Fish community dynamics and nursery habitats in an undeveloped estuary

by

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Thesis Submitted in Partial Fulfillment of the
Requirements for the Degree of
Master of Science

in the
Department of Biological Sciences
Faculty of Science

SIMON FRASER UNIVERSITY
Spring 2020

Approval

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Date Defended/Approved:	January 31, 2020

Ethics Statement

Abstract

Estuaries are potentially critically-important fish habitats. However, their temporal and spatial dynamics challenge understanding of the nursery functions of estuaries. Working in the Koeye River estuary in British Columbia, I used size-spectra analysis to infer production and predation risk across the estuary habitat mosaic and track their changes through the season. The brackish mudflat habitat exhibited the highest fish production and lowest inferred predation risk, suggesting that this area had particularly high nursery value. Spectra coefficients were seasonally dynamic, indicating that temporal shifts in the spatial patterns of risks and reward. I also investigated the potential effects of climate change on the distributions of different estuarine fish assemblages by comparing two climatically-divergent sampling seasons. Marine-oriented species expanded their range up-estuary during the dry, more saline year, but freshwater species did not shift. Collectively, this research advances understanding of the spatio-temporal dynamics of estuary nursery functions.

Keywords: estuary; nursery habitat; habitat mosaic; size-spectra; community dynamics; climate change; *Oncorhynchus* spp.

I dedicate this thesis to all of the wonderful, beautiful, strange, fishy people I’ve encountered since embarking on this piscatorial pursuit. The kindness you showed, the guidance you gave, and the experiences you shared with me have made this journey all the more magical and unforgettable. And I cannot thank you enough for that.

Acknowledgements

This thesis would not have been possible without the help, guidance, and support of numerous people and organizations. First and foremost of those people is Jon Moore, who after only a few emails and a phone call, offered me a position in his lab and then didn’t hear from me for 5 months because I was off gallivanting with bears and swimming with sockeye deep in the Alaskan bush. Thank you so much for all of your trust, guidance, support, and most of all patience. It’s been a long, winding road to this moment, thank you for not losing faith. And where would I be without Will Atlas? You brought me to Koeye, introduced me to Bella Bella, and almost immediately trusted me to keep your field research program afloat in your absence. You built an amazing program and continue to make it better. I look forward to learning more and more from you as we continue to work together and thank you for all that you’ve done for me.

Thank you to Larry Jorgenson, Jess Housty, Louisa Housty, William Housty, everyone at QQs Projects Society, and the whole Kvai Family for all of the field support you have provided to me and the trust you had in me. A huge thank you to all of the field technicians who put up with the long, gruelling hours of seining I made you do, especially Jared Reid, Jeremy Jorgenson, and Richard Wilson-Hall, you guys rock! Thank you to all my Central Coast friends for hanging out and letting me crash on your couches, especially Al LaLiberte, Megan Humchitt, and Allison Dennert and the rest of the Reynold lab crew. Thank you to Ben Millard-Martin and all of the other Hakai folks who came by and seined and seined and seined with me. And thank you to the Heiltsuk Nation as a whole for allowing me to live and work in your beautiful territory for 3 years now.

A special thanks to my other committee members, Brian Hunt and Leithen M’Gonigle, for your helpful guidance and constructive feedback in the preparation of this thesis. Thank you to Michael Arbeider for your friendship and helping me get my field work off the ground. Thank you to Kyle Wilson, Emma Hodgson, and Sam Wilson for sharing your statistical and coding knowledge with me. Thank you to the rest of the Moore Lab and the whole E2O crew, it has been great getting to know you all during my brief office stints between Koeye deployments.

Thank you to all of the organizations which helped fund this research: the Liber Ero Foundation, the Pacific Salmon Foundation, and the McLean Foundation. A very special thanks to Eric Peterson and Christina Munck of the Tula Foundation/Hakai Institute who have generously funded all of the projects at Koeye, supported me through a Mitacs internship, and provided logistical support, sensor data, and given me the opportunity to spend some time working with their staff at their beautiful Calvert Island field station.

I owe a great deal to my parents Michael and Marianne Seitz and want to thank them for all of their love and support through the years even though we don’t always see eye to eye. Thank you to all of my family and friends who support me even though they don’t quite understand what exactly it is that I do, but always have interesting ideas (wrestle bears, fish whisper, date sasquatch). And thank you to my best friend Ryan Santilli who constantly encourages me to leave this life behind and move to Colorado so my friendship can be more convenient to him, maybe one day buddy, one day.

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Chapter 1. Introduction

Estuaries are the highly dynamic transition zones connecting terrestrial freshwaters to the sea (Daborn and Redden 2016). These ecosystems are some of the most biologically productive on the planet, but also some of the most economically valuable (van den Belt 2011). Being at the interface between land and sea, these areas are highly prized by humans, with more than half of the global population living within the coastal zone (Sheaves et al. 2015; Vitousek et al. 1997; van den Belt 2011). Increasing population pressure worldwide has led to rapid, large-scale development in coastal wetland habitats (Sheaves et al. 2015), causing widespread degradation and diminishing ecosystem health (Waycott et al. 2009). The intense threats to these regions of high ecological value makes a detailed understanding of their natural functionality imperative if we hope to manage and protect them for future generations (Elliott and Kennish, 2011).

Estuaries are well known to act as critical nursery grounds for numerous ecologically and economically important fish species (Beck et al. 2001). The shallow, protected waters of estuaries are often turbid and filled with aquatic vegetation, providing juveniles with refuge from predators as well as productive foraging grounds (Rozas and Odum 1988; McIvor and Odum 1988; Levings 2016). Estuary ecosystems are not homogeneous however, but rather are composed of a mosaic of habitat types and juvenile fish tend to show preferences for some habitat types over others (Sheaves 2009; Daborn and Redden 2016). Being naturally dynamic systems, estuarine salinity, temperature, and flow regimes are constantly changing (Fulford et al. 2014; Daborn and Redden 2016), necessitating frequent movement by resident fishes in order to find suitable conditions for their physiology (Selleslagh and Amara 2008; Nagelkerken et al. 2015). Habitat diversity and connectivity are thus essential for optimal nursery function, allowing for juvenile fish to move among the habitat patches as their needs and the conditions change (Sheaves 2009; Nagelkerken et al. 2015; Sheaves et al. 2015).

Estuaries are some of the most dynamic environments on the planet, experiencing major shifts in environmental conditions on the scale of hours or even minutes in cases of extreme tidal flux, but these ecoclines are also subject to change on much longer time scales, such as those being induced by global climate change

(Peterson et al. 2007; Daborn and Redden 2016). Climate change is anticipated to affect the dynamics and structure of estuaries in a myriad of ways, such as: more variable flow regimes, increased water temperatures, inundation, fragmentation, and inland retreat of habitats, and increased up-river saltwater intrusion (Roessig et al. 2004; Gillanders et al. 2011; James et al. 2013; Fulford et al. 2014; IPCC 2014; BC Ministry of the Environment 2016). These long-term and large-scale changes to the estuary environment are predicted, and in some places already being observed, to alter resident fish species distributions and community structure (Love et al. 2008; Gillanders et al. 2011; James et al. 2013; Fulford et al. 2014; Munsch et al. 2019). As nursery habitats for a variety of species, climate-induced changes to estuary ecosystems could have far-reaching effects as any influence on juvenile survival or fitness will alter adult populations which may be vital to distant ecosystems or human communities (Roessig et al. 2004; James et al. 2013; Fulford et al. 2014; Munsch et al. 2019).

This thesis explores how estuary fish distribute themselves across the habitat mosaic, what factors influence those distributions, and how these distributions may be altered in the face of global climate change. My first data chapter (Chapter 2) examined nursery function across the estuary mosaic through the use of size-spectra analysis. My second data chapter (Chapter 3) examined the environmental factors that influence estuary fish community structure and how the distributions of species assemblages differ between years of divergent climatic regimes. Together, these chapters provide insight into the interplay between physical habitat, environmental conditions, and community structure across estuary ecoclines.

My research focused on field sampling at the Koeye River estuary on the Central Coast of British Columbia during 2017 and 2018. The Koeye River watershed is small (180 km2), but relatively pristine, having experienced little industrial development and minimal amounts of logging. The estuary is ~5 km long from the top of tidal influence to where the river empties into Fitz Hugh Sound. Along it’s length there are 6 distinct habitat types; 1) sandy beaches, 2) eelgrass beds, 3) rockweed mudflats, 4) main channel salt marsh, 5) side channel salt marsh, and 6) tidal river. Multiple sites in each habitat type were sampled for fish community and water quality metrics every 10-14 days from April through September each year and continuously running sensors recorded weather conditions and river flow, resulting in a spatially- and temporally-extensive dataset on fish and environmental conditions.

