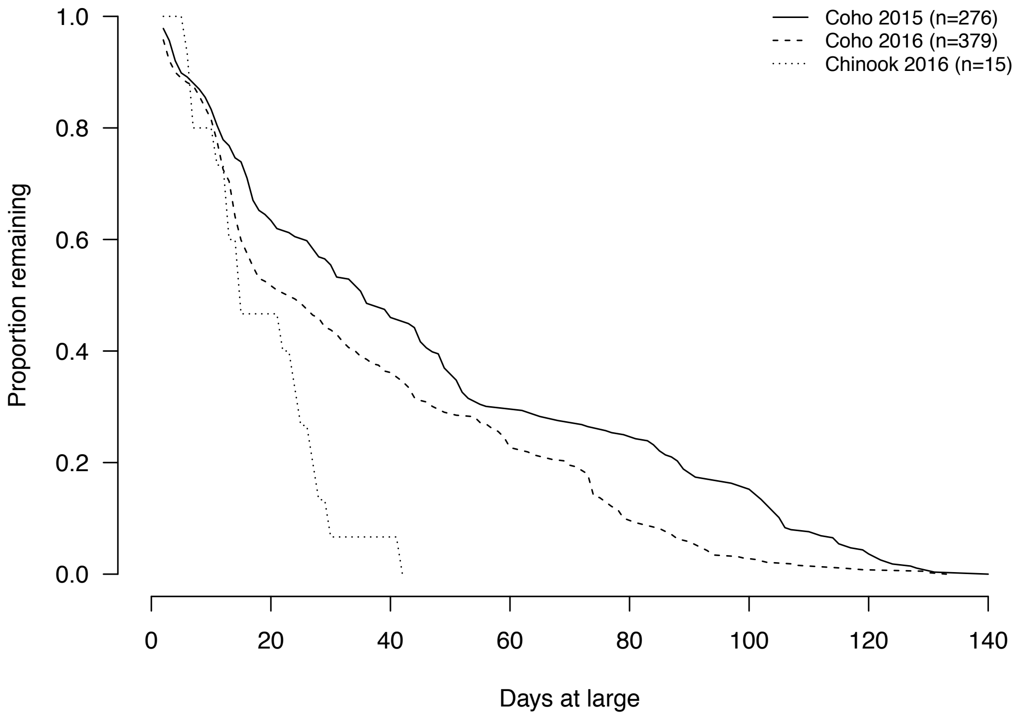

Figure 3. Decay curves of the proportion of juvenile salmon detected at PIT antennas after tagging and release in the Anchor River estuary. The 2015 data were truncated to exclude detection of fish tagged in 2015 that were detected in 2016 since comparable data are not available for fish tagged in 2016.

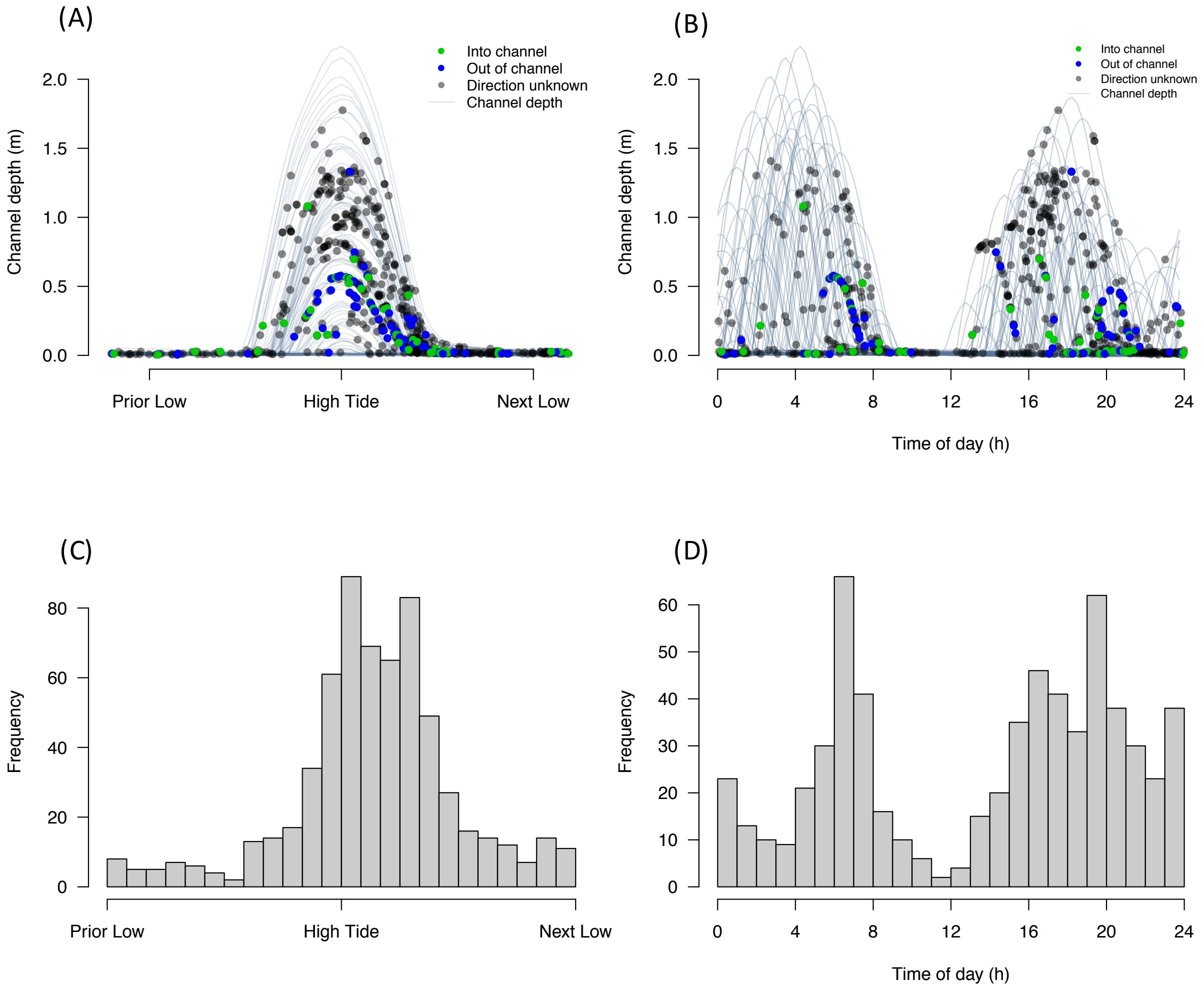

Figure 4. Detections of PIT-tagged juvenile Coho and Chinook salmon by tidal stage, channel depth, and time of day in the marginally connected Lower Marsh channel between 25 May and 1 September 2016. The upper panels display channel depth by normalized tidal stage (A) and by time of day (B). Points denote a PIT tag detection and are colored by movement direction (black points representing unknown direction of movement are semi-transparent to reduce over-plotting). The lower panels show the frequency of PIT tag detections by tidal stage (C) and by time of day (D). Fish could easily pass undetected when PIT antennas were fully submerged at channel depths ≥ 0.6 m.