In Chapter 2, I apply size-spectrum theory to investigate nursery function in the various habitats found in the Koeye estuary. Size-spectra analysis utilizes the distribution of organism body sizes as indicators of ecosystem structure and function (Giacomini et al. 2016). Body size is well known to be correlated with important physiological and ecological processes and is especially relevant in aquatic systems where predator-prey dynamics are often dependent on the size relationship between individuals (Giacomini et al.2016). In open ocean systems, while small individuals greatly outnumber large individuals, the total biomass of each size class is approximately equal (Sheldon et al. 1972). By plotting a measure of abundance as a function of some metric of body size in logarithmic space, one can use the coefficients from the resulting regression, or size-spectra, to study various properties of community structure and ecosystem health (Kerr and Dickie 2001; Guiet et al. 2016). Spectra slopes (λ) measure the relative frequency of body sizes in a community and have been found to be closely related to predator-prey dynamics (Platt and Denman 1978; Kerr and Dickie 2001; Giacomini et al. 2016; Perkins et al. 2018). Intercepts (Γ) have been found to correspond to ecosystem production and are influenced heavily by environmental conditions and nutrient availability (Boudreau and Dickie 1992; Maury et al. 2007; Guiet et al. 2016). High productivity and low predation risk are often cited as the key attributes that estuaries possess which makes them nursery grounds for so many species (Dahlgren and Eggleston 2000; Cocheret de la Morinière et al. 2002; Nagelkerken et al. 2015; Sheaves et al. 2015). For my abundance versus body mass size-spectra, I interpreted the slopes as a measure of predation risk and the intercepts as a measure of production. This allowed me to compare nursery functions of the individual habitat types and track how those values changed across the growing season. I found that the middle estuary mudflat habitat had the lowest median predation risk and the highest median productivity among all of the habitats, indicating this area likely had the highest nursery value for juvenile fish. I also found that size-spectra fluctuated across the season and that these fluctuations correlated with observed biological events. These results provide rare empirical evidence of seasonal shifts in size-spectra across multiple habitats, lending support to the theory that fish can maximize their foraging opportunities while minimizing risk by “surfing” the size-spectrum (Pope et al. 1994), as well as the theory that habitat diversity and connectivity are vital to optimal nursery function (Peterson 2003; Nagelkerken et al. 2015).

In Chapter 3, I investigated how shifting environmental mosaics altered fish community structure and species' distributions. In British Columbia, weather is predicted to become much more variable as global warming continues with summer growing seasons becoming warmer and drier than historic norms (BC Ministry of Environment 2016). As a result, estuaries are likely to experience decreased freshwater input during summer, which should increase saltwater intrusion into the upper reaches of the estuary (BC Ministry of Environment 2016; Munsch et al. 2019). Climate change is also predicted to result in significant sea level rise, which would further increase saltwater intrusion (Roessig et al. 2004; Fulford et al. 2014; BC Ministry of Environment 2016). My two sampling years, 2017 and 2018, were very different climatically; 2017 would be considered typical for the region, while 2018 was extremely dry. This allowed me to investigate how different resident fish species' distributions may be altered as a result of climate change's impact on the estuary environment. Grouping fish according to their salinity tolerances, I modelled their probability of presence across the estuary during each sampling year and found that saltwater-oriented species were able to expand their range and utilize more estuary habitat during the dry year, but the more freshwater oriented species showed no change in distribution between years. These results suggest that increased saltwater intrusion in estuaries due to climate change could be a benefit to marine species, allowing for increased available habitat, but may be a detriment to freshwater species through increased osmotic stress and competition (Love et al. 2008; Fulford et al. 2014).

I conclude this thesis with a brief chapter (Chapter 4) reviewing my key findings and their implications, as well as discussing some caveats of my work and future directions of this research. Overall, my research provides rare empirical evidence and insights into estuary fish community dynamics and nursery function. Insight into how fishes distribute themselves in response to both biotic and abiotic factors could prove valuable to the assessment of critical habitat areas within estuarine environments. Much research has been performed in estuaries that are already highly impacted by humans, such as the Fraser and Columbia Rivers, but data is lacking from pristine sites due to their scarcity and remoteness. This makes my work in the Koeye all the more important as it reveals how estuary ecosystems would function in the absence of anthropogenic influence, providing a baseline for comparative studies with more highly developed sites.

Chapter 2. Size-spectra analysis in the estuary: assessing fish nursery function across a habitat mosaic[1]

2.1. Abstract

Estuaries act as nurseries for a wide variety of fish species, providing vital foraging opportunities and refuge from predation for their juvenile residents. These dynamic environments are comprised of a mosaic of habitat types that span gradients of both salinity and physical habitat structure. Here we present a novel use of size-spectra analysis to infer nursery habitat function across the estuary habitat mosaic. Interpreting slope and intercept values of abundance against body mass size-spectra regressions as indicators of predation risk and production, we constructed spectra for six distinct habitat types across the entire tidal influence of an unindustrialized estuary in coastal British Columbia. Based on catches of >200,000 individual fish representing 30 different species from April through September, the estuary rockweed mudflat habitat had the lowest size-spectra slope and highest intercept, indicative of lower predation risk and higher production. Size-spectra coefficients varied seasonally across the ecotone, indicating spatio-temporal variation in key nursery functions. Size-spectra can provide insight into key ecological processes of productivity and predation risk across dynamic aquatic habitats.

2.2. Introduction

Coastal wetlands, such as estuaries, salt marshes, mangroves and seagrass meadows, are some of the most productive and ecologically significant ecosystems on the planet, yet they are also among the most threatened (van den Belt, 2011). Estuarine environments are notably important to juvenile fishes, providing foraging opportunities, reduced predation risks, and a mosaic of habitats suitable for a variety of life stages (Dahlgren and Eggleston 2000; Peterson 2003; Nagelkerken et al. 2015). Juvenile fish should seek out habitats where there is the best potential to maximize growth and the

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[1] A version of Chapter 2 has been submitted and is in review for the journal *Ecosphere*, with coauthors William I. Atlas, Benjamin Millard-Martin, Jared Reid, Julian Heavyside, Brian P. V. Hunt, and Jonathan W. Moore.

lowest potential for mortality (Werner and Gilliam 1984; Dahlgren and Eggleston 2000; Cocheret de la Morinière et al. 2002). As such, estuaries have been dubbed as nurseries by many scientists, conservation groups, managers, and the public at large (Beck et al. 2001). With nearly 60% of humanity residing within 100 km of the coastline (Vitousek et al., 1997) and associated rapid, large-scale development in coastal habitats (Hughes et al. 2009), assessing fish nursery function within estuary environments can help prioritize protection and restoration (Beck et al. 2001; Peterson 2003; Nagelkerken et al. 2015).

With the rising popularity of ecosystem-based management, managers are asked to account for a multitude of interacting biological and physical factors while simultaneously uncovering the drivers and pressures which cause ecological change (Guiet et al. 2016). The increasingly complex ecological models being employed by ecosystem managers require rich datasets based on extensive field sampling for sufficient parameterization (Guiet et al. 2016). This is particularly challenging for estuaries where both the abiotic and biotic components of the ecosystem are in constant flux (Beck et al. 2001; Nagelkerken et al. 2015; Sheaves et al. 2015). Size distributions, so-called size-spectra, can be employed to infer ecosystem structure and function, while not being overwhelmed by complexity and associated model uncertainty (Giacomini et al. 2016; Guiet et al. 2016).

Size-spectrum theory is based upon the observation that in pelagic systems there are many more small individuals than large ones, but that total biomass is approximately equal across size classes (Sheldon et al. 1972). By plotting either biomass, abundance, or energy as a function of individuals' length, weight, or volume in logarithmic space, size-spectra summarize a complex suite of biophysical and trophic processes with simple linear regressions (Kerr and Dickie 2001; Guiet et al. 2016). The coefficients of spectra regressions, slope (λ) and intercept (Γ), can be used to infer different properties of community structure and ecosystem health (Kerr and Dickie 2001; Guiet et al. 2016). Spectra slopes (λ) measure the relative frequency of body sizes in a community and depend upon predator-prey dynamics and trophic transfer efficiencies (Platt and Denman 1978; Kerr and Dickie 2001; Giacomini et al. 2016; Perkins et al. 2018). When larger individuals are removed from the population, such as in the case of fisheries exploitation, spectra slopes (λ) decrease and the abundance of smaller individuals increases, suggesting that the smaller size classes experienced a release from predation pressure (Gislason and Rice 1998; Bianchi et al. 2000; Blanchard et al.

2005). Thus, slope values can indicate the relative degree of predation risk. Intercepts (Γ) correspond to ecosystem production and are influenced by abiotic environmental factors such as nutrient availability and temperature (Boudreau and Dickie 1992; Maury et al. 2007; Guiet et al. 2016). Highly productive habitats, such as eutrophic lakes and upwelling zones, exhibit higher spectra intercept values than those with low overall productivity, such as oligotrophic regions (Bianchi et al. 2000; Guiet et al. 2016). Size-spectra analysis has been used to provide insight into a variety of ecological processes, including; predator-prey interactions (Thiebaux and Dickie 1992; Blumenshine et al. 2000; Kerr and Dickie 2001), effects of fisheries exploitation on community structure (Gislason and Rice 1998; Bianchi et al. 2000; Blanchard et al. 2005), and the effects of resource subsidies on food-web structure (Hocking et al. 2013; Perkins et al. 2018).

Here we apply size-spectra analysis within the estuary to gain insight into the potential nursery functions of habitats across this ecotone. We hypothesized that size spectra along the estuary gradient from freshwater to the saltwater would reflect spatial gradients of predation risk and productivity. First, we predicted that predation risk, as revealed by higher slopes (λ), would increase closer to the ocean due to the relationship between habitat size and food chain length (McIntosh et al. 2018). Second, we predicted that production, as revealed by higher intercepts (Γ), would also increase in the seaward direction as temperate latitude oceans are more productive than their freshwaters (Gross et al. 1988). Thus, young fish would face trade-offs in predation risk and productivity across the estuary mosaic. However, it is also possible that particularly important nursery habitat areas break this trade-off and have lower slopes and higher intercepts. We produced spectra based on abundance and body weight to describe the fish communities across the full tidal influence of an unindustrialized estuary in the Great Bear Rainforest region of British Columbia, Canada (Fig. 1). Given that seasonal shifts in environmental conditions and biotic community structure can alter size-spectra (Pope et al. 1994; Maury et al. 2007; Guiet et al. 2016), we also examined how spectra coefficients fluctuated through time across the mosaic.

2.3. Methods

The Koeye River estuary (51.7782°N, 127.8737°W) is located on the Central Coast of British Columbia, Canada, ~50km south of the Heiltsuk village of Bella Bella (Figure 2.1a). Sampling sites spanned the entirety of the tidal influence, ranging from the marine Fitz Hugh sound to ~5 km upstream of the river mouth. We divided the estuary into six reaches based on habitat characteristics (Figure 2.1a) (Reshitnyk 2015); Reach 1 is fully saltwater with sandy beaches, Reach 2 is highly saline with dense eelgrass

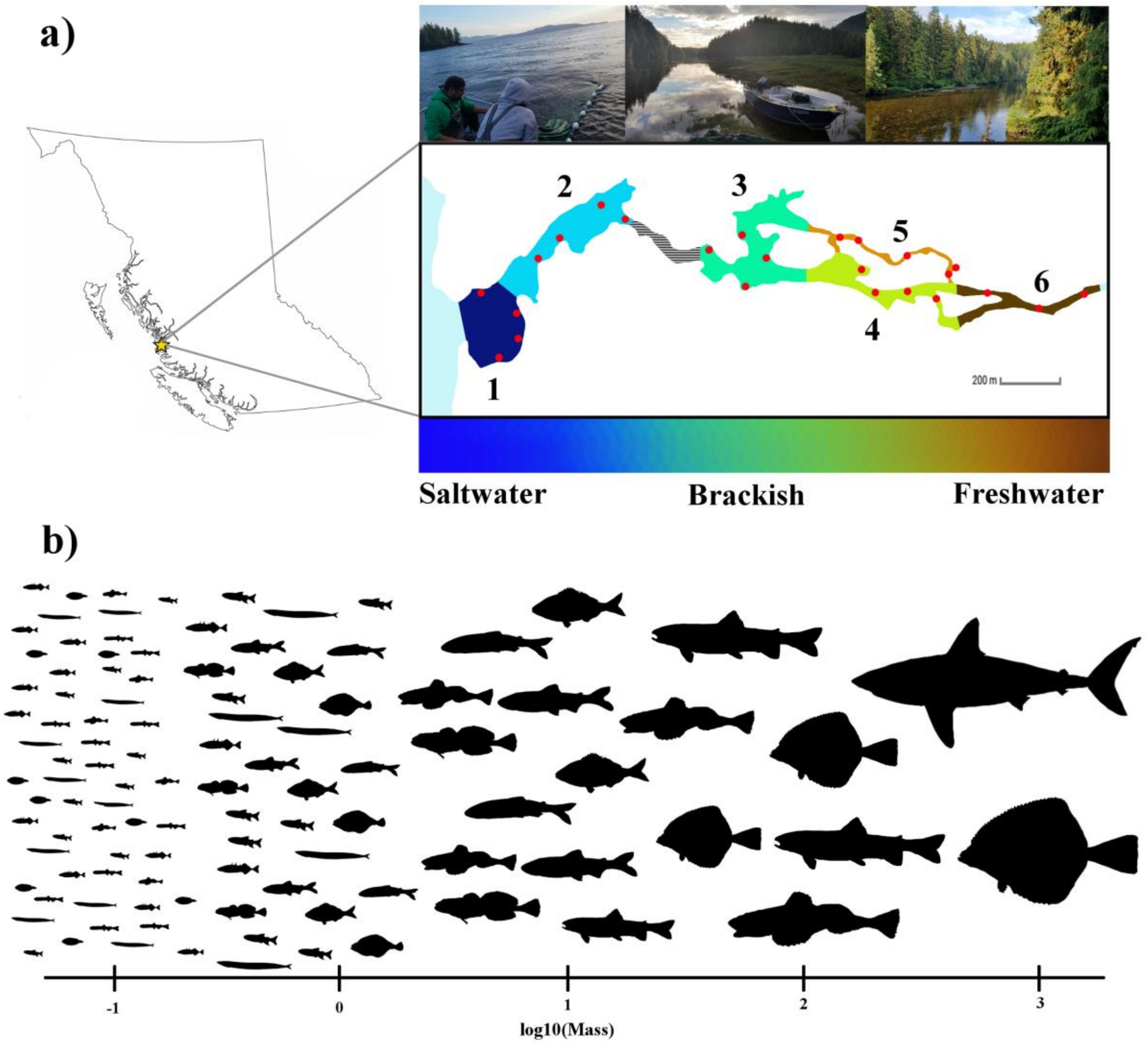

Figure 2.1 **a) Map of the Koeye River Estuary showing reach area designations (colored regions), the most frequently used beach seine sites (red dots), and the general salinity gradient across the estuary. The grey shaded area between reaches 2 and 3 is a narrow canyon with steep rock walls and swift currents that make beach seining nearly impossible and thus was not sampled. b) A pictorial representation of the Koeye estuary size-spectra, showing approximate abundances of typical fish species caught in each size class.**

(*Zostera marina*) beds, Reach 3 has variable salinity with muddy substrate and large expanses of rockweed (*Fucus* spp.), Reach 4 has variable salinity and is the mainstem salt marsh, Reach 5 has variable salinity and is side-channel salt marsh, and Reach 6 is primarily freshwater with classic stream riffle-pool characteristics (Appendix A: Table A.1.). Each reach had three to four sampling areas for a total of 19 sites across the estuary which were beach seined every two weeks from mid-April until the end of September. In total, we performed 188 seine sets over 10 rounds of sampling in 2018.

During each seine set, we measured water chemistry parameters (temperature, salinity, dissolved oxygen, pH) using a YSI ProDSS multiparameter water quality meter. The sensor was submerged to the middle of the water column at the deepest area of the seine and was calibrated prior to the start of each sampling round (Appendix A: Table A.1.). Three different juvenile beach seines were employed based on site-specific bathymetry in order to ensure equal sampling coverage of the water column at all sites: a 22m x 3.1m net was used primarily for deep saltwater sites, a 30m x 1.8m net was used for most other sites when water levels were high enough for boat operation, and a 13.7m x 1.2m pole seine was used in shallow/confined areas. During each set, we identified and enumerated all fish species then measured the fork-length of up to ten randomly selected individuals of each species. We only measured a small subsample of each species during each seine set due to time and logistical constraints associated with the large variety and abundance of fish caught and our tight sampling schedule. Most sampled fish were measured without the use of anesthetics, but larger individuals were briefly anesthetized in MS-222 (0.05 g/l) and allowed to recover in aerated water prior to release (University Animal Care Committee at Simon Fraser University protocol number 1270B-14). Direct mass measurements were not taken because of difficulties in obtaining accurate measures under variable field conditions.