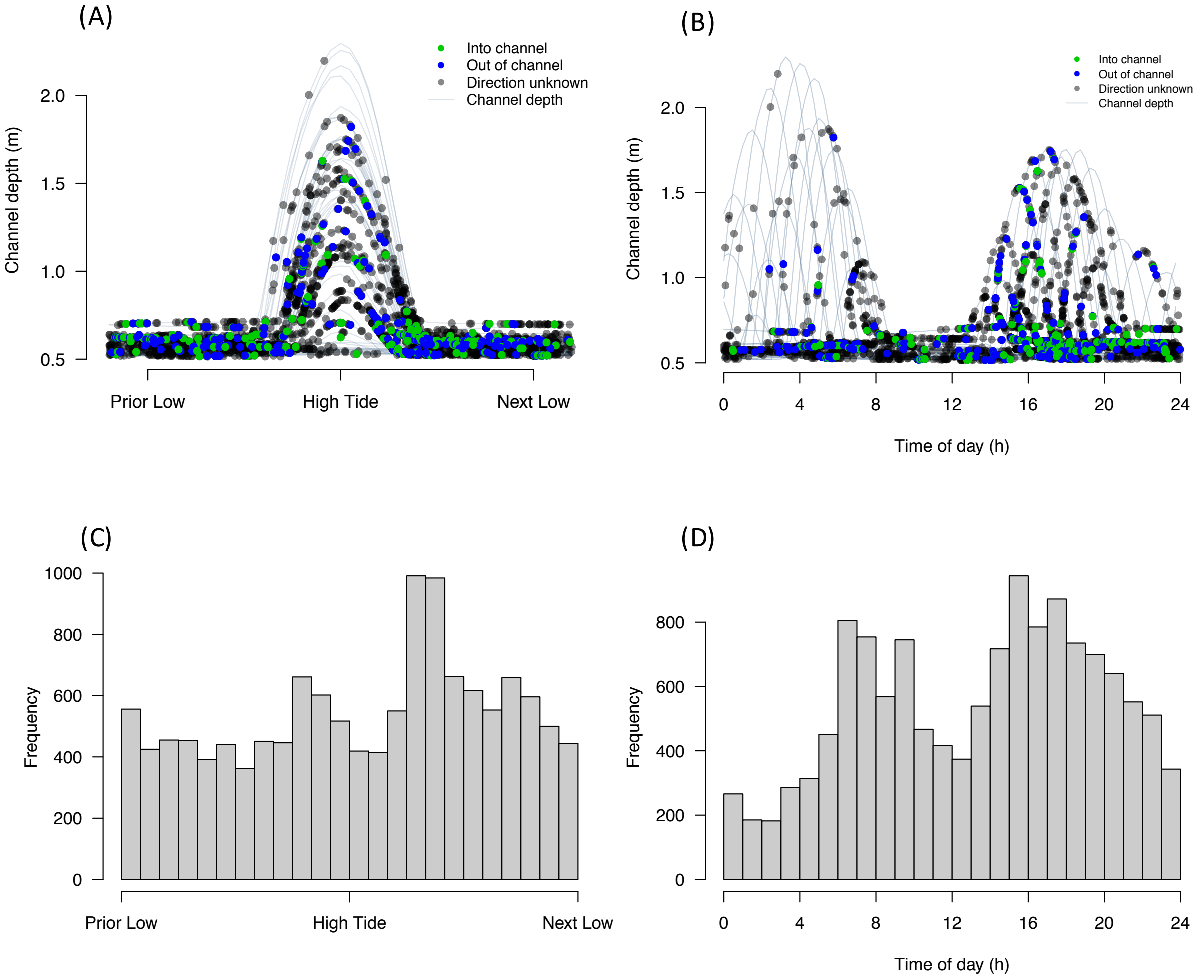

Figure 5. Detections of PIT-tagged juvenile Coho and Chinook salmon by tidal stage, channel depth, and time of day in the continuously connected Upper Marsh channel. The upper panels display channel depth by normalized tidal stage (A) and by time of day (B) for July 2016. Points denote a PIT tag detection and are colored by movement direction (black points representing unknown direction of movement are semi-transparent to reduce over-plotting). The lower panels show the frequency of PIT tag detections by tidal stage (C) and by time of day (D) between 25 May and 2 September 2016. PIT antennas became submerged when the channel depth was approximately > 1 m.

CHAPTER 3: FISHY FRIENDS OR COMMON HANG-OUTS? PRELIMINARY EXPLORATION OF JUVENILE PACIFIC SALMON SOCIAL STRUCTURE USING A DYNAMIC SOCIAL NETWORK ANALYSIS

Abstract

Social relationships between individual organisms can have profound influences on the ecology of populations, including the spatial and temporal distribution of individuals. Individuals may co-occur over time because they form preferential associations or because they independently exhibit fidelity to the same habitat. Social network analysis has emerged as a powerful way to describe the social structure of animal groups. In the present study, I present a preliminary exploration of the presence and stability of associations among individual juvenile Coho Salmon *Oncorhynchus kisutch* in the Anchor River estuary, southcentral Alaska, USA. Beginning with a data stream of timestamped detections of PIT-tagged fish, I create a dynamic social network to explore how individual relationships persist or change through time. Initial results indicate that juvenile Coho Salmon do not form strong individual associations but tend to break and form new associations regularly. This study demonstrates the feasibility of using a temporal data stream of fish detections to infer social relationships and examine their persistence through time.

Introduction

Animal social behavior influences ecological and evolutionary processes at every level of biological organization, from individuals to ecosystems (Wilson 1975, Kurvers et al. 2014). Beyond a fundamental understanding of animal behavior, the nature of interactions among individual organisms has implications in such topics as the transmission of information (Couzin et al. 2005) or disease (Drewe and Perkins 2014), mate selection (Pizzari and Gardner 2012), foraging success (Marshall et al. 2015), and predator avoidance (Croft et al. 2006). Furthermore, social relationships may be confounded with or superimposed upon observed ecological patterns such as species distribution in a heterogeneous environment and site fidelity (Wolf et al. 2007). Thus, it is beneficial to consider the social context of individuals in conjunction with population-level ecological patterns.

The impetus for the present study developed from observations during a study on the habitat use and movement patterns of juvenile Coho Salmon *Oncorhynchus kisutch* in an Alaskan estuary (Chapter 2). Fish tagged with passive integrated transponder (PIT) tags showed strong site fidelity in tidal marsh channels. Although fish would occasionally venture between marsh channels, the vast majority of detections at stationary antennas within each channel were from fish tagged within that channel weeks or months previously. Furthermore, it was not uncommon for simultaneously recaptured fish to have been tagged during the same sampling event, even if tagging was 4-6 weeks prior to recapture. This led to the question: Do juvenile Coho Salmon form and maintain stable relationships for prolonged periods? Or were fish observed together at tagging and recapture merely because they shared common site fidelity? Similarly, do fish prefer to school with similarly sized fish? I used a dynamic social network analysis to address these hypotheses.

Within the last decade, social network analysis has emerged as a powerful tool for studying animal social interactions (Krause et al. 2007, Wey et al. 2008, Croft et al. 2008). A social network is a formalized way of describing who interacts with whom, and consists of discrete entities (“nodes” or “vertices”) that can be connected by some interaction (“links” or “edges”) (Croft et al. 2008). In the present study, nodes represent individuals and links represent joint group membership. Associations among individuals and, thus network structure, change over time as groups break up and new associations are formed. Network theory provides a quantitative framework to evaluate static, temporal, and spatial patterns in social interactions that are formed at the level of individuals but influence groups and populations.

My specific objectives were to:

(1) determine if a social network could be constructed from detections of PIT tagged fish and if/how networks constructed from different antennas differed, and

(2) conduct preliminary explorations to test the hypotheses that

  (a) fish maintain social connections through time, and

  (b) fish preferentially associate with similarly sized fish.

Methods

Network construction

A primary and highly influential step in animal social network analysis is determining what constitutes an association or link between individuals (Castles et al. 2014). While some studies can directly observe an interaction, many must infer an interaction, often through spatial and temporal co-occurrence (Whitehead 1997). One co-occurrence methodology, often referred to as "gambit of the group," assumes that all individuals that co-occur in space and time comprise a "group" and all members of the group associate with all other members of the group. While gambit of the group may be subject to sampling biases (Franks et al. 2009), technological advances in automated data collection yield considerably larger datasets than traditional sampling methods, providing a greater degree of certainty in inferred associations (Farine and Whitehead 2015).

In the present study, observational data consists of timestamped detection records of PIT-tagged fish passing stationary, in-channel antennas. Thus, social interaction or group membership is not readily apparent and must be inferred. One way to infer associations from temporal data is to divide the data stream into discrete time intervals and assume an interaction between individuals detected during the same interval (Lauw et al. 2005, Krings et al. 2012). However, the time interval is assumed to be fixed throughout the data stream and the selection of the interval size influences the resultant social network (Psorakis et al. 2012). Alternatively, when detection events are clustered in time (like when a school of tagged fish swims past an antenna) a Gaussian mixture model can be used to identify detection-rich portions of the data stream and assign group membership based on the probability of detections belonging to each group (Psorakis et al. 2012).

I applied the group detection methods of Psorakis et al. (2012) to temporal data streams obtained from the detection of PIT-tagged juvenile Coho Salmon. For fish sampling and tagging procedures, see Chapter 2. As this is an initial exploration, I reduced the extent of the data to only those detections that occurred in July 2016. I excluded fish that were tagged after June 30th so that the appearance of new tags would not obscure temporal patterns. Occasionally, a single fish would remain near the antenna and generate hundreds of detections in the span of a couple of minutes, thereby artificially inflating the detection density. Therefore, I reduced the dataset to keep only the first detection per minute for each tag (commercially available PIT tag readers often perform similar 1-minute unique detection reductions automatically). Using the methods of Psorakis et al. (2012), clusters of detection events were identified using a Gaussian mixture model such that detections occurring closely in time were assigned to the same gathering event (i.e. group). This method assumes that each detection is a draw from a mixture of K Gaussian distributions and uses a machine learning algorithm to determine the appropriate number of clusters K and assigns each detection to a cluster k based on its posterior probability (for model specifics, see Supplementary Material in Psorakis et al 2012). This results in an observation-by-group matrix, which can be reduced to an individual-by-group matrix. The individual-by-individual *adjacency matrix* (or *sociomatrix*) can then be constructed where each cell represents the total number of co-occurrences (joint group membership) for each pair of fish. The values of the adjacency matrix are effectively link weights between each pair of individuals. There are additional association indices that can be used, including the simple ratio association index or half-weight association index which may be particularly appropriate for gambit of the group data inferred from spatio-temporal data stream observations (Psorakis et al. 2015). Furthermore, randomizations can be used to test if associations are greater than would be observed in a random network (Krause et al. 2009). However, for the present, I have simply used the link weights or binary presence/absence of association.

Network analysis

Psorakis et al. (2012) constructed their social networks using data of PIT-tagged birds detected at 16 antennas placed near feeders. However, in our system, each antenna had a unique configuration based on the physical characteristics of the channel at that location and correspondingly varied in detection efficiency. Additionally, channel depth and connectivity influenced habitat use (see Chapter 2). Therefore, I postulated that the network structure would vary among sites. To evaluate this, I compared the networks derived from detections at three antennas (upstream antenna of Lower Marsh, upstream antenna of Upper Marsh Array 1, and downstream antenna of Upper Marsh Array 2; Figure 1).

I used a dynamic network approach to evaluate if juvenile Coho Salmon maintained stable relationships over time. The data stream was divided by day, and an association matrix was computed for each day. The association matrices were used to construct binary networks, where a link was present between two fish if they co-occurred at least once during that day. If juvenile

Coho Salmon maintain relationships, this link would be expected to perpetuate at each time step (or at least at each time step where the fish were present). Conversely, if juvenile Coho Salmon exhibit fission-fusion relationships, we would expect to see associations continually break and form over time.

Once a network has been established, further social patterns can be explored using the attributes of the individuals in the network. To explore this, I tested if juvenile Coho Salmon preferentially associated with similarly sized conspecifics, a pattern that has been observed in other fishes (Croft et al. 2005). I created a matrix of the size (fork length) differences between each pair of fish. Because fish were measured and tagged on different dates, I used the fish lengths estimated on a fixed date (see Chapter 2 for growth rate and size estimation). A Mantel test was used to test the correlation between the size difference matrix and the aggregate (full month) association matrix for each antenna.

Adjacency matrices were constructed in MATLAB R2017a (The MathWorks, Inc. 2017) using the script *GMMevents* from Psorakis et al. (2012). Further analyses and data visualization were conducted in R 3.3.2 (R Core Team 2016) using the following packages: *networkDynamic* (Butts et al. 2016), and *ndtv* (Bender-deMoll 2016). Data visualization also utilized the MDSJ Java library (Algorithmics Group 2009).

Results

In July 2016, 43 Coho Salmon were detected 256 times at the Lower Marsh antenna and composed 31 groups. At the Upper Marsh Array 1, 41 fish were detected 299 times comprising 70 groups, and at Array 2, 113 fish were detected 1,499 times comprising 151 groups. As anticipated, network topology varied considerably among antennas (Figure 2). I selected data from the Array 1 antenna for the dynamic network analysis. While several Coho Salmon were present for multiple days during the month, they did not show stable social associations, with the possible exception of two fish that were detected together on six non-consecutive days (Figures 3 and 4). By animating the dynamic network on a daily time step (Video S1) we can see how individual associations change over time and contribute to the aggregated (full month) static network depicted in Figure 2B. The number of detected fish varied considerably from day to day with few detections during the moderate neap tides (approx. July 9-17). Thus, environmental factors influenced the observed social patterns. Juvenile Coho Salmon did not preferentially associate with fish of similar size (Table 1). However, this might change when a more appropriate association index is used (see Discussion).