To account for the wide variety of body plans exhibited by fish species in our study, we calculated our size-spectra based on individuals' body mass rather than length (Kerr and Dickie 2001; Sprules and Barth 2016). To do this, we calculated the mass of sampled individuals of most species from their fork-lengths using species-specific Bayesian length−weight conversions found on FishBase (Froese et al. 2014; Froese and Pauly 2018). Exceptions were coho salmon (*Oncorhynchus kisutch*), sockeye salmon (*Oncorhynchus nerka*), and Dolly Varden trout (*Salvelinus malma*) for which previously collected data on lengths and mass from Koeye were used and lingcod (*Ophiodon elongatus*) for which conversions were found in Forrester and Thomson (1969). Estimated masses were rounded up to the nearest 0.1g. Returning adult salmon were removed from the dataset at this point because they do not feed during this life stage and thus are essentially inert members of the estuary fish community.

Once we had individual body mass estimates for our measured fish, we sampled with replacement from these measures to produce a body mass sample set of the full catch abundance of each species in each seine set. To account for our different net sizes, we corrected catch abundances from all sets to the 30m net size using the ratio of the surface area seined (net lengths = 30m, 22m, 13.7m; surface areas seined = 143.24m2, 77.03m2, 29.87m2; catch abundance correction ratio = 1 : 1.86 : 4.78). To produce our size distributions, body mass sample sets for all species were combined for each reach during each sampling round and individuals were sorted into log10 equal body size classes, or mass bins (0.1-0.9g, 1.0–9.9g, 10.0–99.9g, 100.0-999.9g, 1000.0-9999.9g). Size-spectra were estimated for each reach-round combination with a simple linear regression relating the distribution of abundance across size classes (log10(n + 1) ~ log10(mass bin), with mass bins represented as 0.1, 1, 10, 100, and 1000)(Fig. 2a). We then bootstrapped this process 1000 times to reduce any random sampling bias, retaining slope (λ) and midpoint height (ΓH) values for each of the regressions and using the mean values of the size-spectra coefficients found for each reach-round combination for the remainder of the analysis. Midpoint height (ΓH) values were used instead of y-intercept (Γ) values to avoid correlation of the spectra coefficients which produces the statistical artefact of increasing intercept with decreasing slope (Daan et al. 2005; Guiet et al. 2016). Following best practices, we interpret these midpoint heights (ΓH) in the same way as we would y-intercepts and so will refer to them simply as intercepts for purposes of clarity in the remainder of the paper.

To examine differences between habitat slope (λ) and intercept (ΓH) values across the six reaches, we performed the non-parametric Kruskal-Wallis test followed by the Conover-Iman test for stochastic dominance using the R package ‘conover.test’ (Appendix S1: Tables S3 and S4) (Kruskal and Wallis 1952; Conover and Iman 1979; Conover 1999; Dinno 2017). We used these non-parametric tests because the relatively small sample size (10 spectra regressions per reach), did not allow consistent assessment of normality.

We also examined how size-spectra shifted seasonally across the ecotone. We first constructed whole estuary models for both slope (λ; predation risk) and intercept

(ΓH; productivity) and compared six sequential polynomial models to determine the polynomial orders which best described the overall variation in coefficient values over the season (Table 2.3). We then tested whether the different habitats showed synchronous, lm(coefficient ~ poly(week, order) + reach), or independent, lm(coefficient ~ poly(week, order) * reach), variation in spectra coefficients over time (Table 2.4). Models were compared using Akaike's Information Criterion for small sample sizes (AICc).

All analyses and graphics were produced in the R statistical environment version 3.6.1 (R Development Core Team 2019) using the packages 'conover.test', 'AICcmodavg', 'dplyr', and 'ggplot2'.

2.4. Results

In total, we caught 216,717 fish of 30 different species, sampling 3999 individuals for fork-length. Sand lance (*Ammodytes hexapterus*) were the most abundant species in our catch, followed by juvenile coho salmon (*Oncorhynchus kisutch*) which were also the most ubiquitous species across the estuary, then three-spined stickleback (*Gasterosteus aculeatus*), and shiner perch (*Cymatogaster aggregata*)(Appendix A: Table A.2. and Figure A.1.; Table 3.4). Community structure and abundance varied greatly across the estuary, with overall richness and abundance increasing with salinity but diversity and evenness peaking in the middle estuary (Appendix A: Table A.2.). For example, in the marine beach habitat we caught a total of 194,562 individual fish comprising 24 species, while in the tidal freshwater habitat, we caught a total of only 2,040 individuals from 10 different species (Appendix A: Table A.2.). The marine reach also had the greatest number of species, with 5 being found nowhere else in the estuary, including a juvenile salmon shark (*Lamna ditropis*) (Appendix A: Table A.2.).

Size-spectra varied across the estuary ecotone (Figure 2.2). Contrary to the prediction that there would be contrasting spatial gradients across the ecotone, the intermediate estuary habitat (mudflat and rockweed habitat, Reach 3) had the lowest median slope (λ; predation risk) and the highest median intercept (ΓH; productivity) among the various habitat types (Figure 2.2). The Conover-Iman test revealed that the mudflat reach was significantly different ($p < 0.05$) from all other habitats in both slope (λ; predation risk) and intercept (ΓH; productivity), with the exception of similar estimates of

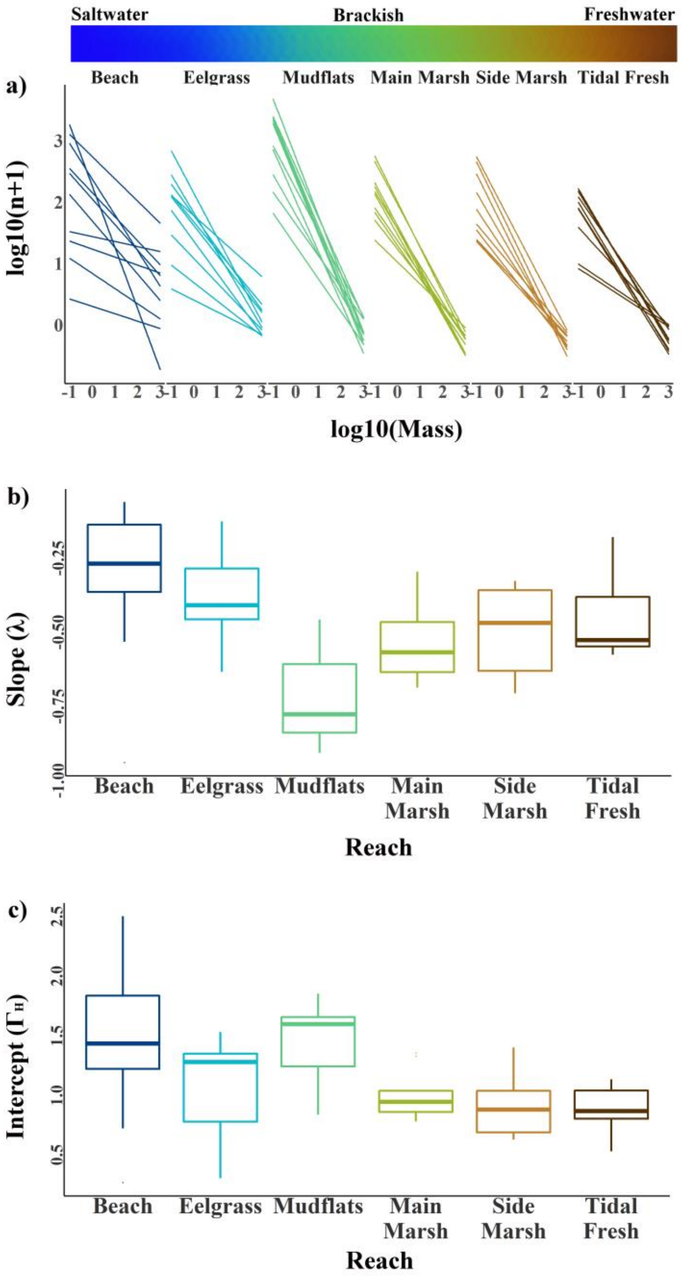

Figure 2.2 **a) Size-spectra produced using the linear model log10(n + 1) ~ log10(mass bin) in each of the reaches during each sampling round. Spectra are seen to vary between reaches, but also display temporal variation within each. Boxplots of the b) slope (λ) and c) intercept (ΓH) values found in each reach using mean values for each reach-round combination the mass sample extrapolation. Using the Conover-Iman test, the mudflats were found to be significantly different ($p < 0.05$) from all other reaches in slope (λ) and intercept (ΓH), except for marginally non-significant results for the main marsh slope ($p = 0.0614$)(Table 2.1) and with the beach intercept ($p = 0.5788$) (Table 2.2).**

Table 2.1 Pairwise multiple comparison results for slope (λ) using Kruskal-Wallis and Conover-Iman tests.