Discussion

The findings in this preliminary study indicate that juvenile Coho Salmon do not appear to maintain stable relationships, but exhibit the patterns of a fission-fusion society where associations between individuals dissolve and re-form on a regular basis. This would indicate that individuals likely co-occur due to joint site fidelity as opposed to preferential association. This has important implications, as the spread of both information and disease is influenced by network connectivity (Croft et al. 2005, Wey et al. 2008). However, even in groups with high fission-fusion dynamics, individuals may be able to maintain lasting relationships (Kerth et al. 2011) or at least preferential associations (Croft et al. 2005). The analyses presented here are rather preliminary and will benefit from more rigorous evaluation. I used either binary links (presence/absence of association) or links weighted by the number of times two individuals co-occurred in a group. However, for data where individuals are present but not detected, the half-weight index is considered to give a less-biased estimate of association (Whitehead 2008). Metrics such as the lagged association rate (Whitehead 2008) or the [perhaps unfortunately named] lagged rate of association (Farine 2013) will allow a more formalized way of evaluating the persistence or stability of associations between fish. Additionally, the observed relationship stability patterns will need to be tested against an appropriate null network that maintains the social grouping structure while permuting the identities of individuals. Future work will incorporate the use of these metrics and appropriate null models.

To my knowledge, this is the first study to utilize a detection time series from PIT-tagged fish to construct a social network, which is, perhaps, surprising because some of the earliest animal social networks were develop for fish populations (Wilson et al. 2014), and PIT tag technology has long been used in the study of fishes (Prentice et al. 1990). However, the present study does bring to light certain challenges and considerations when using PIT tag data streams to explore fish social patterns. The unique habitat characteristics at each antenna and the antenna configurations themselves resulted in markedly different network topologies that are not directly comparable. This differs from the studies of PIT-tagged birds detected at essentially identical feeding stations (Psorakis et al. 2012, 2015, Farine et al. 2015). Additionally, in the present study as well as in most fish PIT tag studies, only a fraction of the population was tagged. Thus, care must be taken in interpreting network results; network-level (and some node-level) metrics should be avoided (Farine and Whitehead 2015). Despite these considerations, social networks developed from timestamped detections of PIT-tagged fish have the potential to provide valuable insight into how associations between pairs of individuals influence population-level patterns, which in turn influence the ecology and evolution of the species.

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Tables

Table 1. Mantel's test results for the correlation between the association matrix and a matrix of the pairwise size difference (fork length) of juvenile Coho Salmon. The association matrices were either weighted by the number of times two fish co-occurred in the same group or were binary for the presence or absence of joint group membership.

	Range of size	Weighted associations		Binary associations	
Antenna	differences	Mantel's *r*	*p*	Mantel's *r*	*p*
Lower Marsh	0-41 mm	0.027	0.22	0.021	0.31
Upper Marsh, Array 1	0-25 mm	0.008	0.42	0.007	0.46
Upper Marsh, Array 2	0-46 mm	-0.14	1	-0.13	0.99

Figures

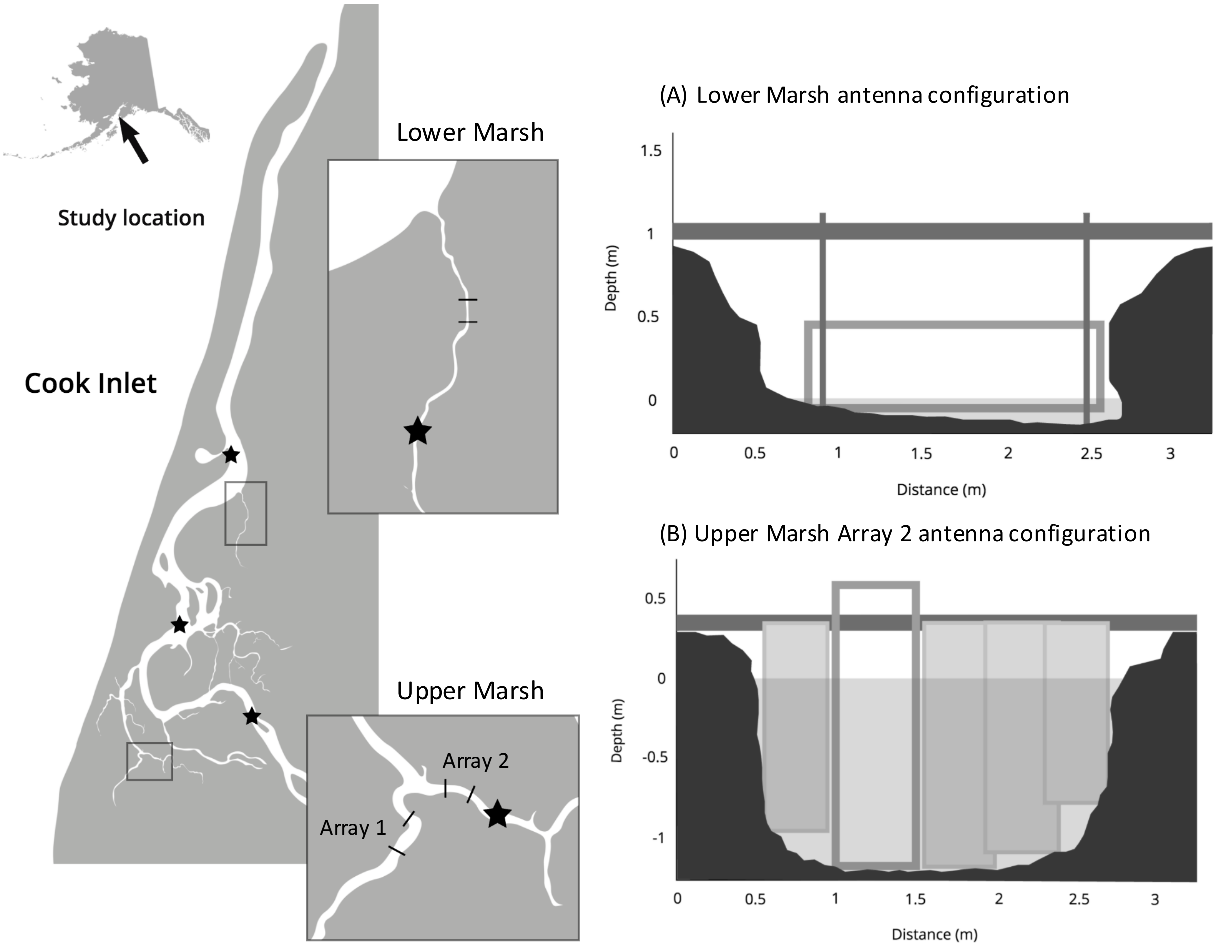

Figure 1. Location and design of PIT antennas used to collect the temporal data stream used in this study. Stars indicate locations where Coho Salmon were tagged and released. Insets show a close-up view of the marsh channels fitted with PIT antennas (black lines). Panels on the right provide cross-sectional schematics of PIT antennas used in the Lower Marsh (A) and Upper Marsh Array 2 (B). Black polygons represent approximate channel cross-sectional profiles, shading within the channel represents average water depth at low tide, open grey rectangles represent PIT antennas, solid light grey rectangles represent rubber mats used to direct fish through the antenna. Only data from the upstream antenna at the Lower Marsh, upstream antenna of Array 1, and downstream antenna of Array 2 were used in the present study. The upstream Array 1 antenna was similar in design to the Lower Marsh antenna, although water maintained a depth of 0.3 m in that channel.

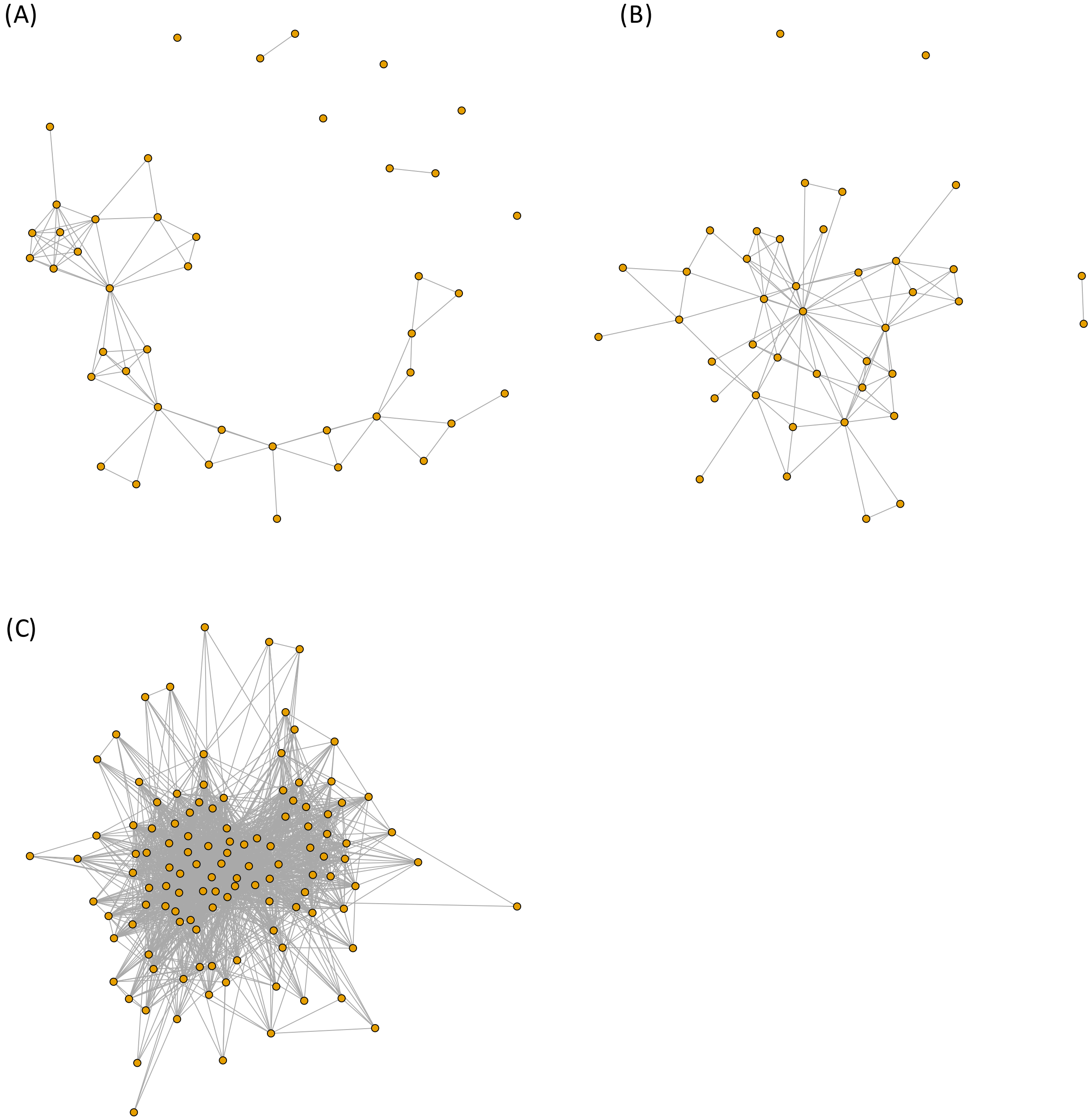

Figure 2. Social networks for juvenile Coho Salmon detected at antennas in the Lower Marsh (A) and Upper Marsh Array 1 (B) and Array 2 (C) in July 2016. Nodes represent individual fish, and links represent associations inferred from joint group membership. Links are weighted such that fish that occur together more frequently are closer together in the graph.