Kruskal-Wallis chi-squared = 21.7075, df = 5, *p*-value = 0.000595					
Reach	1	2	3	4	5
2	*T* = 0.770355 *p* = 0.4444	-	-	-	-
3	*T* = 5.007313 *p* = 0.0000*	*T* = 4.236957 *p* = 0.0001*	-	-	-
4	*T* = 3.096831 *p* = 0.0031*	*T* = 2.326475 *p* = 0.0238*	*T* = -1.910482 *p* = 0.0614	-	-
5	*T* = 2.388103 *p* = 0.0205*	*T* = 1.617747 *p* = 0.1115	*T* = -2.619210 *p* = 0.0114*	*T* = -0.708727 *p* = 0.4815	-
6	*T* = 1.864261 *p* = 0.0677	*T* = 1.093905 *p* = 0.2789	*T* = -3.143052 *p* = 0.0027*	*T* = -1.232569 *p* = 0.2231	*T* = -0.523842 *p* = 0.6025

*Significant *p*-value ($p \leq \alpha$)
alpha (α) = 0.05, no *p*-value adjustment

Table 2.2 Pairwise multiple comparison results for intercept (ΓH) using Kruskal-Wallis and Conover-Iman tests.

Kruskal-Wallis chi-squared = 18.0223, df = 5, *p*-value = 0.0002919					
Reach	1	2	3	4	5
2	*T* = 1.557987 *p* = 0.1251	-	-	-	-
3	*T* = -0.558523 *p* = 0.5788	*T* = -2.116511 *p* = 0.0389*	-	-	-
4	*T* = 2.234095 *p* = 0.0296*	*T* = 0.676107 *p* = 0.5019	*T* = 2.792619 *p* = 0.0072*	-	-
5	*T* = 2.968995 *p* = 0.0044*	*T* = 1.411007 *p* = 0.1640	*T* = 3.527519 *p* = 0.0009*	*T* = 0.734899 *p* = 0.4656	-
6	*T* = 3.145371 *p* = 0.0027*	*T* = 1.587383 *p* = 0.1183	*T* = 3.703895 *p* = 0.0005*	*T* = 0.911275 *p* = 0.3662	*T* = 0.176375 *p* = 0.8607

*Significant *p*-value ($p \leq \alpha$)
alpha (α) = 0.05, no *p*-value adjustment

intercept (ΓH) in the beach habitat (Reach 1) ($p = 0.5788$) (Table 2.1) and a marginally non-significant difference in slope (λ) with the mainstem marsh habitat (Reach 4) ($p = 0.0614$)(Table 2.2).

Size-spectra shifted seasonally across the estuary (Figure 2.3). AICc comparisons of the whole estuary models indicated that seasonal patterns for slopes (λ; predation risk) were best described by a 4th order polynomial and intercepts (ΓH; productivity) were best described by a 2nd order polynomial (Table 2.3). Habitats varied synchronously for slopes (λ; predation risk), decreasing from early spring to summer and then rising again into the fall (Figure 2.3a, Table 2.4). In contrast, size-spectra intercepts (ΓH; productivity) exhibited different seasonal patterns across the reaches, with the marine reaches having more variable intercepts representing more pulsed fish communities whereas freshwater reaches were more consistent across the season (Figure 2.3b, Table 2.4).

Table 2.3 Polynomial selection results for global slope (λ) and intercept (ΓH) models using Akaike's Information Criterion for small sample sizes (AICc).

Model equation[1] = lm(coefficient[2] ~ poly(week[3], m)

Polynomial order (m)	Slope (λ)				Intercept (Γ_H)			
	K[4]	AICc	ΔAICc	LL[5]	K[4]	AICc	ΔAICc	LL[5]
1	3	-13.43	8.87	9.93	3	73.42	15.97	-33.50
2	4	-17.03	5.27	12.88	4	57.45	0.00	-24.36
3	5	-21.08	1.23	16.09	5	59.38	1.93	-24.13
4	6	-22.30	0.00	17.94	6	60.45	3.00	-23.43
5	7	-19.87	2.44	18.01	7	63.01	5.56	-23.43
6	8	-17.86	4.45	18.34	8	65.59	8.14	-23.38

[1] Model written in base R linear model format
[2] Either slope (λ) or intercept (Γ_H)
[3] Week of the year in which sampling was performed
[4] Number of parameters
[5] Log-likelihood

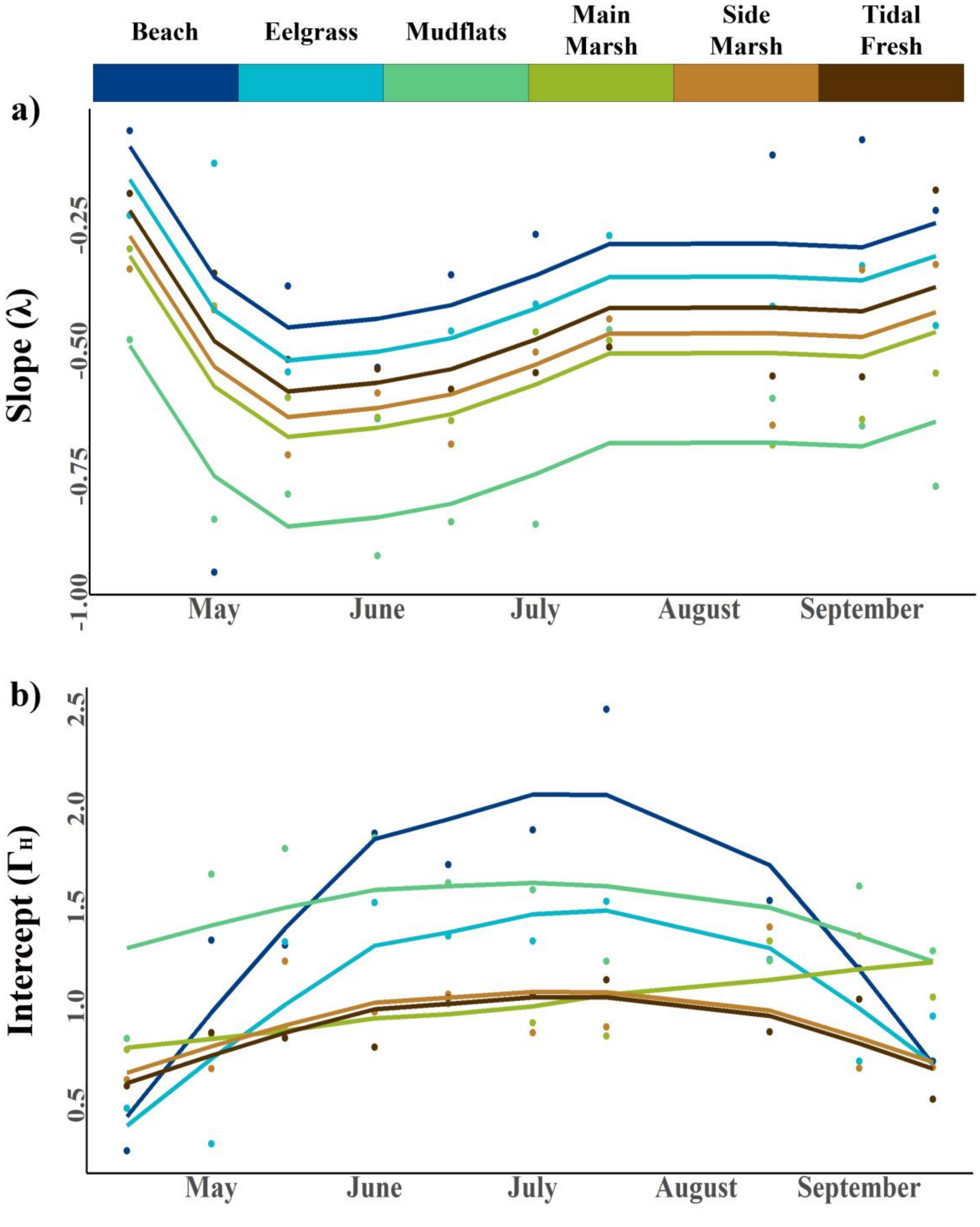

Figure 2.3 Model fits for the temporal variation associated with a) slope (λ), lm(λ ~ poly(round, 4) + reach)(multiple R2 = 0.6085, adjusted R2 = 0.538, df = 50, p = 1.144e-7), and b) intercept (ΓH), lm(coefficient ~ poly(round, 2) * reach)(multiple R2 = 0.7823, adjusted R2 = 0.6941, df = 42, p = 4.981e-9). Habitats were found to vary synchronously in predation risk (slope (λ)), but independently in productivity (intercept (ΓH)). Model selection results can be found in Tables 2.3 and 2.4.