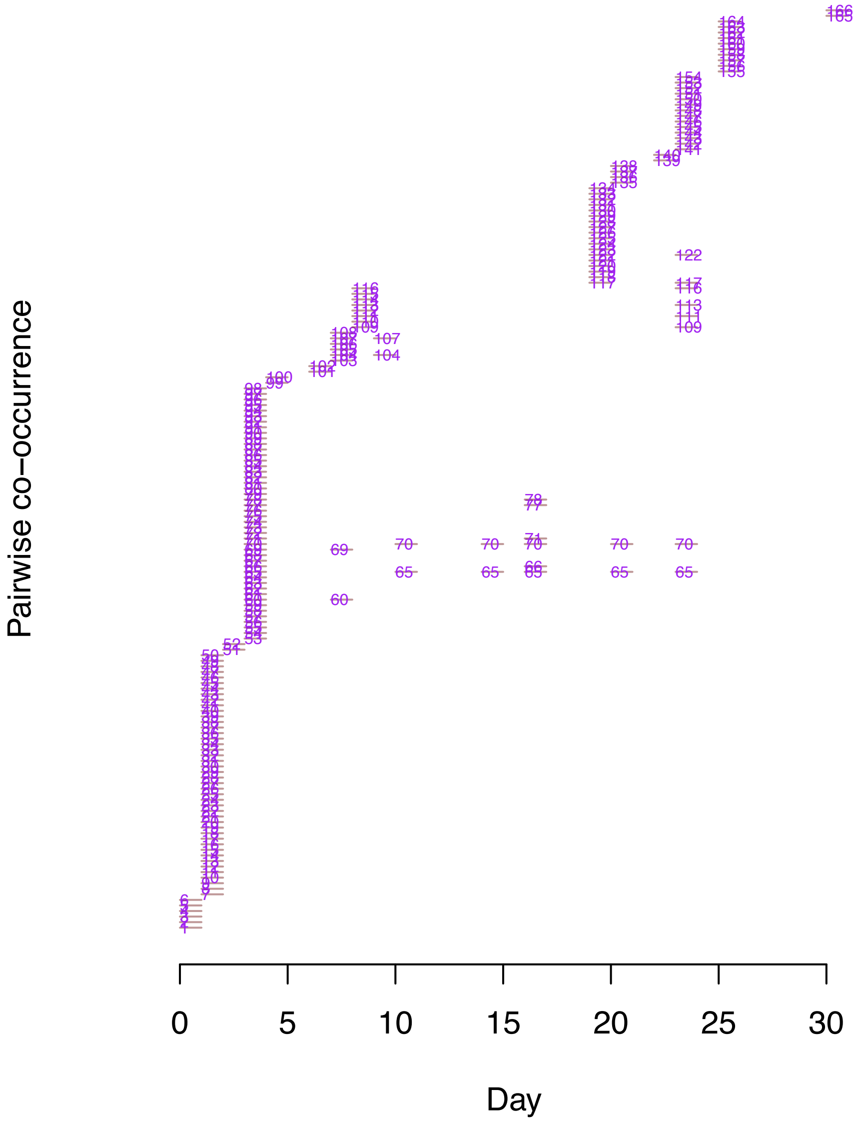

Figure 3. Timeline of pairwise associations of juvenile Coho Salmon (N=41). Each segment (numbered to facilitate identification over time) represents a co-occurrence of two tagged fish. Note that no fish pairs were detected together on consecutive days and most pairs only co-occurred once.

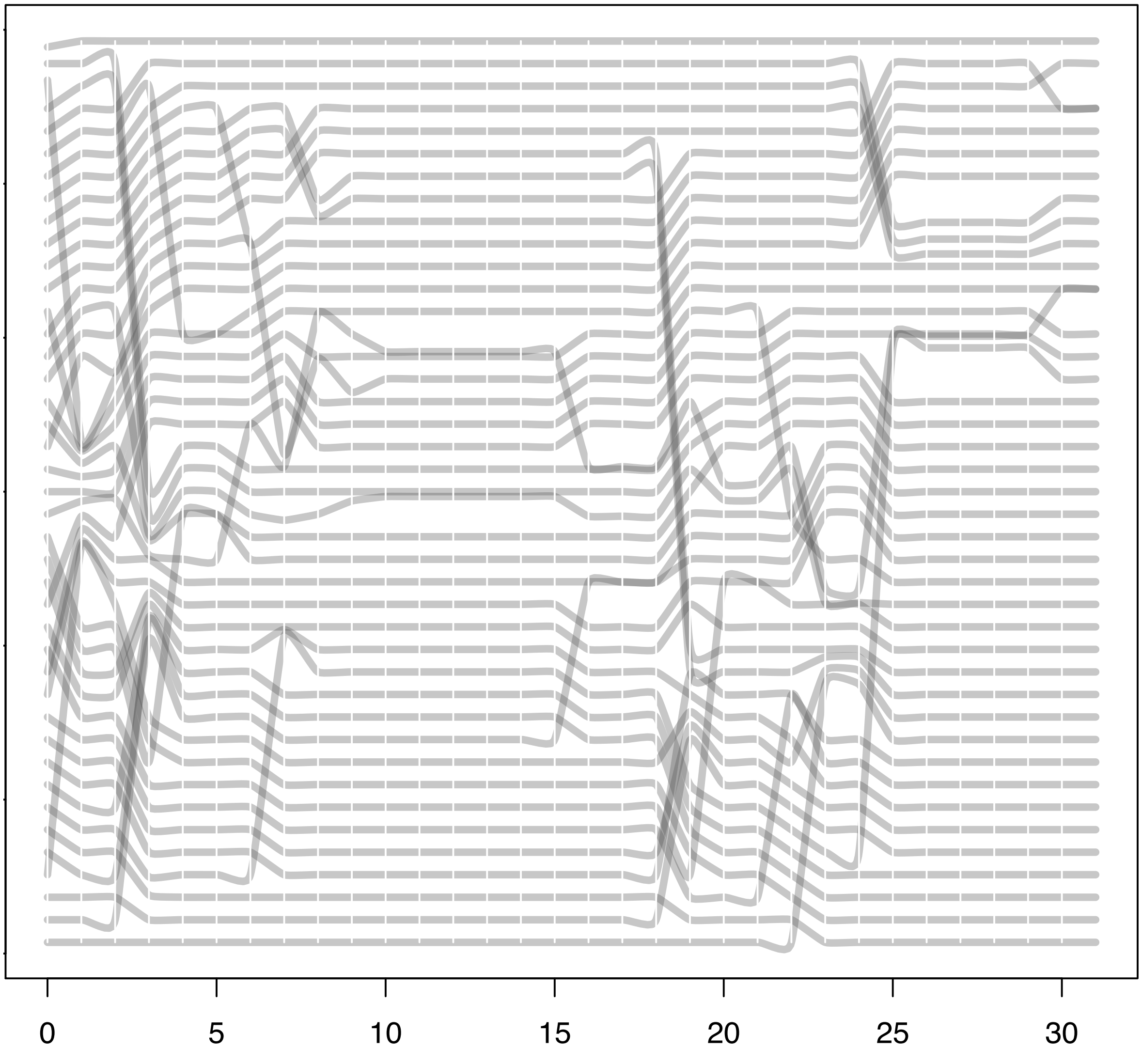

Figure 4. Proximity timeline of fish associations. Each line represents an individual fish (initial ordering on the y-axis is arbitrary). When fish associate, their lines shift so that they are together for that time period. Note that there are distinct gathering events, followed by a period of few detections, and then another series of gathering events with new associates.

APPENDIX

Table A1. Diet composition by frequency of occurrence (*FO*), prey-specific percent number (*%PN*), prey-specific percent weight (*%PW*), and Prey-Specific Index of Relative Importance (*%PSIRI*) for juvenile Coho and Chinook salmon during the late-June sampling events at Main Mid and Main Down (these were the only two sampling events that had adequate (n ≥ 6) sample sizes for both species).

				Coho Salmon (n = 15)				Chinook Salmon (n = 16)			
Prey Taxa				FO	%PN	%PW	%PSIRI	FO	%PN	%PW	%PSIRI
Arachnida							*0.1*				*2.1*
	Acari							6.3	58.7	8.0	2.1
	Araneae			6.7	1.5	0.9	0.1				
Clitellata											
Collembola				13.3	18.2	2.3	1.4				
Insecta							*57.5*				*84.7*
	Coleoptera			20.0	2.4	6.2	0.9				
	Diptera						*49.9*				*81.4*
		Brachycera		26.7	3.3	10.7	1.9	12.5	3.6	33.4	2.3
		Nematocera					*42.8*				*73.1*
			Unidentified Nematocera	6.7	0.7	1.7	0.1	12.5	1.4	4.3	0.4
			Chironomidae, adult/emergent	20.0	3.8	9.2	1.3	31.3	20.0	23.2	6.8
			Chironomidae, larva	66.7	14.3	5.9	6.7	81.3	38.0	32.5	28.7
			Chironomidae, pupa	93.3	42.2	32.2	34.7	93.8	42.7	36.9	37.3
		Unidentified Diptera, larva		20.0	16.2	36.1	5.2	12.5	44.2	51.8	6.0
	Hemiptera							12.5	1.6	4.4	0.4
	Hymenoptera			13.3	1.8	0.9	0.2	12.5	1.4	3.3	0.3
	Orthoptera			6.7	5.6	59.0	2.2				
	Plecoptera, nymph			13.3	5.8	4.4	0.7	25.0	3.4	14.9	2.3
	Thysanoptera, nymph							6.3	6.7	3.8	0.3
	Unidentified Insecta, larva			20.0	13.6	23.9	3.8				
Crustacea							*34.2*				*11.0*
	Amphipoda			60.0	56.9	46.0	30.9	37.5	25.8	27.4	10.0
	Decapoda, larva			6.7	4.3	8.4	0.4				
	Arguloida			13.3	3.7	6.9	0.7	6.3	0.6	31.1	1.0
	Harpacticoida			6.7	33.9	15.1	1.6				
	Other Copepoda			20.0	5.5	0.3	0.6				
Teleostei	Teleostei, larva/juvenile			20.0	3.8	64.1	6.8	6.3	26.3	46.6	2.3

Note: Italicized *%PSIRI* values are sums of the constituent taxa.

Table A2. Diet composition by frequency of occurrence (*FO*), prey-specific percent number (*%PN*), prey-specific percent weight (*%PW*), and Prey-Specific Index of Relative Importance (*%PSIRI*) for juvenile Coho Salmon at each sampling event (all sites combined).

	Late-June (n = 36)				Early-August (n = 28)				Early-September (n = 15)			
Prey Taxa	FO	%PN	%PW	%PSIRI	FO	%PN	%PW	%PSIRI	FO	%PN	%PW	%PSIRI
Arachnida				*1.4*				*3.0*				*2.4*
Acari					17.9	14.0	8.0	2.0				
Araneae	22.2	5.1	7.8	1.4	7.1	5.3	24.8	1.1	26.7	7.2	10.9	2.4
Clitellata									6.7	100.0	100.0	6.7
Collembola	33.3	36.8	13.0	8.3	32.1	57.4	26.2	13.4	26.7	49.4	36.4	11.4
Gastropoda					3.6	10.0	96.4	1.9				
Insecta				*61.4*				*55.0*				*36.7*
Coleoptera	27.8	3.5	12.3	2.2	7.1	8.7	24.2	1.2				
Diptera				*51.7*				*42.0*				*31.7*
Brachycera	36.1	3.0	17.2	3.7	17.9	4.4	31.8	3.2	26.7	22.3	37.2	7.9
Nematocera				*43.7*				*35.7*				*23.8*
Unidentified Nematocera	11.1	3.2	28.5	1.8	10.7	21.1	34.7	3.0	13.3	24.2	1.4	1.7
Chironomidae, adult/emergent	50.0	8.9	17.1	6.5	14.3	19.8	6.5	1.9	13.3	4.8	18.6	1.6
Chironomidae, larva	69.4	31.5	10.1	14.4	60.7	30.2	17.7	14.6	40.0	37.0	24.8	12.4
Chironomidae, pupa	80.6	27.1	25.0	21.0	50.0	38.3	26.8	16.3	46.7	18.5	16.5	8.2
Unidentified Diptera, larva	22.2	9.7	29.4	4.3	14.3	16.9	25.5	3.0				
Ephemeroptera					14.3	25.5	18.9	3.2				
Hemiptera	16.7	12.5	26.0	3.2	3.6	3.1	26.1	0.5				
Hymenoptera	11.1	3.0	4.0	0.4	7.1	9.9	37.7	1.7	13.3	29.2	12.3	2.8
Orthoptera	2.8	5.6	59.0	0.9								
Plecoptera, nymph	16.7	3.3	5.2	0.7	14.3	16.2	12.9	2.1				
Thysanoptera, nymph	2.8	1.3	4.5	0.1	3.6	1.4	7.6	0.2	6.7	14.3	17.5	1.1
Trichoptera, nymph												
Unidentified Insecta, larva	19.4	9.8	13.9	2.3	17.9	18.2	29.7	4.3	13.3	10.5	6.2	1.1
Crustacea				*25.4*				*26.4*				*28.0*
Amphipoda	52.8	32.5	32.4	17.1	46.4	40.2	61.2	23.5	53.3	45.6	49.3	25.3
Decapoda, larva	2.8	4.3	8.4	0.2								
Arguloida	5.6	3.7	6.9	0.3	3.6	2.9	4.3	0.1				
Harpacticoida	11.1	66.4	38.9	5.9	3.6	71.9	64.6	2.4	6.7	78.3	3.8	2.7
Other Copepoda	25.0	12.1	3.6	2.0	7.1	2.8	6.6	0.3				
Ostracoda	2.8	1.4	0.6	0.0								
Teleostei				*3.4*				*0.2*				*14.8*
Teleostei, egg	2.8	0.8	0.7	<0.1					13.3	38.3	69.8	7.2
Teleostei, larva/juvenile	11.1	7.9	52.3	3.3	3.6	7.7	1.9	0.2	20.0	20.6	55.0	7.6

Note: Italicized *%PSIRI* values are sums of the constituent taxa.