Table 2.4 Synchronous and independent model comparison results using Akaike's Information Criterion for small sample sizes (AICc).

Model[1]	Slope (λ)				Intercept (Γ_H)			
	K[2]	AICc	ΔAICc	LL[3]	K[2]	AICc	ΔAICc	LL[3]
Synchronous **lm(coefficient[4] ~ poly(week[5], m[6]) + reach**	11	-48.07	0.00	37.79	9	36.17	2.56	-7.29
Independent **lm(coefficient[4] ~ poly(week[5], m[6]) * reach**	31	22.86	70.93	55.00	19	33.17	0.00	11.70

[1] Model written in base R linear model format

[2] Number of parameters

[3] Log-likelihood

[4] Either slope (λ) or intercept (Γ_H)

[5] Week of the year in which sampling was performed

[6] Polynomial order

2.5. Discussion

Here we applied size-spectra to examine potential spatial gradients of predation risks and productivity and provide insight into estuary nursery function. Our analysis of size-spectra in the unindustrialized Koeye River estuary revealed that the middle of the estuary habitat, Reach 3, characterized by muddy-substrate and large rockweed expanses, had size-spectra coefficients that indicated higher production (higher Γ¬H) and lower predation risk (lower λ) in the fish community (Figure 2.2). The combination of high productivity and low predation risk has been suggested as a key reason why estuaries function as nurseries for so many species (Dahlgren and Eggleston 2000; Cocheret de la Morinière et al. 2002; Nagelkerken et al. 2015; Sheaves et al. 2015).

Estuaries are comprised of a mosaic of habitat types that vary in structure, extent, and abiotic conditions (Peterson 2003; Nagelkerken et al. 2015), which likely contributes to the observed patterns in size-spectra and inferred estuary nursery function. For example, predator abundance, size, and trophic position tend to increase with habitat size and stability (Kushlan 1976; McHugh et al. 2018). Indeed, we observed the overall largest fish (a juvenile salmon shark) as well as the highest abundance of upper size-class individuals in the more spatially expansive marine sites, while the fish communities of the more constrained, environmentally-variable middle and upper estuary reaches were almost exclusively comprised of smaller size-class individuals

(Figure 2.2a; Appendix A: Table A.1. and A.2.). Size-spectra are the emergent patterns that arise from this complicated and dynamic nature of fish communities and habitats in estuaries.

Spectra coefficients have been shown to reflect changes in environmental conditions (Maury et al. 2007; Guiet et al. 2016) and oscillate through time in response to shifting ratios in predator and prey size and abundance (Blumenshine et al. 2000; Law et al. 2009). In temporally dynamic systems, fish size cohorts are thought to track moving waves of productivity and predation risk, “surfing” the size-spectrum to maximize their foraging opportunities while minimizing their risk of predation (Pope et al. 1994). Seascape studies have shown that animals move among habitat patches daily, following tidal movements in search of food and shelter, but also show ontogenetic shifts in habitat use on longer time-scales as their resource needs change with growth (Dahlgren and Eggleston 2000; Cocheret de la Morinière et al. 2002; Peterson 2003; Nagelkerken et al. 2015). Here we present rare empirical evidence for seasonal shifts in size-spectra across multiple habitat types (Figure 2.3), lending support to the surf-riding and mosaic seascape nursery hypotheses (Pope et al. 1994; Peterson 2003; Nagelkerken et al. 2015). Migration events, such as Pacific salmon smolt outmigration, brings large influxes of small size class fishes to the estuary for a brief period, saturating the ecosystem with prey and presumably lowering the predation risk for any individual fish (May in Figure 2.3a). Similarly, reproduction events within the estuary, such as those of shiner perch and sticklebacks, also create pulses in small fish abundance which affect individual predation risk (August in Figure 2.3a). Such temporal dynamics in size spectra are also likely linked to seasonal patterns of plankton blooms, plant growth, and macroinvertebrate abundance across the estuary habitat mosaic (Figure 2.3b). Thus, estuary fish communities reveal spatially and temporally dynamic patterns of productivity and predation risk. Rather than consistent trade-offs between productivity and risk, the habitat with the least risk is not necessarily also the least productive (Figure 2.3). In autumn, it appears that many fish move to overwintering habitats outside of the estuary and the community shifts back to its pre-growing season configuration, demonstrating the seasonality of nursery function in temperate estuaries (Figure 2.3). Examining temporal shifts in spectra coefficients across the entire mosaic of estuary environments, allows for not only the identification of nursery function in discrete habitats (Beck et al.

2001), but also the study of more spatially and temporally dynamic processes shaping estuary fish communities (Peterson 2003; Nagelkerken et al. 2015; Sheaves et al. 2015).

By integrating abundance and relative body size frequencies, size-spectra analysis provides a relatively easy to sample and statistically simple method for studying the underlying ecological energetics of complex aquatic ecosystems (Kerr and Dickie 2001; Giacomini et al. 2016; Guiet et al. 2016; Sprules and Barth 2016). Thus, size-spectra analysis may prove to be an important new tool for understanding estuary fish ecology and habitat function.

Chapter 3. Climate-altered salinity regimes and its effect on fish communities across an estuary habitat mosaic[2]

3.1. Abstract

The spatial and temporal variability of estuaries may create a complicated mosaic of habitat types and conditions for the species that depend on them. Estuary environmental conditions, such as temperature and salinity, vary across time according to tides, weather, seasons, and climate patterns. In addition, estuaries are not a single habitat, but a mosaic of habitat types spread across the estuary gradient, ranging from mudflats to eelgrass to marsh meadows. Thus, mobile species such as fish that rely on estuaries are confronted with a relatively static mosaic of habitat types, and a shifting mosaic of environmental conditions. Environmental conditions may be further modified by climate change, challenging mobile fish to respond to shifting gradients of environmental conditions. Here we investigate how changing environmental conditions affect fish species distributions and community structure across an estuary ecotone. To address this question, we performed an extensive study of the dynamics of fish communities in a remote and undeveloped estuary on the remote Central Coast of British Columbia, Canada, across a typical wet year (2017) and an atypical dry year (2018). We found that fish communities differed between physical habitat types and that they were closely aligned with the underlying salinity gradient of the estuary. During the dry year, there was substantial saltwater intrusion up the estuary, shifting the location of salinity and other environmental conditions relative to habitat types such as marsh meadows. This alteration of environmental conditions within the physical habitat types was associated with changes in the structure of the fish communities found therein. Different fish assemblages (e.g., marine vs. brackish vs. freshwater assemblages) showed disparate probabilities of presence across the estuary mosaic as well as differential responses to changes in environmental conditions. Specifically, marine origin species expanded their range up-estuary and utilized new habitats in the year with increased saltwater intrusion, while brackish and freshwater origin species retained their

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[2] A version of Chapter 3 is in preparation for journal submission, with coauthors William I. Atlas, Benjamin Millard-Martin, Jared Reid, Michael Arbeider, Julian Heavyside, Brian P. V. Hunt, and Jonathan W. Moore.

overall range despite changing conditions. With the British Columbian coastal rainforest heading towards a warmer, more variable climate, and more saltwater intrusion events, additional habitats in the estuary may become available for exploitation to more traditionally marine species, but those estuary residents originating in brackish or freshwater may be subject to higher stress levels from both more extreme abiotic conditions and additional biotic interactions such as competition or predation.

3.2. Introduction

Landscapes are rarely homogeneous and constant, but rather are composed of a complex mosaic of environmental and physical habitat features (Stanford et al. 2005; Fulford et al. 2011; Brennan et al. 2019). These habitat features are also dynamic, as variations in environmental conditions and geomorphic structure can cause shifts in the habitat mosaic on multiple time scales (Stanford et al. 2005; Brennan et al. 2019). In order to thrive in such spatially- and temporally-dynamic habitat mosaics, organisms can either cope with the environment challenge (high tolerance), rapidly recolonize (weedy species), or move to more favorable locations as conditions change (mobile species) (Stanford et al. 2005; Brennan et al. 2019). In a time of rapid, anthropogenic alterations of the spatial and temporal dynamics of habitats, it is increasingly important to understand how dynamic habitat mosaics influence the structure, distribution, and persistence of biological communities (Vörösmarty et al. 2010: Brennan et al. 2019).