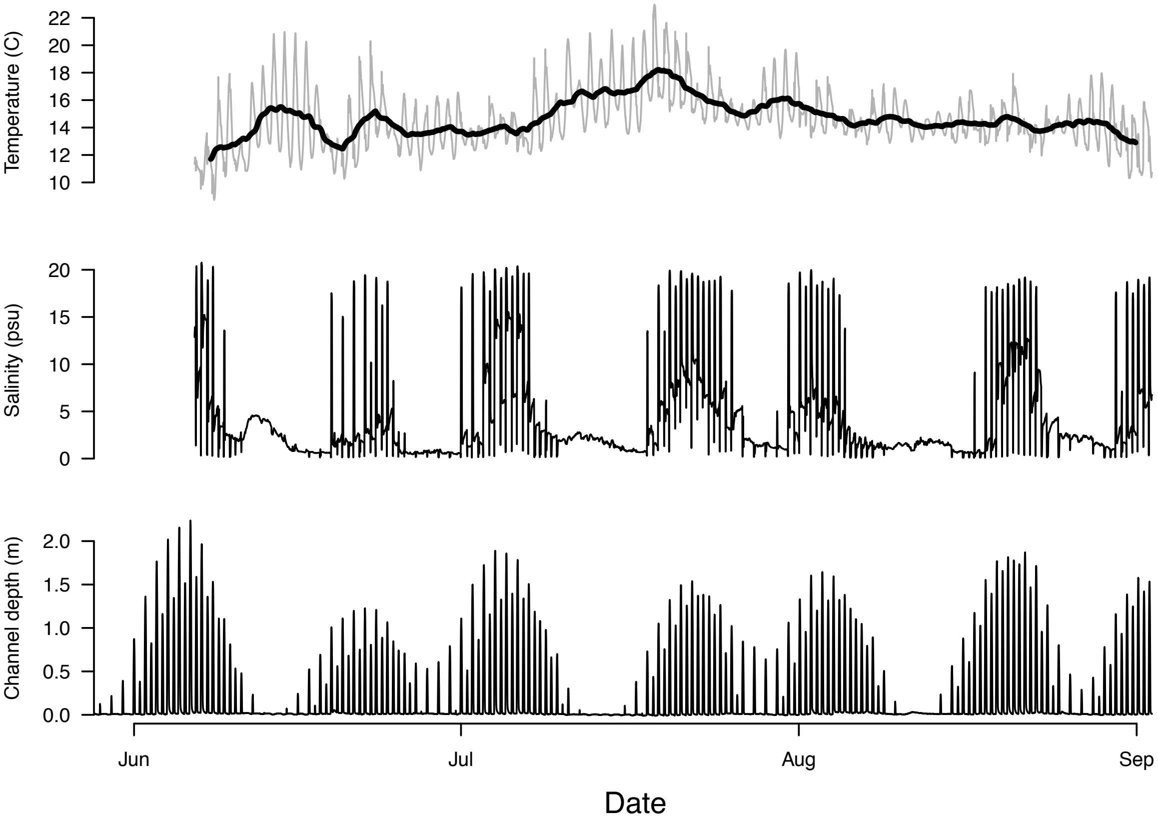

Figure A1. Time series of environmental variables recorded at the in-channel loggers in the Lower Marsh channel in 2016. Temperature is presented as the observed value (grey line) and three-day running average (black line).

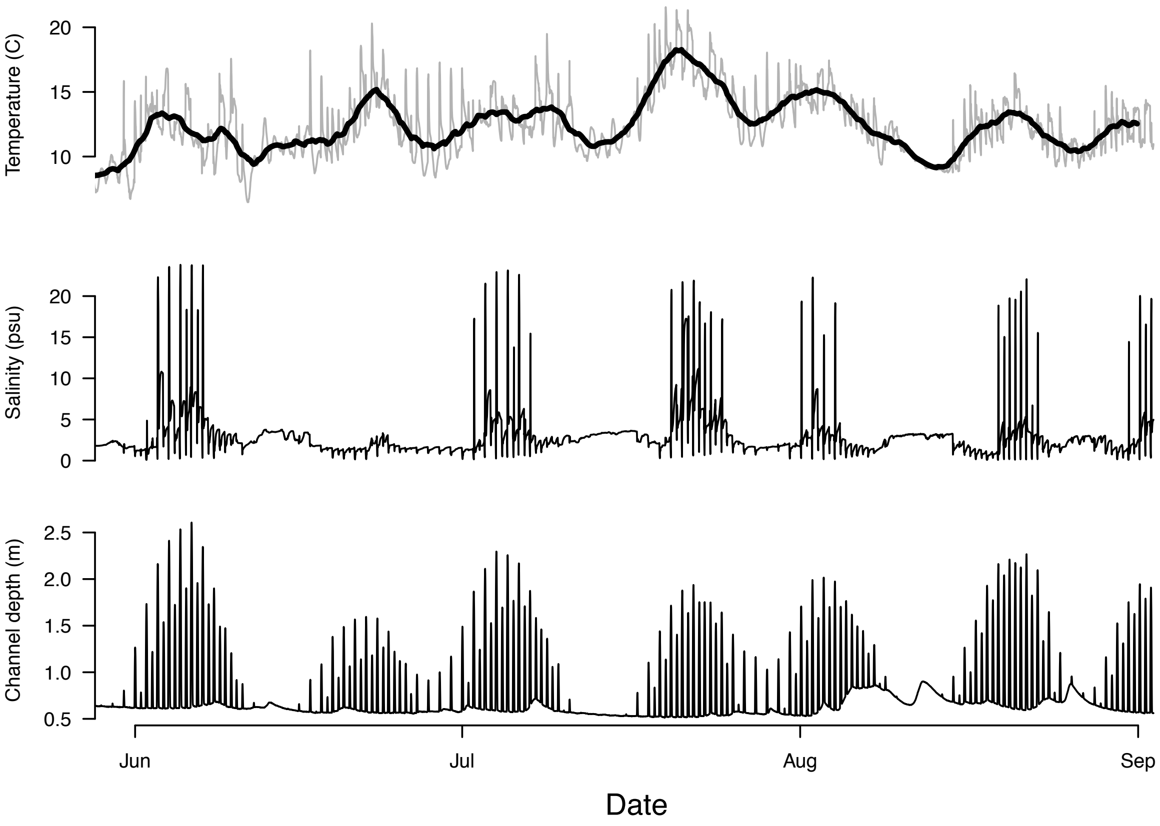

Figure A2. Time series of environmental variables recorded at the in-channel loggers in the Upper Marsh channel in 2016. Temperature is presented as the observed value (grey line) and three-day running average (black line).

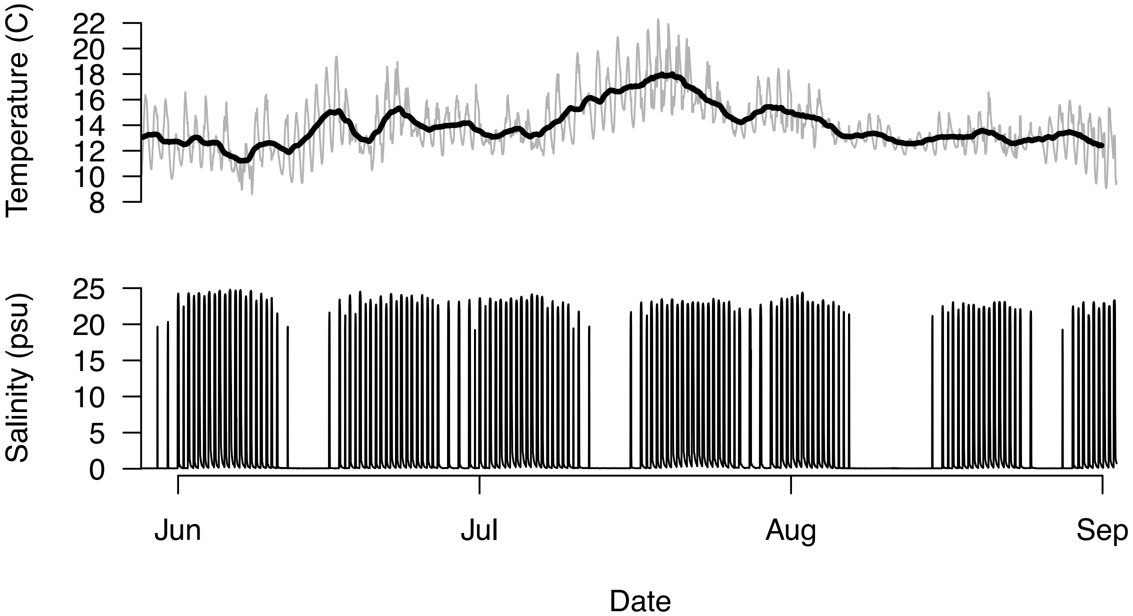

Figure A3. Time series of environmental variables recorded at the in-channel loggers in the main channel near the Main Down sampling site in 2016. Temperature is presented as the observed value (grey line) and three-day running average (black line).