Estuaries are some of the most dynamic and biologically productive ecosystems on the planet but are also some of the most threatened (van den Belt, 2011; Daborn and Redden 2016). As the ecocline between freshwater and the sea, the estuary mosaic is influenced by both marine and terrestrial conditions leading to highly variable environmental conditions across a diverse assemblage of stationary habitat features (Fulford et al. 2014; Daborn and Redden 2016). Shifts in the mosaic occur on the scale of hours (tidal flood and ebb), weeks (lunar cycle), months (seasonal variation), years (climatic oscillations), and beyond (global climate change, land subsistence) (Peterson 2003; Daborn and Redden 2016). The near constant flux of environmental factors within estuaries makes them stressful environments for most aquatic organisms (Elliott and Quintino 2007), leading to generally low biodiversity but high abundance and productivity of species most tolerant to the shifting conditions (Daborn and Redden 2016; Teichert et al. 2017). Despite their stressful nature, estuaries are known to be important nursery grounds for many ecologically and economically important species (Beck et al. 2001; Dahlgren et al. 2006; Nagelkerken et al. 2015; Sheaves et al. 2015). Their key location at the mouths of rivers and streams make estuaries prime sites for human habitation, exposing these systems to further stresses from development, pollution, flow regulation, and many other actions (Basset et al. 2013; Sheaves 2016). In naturally stressed ecosystems, it is difficult to tease apart anthropogenically-induced and intrinsic stresses (Elliott and Quintino 2007), making it all the more important to understand the drivers of community structure and productivity across the estuary complex.

Within an individual estuary, environmental factors, especially temperature and salinity, tend to be the primary determinants of fish community structure and species distributions (Harrison and Whitfield 2006; Selleslagh and Amara 2008; Sheaves 2016). Thermal and salinity tolerances of each species limit the extent and duration of their estuary use, with only the most tolerant species inhabiting the middle mixing zone for extensive periods (Harrison and Whitfield 2006; Sheaves 2016; Teichert 2017). Physical habitat structure (e.g., vegetation such as marsh meadows or eelgrass beds) further influences species distributions due to species- or life-stage-specific habitat requirements or physical impediments to movement (Dahlgren and Eggleston 2000; Harrison and Whitfield 2006; Sheaves 2016; Sharpe et al. 2019). Ecological drivers such as migrations, reproductive events, larval delivery, food availability, predator-prey interactions, and competition also play a key role in the structuring of estuarine fish communities (Dahlgren and Eggleston 2000; Sheaves 2016). All of these drivers can be affected by climatic patterns, changing habitat suitability and altering species distributions on both short and long timescales (Peterson et al. 2007; Daborn and Redden 2016).

Climate change and its effects on river flow and sea level rise may alter the juxtaposition of estuary habitats and their dynamic environmental conditions such as salinity (Roessig et al. 2004; Fulford et al. 2014; BC Ministry of Environment 2016; Munsch et al. 2019). Warmer air temperatures are leading to increases in global precipitation, and the timing and type of precipitation has become more variable, leading to variation in river flow from historical norms (BC Ministry of Environment 2016; Munsch et al. 2019). In systems in northwestern North America, spring freshets have generally become earlier, and summer flows have decreased, which has enabled more extreme tidal salinity fluxes and increased water temperatures in estuaries (BC Ministry of

Environment 2016; Munsch et al. 2019). In addition, thermal expansion of ocean waters and, to a lesser extent, the conversion of ice to liquid water at the poles, is increasing sea levels that will persist for many years even if atmospheric warming were to stop immediately (IPCC 2014; BC Ministry of Environment 2016). As sea levels rise, estuary habitats are at risk of inundation, fragmentation, and inland retreat due to increased saltwater intrusion (Roessig et al. 2004; Fulford et al. 2014; BC Ministry of Environment 2016). The combined effects of climate-driven alterations in river flow and sea level rise are likely to affect estuarine fish communities, though the manner in which individual species, or different assemblages, will be affected is not clear. Thus, there is a need for studies that connect the spatial and temporal dynamics of key abiotic factors with the spatial and temporal dynamics of estuary fish communities.

Here we investigated how shifting environmental mosaics altered fish community structure and species' distributions across two climatically different years in an unindustrialized estuary on the Central Coast of British Columbia, Canada. We hypothesized that shifts in fish community structure within the static habitats would correspond to climate-driven alterations in the environmental conditions such as salinity and, more specifically, that different species/assemblages would react diversely to environmental dynamics. Most studies along the North American west coast have focused on large or highly impacted estuaries and rarely cover the full extent of tidal influence. This paper provides a rare glimpse into the dynamics of an entire estuary complex under near pristine conditions. Due to the extreme difference in climatic conditions between sampling years, this study also provides some insights into how estuarine fish communities may react in the face of global climate change.

3.3. Methods

3.3.1. Study system

The Koeye River estuary (51.7782°N, 127.8737°W) is located on the Central Coast of British Columbia, Canada, ~50km south of the Heiltsuk village of Bella Bella. Characteristic of British Columbia coastal, temperate rainforest watersheds, the Koeye River estuary typically experiences cool, wet springs and autumns, where river discharge is high and freshwater comprises much of the estuary, separated by warmer, drier summers, where river discharge is reduced, and saltwater intrusion increases. Both

Table 3.1 **Weather conditions, air temperature, precipitation, and solar radiation, experienced at Koeye during each month of the 2017 and 2018 sampling seasons.**

Month	Air temperature (°C)[1]		Solar radiation (MJ/m²)[2]		Precipitation (mm)[3]		River elevation (m)[4]	
	2017	**2018**	**2017**	**2018**	**2017**	**2018**	**2017**	**2018**
April	7.63 (-0.67 – 16.09)	7.31 (-1.50 – 19.95)	18.22 (7.41 – 25.22)	18.83 (5.35 – 24.93)	214.0	237.8	1.01 (0.83 – 1.37)	1.12 (0.89 – 1.42)
May	10.52 (1.81 – 18.48)	11.35 (2.70 – 20.11)	18.62 (3.59 – 29.26)	24.89 (6.81 – 30.17)	255.0	76.4	1.00 (0.65 – 1.55)	0.81 (0.57 – 1.08)
June	12.27 (5.90 – 20.99)	12.73 (6.72 – 22.39)	23.75 (7.90 – 31.76)	20.39 (5.66 – 31.03)	149.0	188.8	0.77 (0.45 – 1.41)	0.82 (0.45 – 1.43)
July	14.27 (7.50 – 22.91)	15.30 (7.96 – 24.29)	24.55 (6.42 – 29.97)	25.15 (12.67 – 30.02)	67.6	72.0	0.54 (0.43 – 0.76)	0.47 (0.26 – 1.10)
August	14.81 (9.32 – 23.09)	14.40 (7.72 – 24.33)	15.15 (6.01 – 26.86)	20.45 (8.31 – 24.60)	140.8	36.2	0.69 (0.26 – 1.20)	0.20 (0.16 – 0.26)
September	13.37 (4.91 – 25.15)	12.19 (5.39 – 22.85)	14.56 (4.17 – 19.68)	14.12 (6.00 – 19.94)	181.4	174.4	0.76 (0.54 – 1.48)	0.75 (0.29 – 1.27)

[1] Minimum, maximum, and average daily temperature data were computed as the mean of those values recorded at two separate sensors at Koeye. Monthly median values were calculated using average daily air temperature values, while ranges were calculated using the lowest daily minimum and highest daily maximum air temperatures.

[2] Median and range values of maximum daily solar radiation measured at Koeye.

[3] Sum of daily rainfall measurements for each month measured at Koeye.

[4] Median and range values of average daily river gauge depth. Gauge sensor is located just upstream of the maximum extent of tidal influence

the 2017 and 2018 sampling seasons followed this general pattern, but 2018 was much drier, receiving almost 30% less rain than the 2017 season (Table 3.1). This resulted in river elevations being on average 10cm lower and average estuary-wide salinity being almost double that in 2017 (Table 3.1; Table 3.2).

3.3.2. Field sampling

We performed extensive field sampling of the estuary fish community and key environmental parameters across two years. Sampling sites spanned the entirety of tidal influence which extends ~5km from the river mouth. We divided the estuary into six reaches based on habitat characteristics (Figure 2.1a) (Reshitnyk 2015); Reach 1 is primarily marine with sandy beaches, Reach 2 is highly saline with dense eelgrass (*Zostera marina*) beds, Reach 3 has variable salinity with muddy substrate and large expanses of rockweed (*Fucus* spp.), Reach 4 has variable salinity and is the mainstem salt marsh, Reach 5 has variable salinity and is side-channel salt marsh, and Reach 6 is primarily freshwater with classic stream riffle-pool characteristics.

Each reach had three to four sampling areas for a total of 19 sites across the estuary which were beach seined every 10-14 days from April through September. In total, we performed 500 seine sets over 28 rounds of sampling during the 2017 and 2018 field seasons. Three different juvenile beach seines were available for use and were employed based on the bathymetry of the site being sampled: a 22m x 3.1m net was used primarily for deep saltwater sites, a 30m x 1.8m net was used for most other sites when water levels were high enough for boat operation, and a 13.7m x 1.2m pole seine was used in shallow/confined areas. All fish caught during sampling were enumerated and identified to species. *Cottus asper* and *Cottus aleuticus* were grouped together under the term “freshwater sculpin” and *Pholis laeta* and *Pholis ornata* were grouped under the term “gunnel” due to difficulties in field identifications (Table 3.4). Extremely large catches (5000+ individuals) of Pacific sand lance (*Ammodytes hexapterus*) were estimated by enumerating several full dipnets then multiplying the average count by the number of netfuls required to empty the seine. To account for our different net sizes, we corrected catch abundances from all sets to the 30m net size using the ratio of the surface area seined (net lengths = 30m, 22m, 13.7m; surface areas seined = 143.24m2, 77.03m2, 29.87m2; catch abundance correction ratio = 1 : 1.86 : 4.78).

Table 3.2 Water chemistry parameters, temperature and salinity, during each sampling season and habitat characteristics, substrate and vegetation found in each sampling reach.

Reach	Aquatic conditions[1]				Habitat characteristics	
	Temperature (°C)		Salinity (PSU[a])		Substrate[2]	Vegetation[3]
	2017	2018	2017	2018		
1	13.5 (9.9 – 16.1)	12.7 (7.7 – 15.4)	28.91 (3.13 – 34.93)	30.10 (20.50 – 46.80)	SD	-
2	14.0 (6.8 – 16.7)	13.3 (6.7 – 15.9)	6.50 (0.05 – 36.86)	26.92 (0.06 – 37.62)	SD, GV, CB	EG, RW
3	14.0 (7.3 – 22.8)	14.2 (6.8 – 19.0)	0.97 (0.01 – 29.89)	9.45 (0.02 – 37.14)	MD	RW, EG, MG
4	14.0 (7.2 – 18.8)	14.7 (6.0 – 18.5)	0.11 (0.01 – 23.67)	1.82 (0.01 – 33.73)	GV, CB	MG, RW
5	14.2 (7.2 – 19.6)	15.2 (6.1 – 21.6)	0.03 (0.01 – 10.91)	0.71 (0.01 – 23.19)	GV	MG
6	14.4 (7.0 – 20.1)	14.5 (5.1 – 21.0)	0.01 (0.01 – 3.41)	0.01 (0.00 – 28.22)	CB	MG

[1] Median and range values of aquatic conditions. [a] Practical Salinity Unit.
[2] Substrates observed at sampling sites. (SD = sand, GV = gravel, CB = cobble, MD = mud).
[3] Aquatic and shoreline vegetation observed at sampling sites. (EG = eelgrass, RW = rockweed, MG = marsh grass)

Aquatic conditions (temperature, salinity, dissolved oxygen, pH) were measured during each set using either a YSI 556 MPS (2017) or a YSI ProDSS (2018) multiparameter water quality meter with the sensor submerged to the middle of the water column at the deepest area of the seine. Water quality meters were calibrated prior to the beginning of each sampling round. River elevation was recorded using an Onset HOBO U20 water level data logger mounted in the river just above the extent of tidal influence. Weather data (air temperature, rainfall, and solar radiation) were procured from the Hakai Institute who have a weather station located at the mouth of the Koeye River (Reach 1) (Hakai 2019). Air temperature was measured using a Rotronic HC2S3 temperature and relative humidity probe, rainfall was measured using a Hyquest Solutions TB4 tipping bucket rain gauge, and solar radiation was measured using a Kipp and Zonen CMP3 pyranometer (Hakai 2019).

Monthly river elevation data are the median values of average daily measurements recorded each month of the sampling seasons. Monthly rainfall values are the sum of daily rain measurements recorded each month by a tipping bucket rain gauge. Dual air temperature measurements are recorded continuously at the Koeye weather station and monthly values were calculated as the median of the averaged daily air temperatures. Solar radiation was reported in hourly intervals and monthly values correspond to the median of the maximum daily values recorded.

3.3.3. Analyses

We examined how fish communities found in each habitat type differed between wet and dry years and how these shifts aligned with the salinity and temperature gradients of the estuary. For the community analyses, corrected catch data from all sites within a reach were combined for each month of the sampling seasons. Similarly, salinity and water temperature measurements from all sites within a reach were combined and the median values were used to represent monthly conditions. Species richness, Shannon-Weiner diversity, and Pielou’s evenness was calculated for all reaches during each month of both sampling seasons, as well as overall for the whole estuary and the entire sampling period. NMDS ordination was constrained to 2 dimensions and based upon Bray-Curtis dissimilarity of log10 transformed corrected catch abundances of the 14 most abundant and frequently caught species in the Koeye estuary. Not all species were included in order to facilitate model convergence in 2 dimensions and maintain acceptable stress levels. To be included, species had to be caught in both sampling years and their log10 transformed total abundance had to be greater than 2.

We explored seasonal and between year differences in, as well as correlations between, environmental conditions (weather, river, and aquatic conditions) and major community attributes (abundance and richness). Weather, aquatic, and river conditions, as well as, total catch abundance, and species richness were compared between years, months, and reaches using the non-parametric Kruskal-Wallis test (Kruskal and Wallis 1952). If groups were found to be significantly different, further pairwise comparisons were performed using the Conover-Iman test for stochastic dominance using the Holm method of p-value adjustment (Conover and Iman 1979; Conover 1999; Dinno 2017). Correlations between set-level total catch abundance and species richness and salinity, water temperature, and estuary location (reach) were evaluated using Kendall’s tau coefficient (Kruskal, 1958). Non-parametric tests were employed because not all data conformed to a normal distribution as tested by the Shapiro-Wilk normality test.

We examined how species and assemblage distributions shifted across the estuary under varying levels of saltwater intrusion. Year to year differences in the distributions of individual fish species were examined directly by plotting catch abundance in each reach each year. We classified fish species into four different estuary assemblages based on the aquatic environments they are listed to inhabit on FishBase (Froese and Pauly 2018). The ‘marine’ category includes species only known to inhabit fully saline waters; the ‘brackish’ category includes species known to inhabit both fully saline and brackish waters, but not freshwater; the ‘freshwater’ category includes the most euryhaline species known to inhabit waters from fully fresh to fully saline; and the ‘outmigrant salmonid’ category includes those salmonid species which are passing through the estuary on their way out to sea. ‘Outmigrant salmonids’ (chum (*Oncorhynchus keta*), coho (*O. kisutch*), pink (*O. gorbuscha*), sockeye (*O. nerka*), and steelhead (*O. mykiss*) smolts) were separated from the ‘freshwater’ assemblage due to their highly transient nature in the estuary. Young of year coho salmon which rear long-term in the estuary were included in the ‘freshwater’ assemblage. Yearly variations in the distributions of estuarine fish assemblages were examined by modelling the presence/absence of individual species using a binomial generalized linear mixed effects model. The model’s fixed effects are the median monthly estuary-wide salinity and the various physical habitats (reaches), both with interactions with fish assemblage ((assemblage*median salinity) + (assemblage*reach)). The random effects attempt to incorporate species-level differences in distribution based on general differences (1|species), timed migration and reproduction events (month|species), and seasonal variations (month^2|species). Fish assemblage distributions were also directly examined by plotting seasonal catch abundances across the reaches.

All analyses were performed and graphics produced in the R statistical environment version 3.6.1 (R Development Core Team 2017) using the packages ‘vegan’, ‘conover.test’, ‘NSM3’, ‘dplyr’, ‘ggplot2’ and ‘ggvegan’ (Oksanen et al. 2019; Dinno 2017; Schneider et al. 2018; Wickham et al. 2019; Wickham 2016; Simpson 2019).

3.4. Results

3.4.1. Shifting environmental mosaic

The Koeye estuary had strong gradients in salinity and water temperature that shifted across the season and differed between years (Figure 3.1; Table 3.2). For example, salinities differed between the lower (Reach 1) and upper estuary (Reach 6) by an average of 27.92 PSU in 2017 and 28.62 PSU in 2018, while water temperatures differed by an average of 1.50°C in 2017 and 2.54°C in 2018. Saltwater intrusion into the upper estuary increased in the summer when river levels dropped, and precipitation decreased (Figure 3.1). During the driest months, average whole estuary salinity was 1.44 times higher in 2017 (July) and 2.11 times higher in 2018 (August) than the seasonal average. Water temperatures also increased throughout the estuary during summer (Figure 3.1). Interestingly, the temperature gradient across the estuary flipped from colder in freshwater reaches and warmer in marine reaches during the spring to warmer in freshwater and cooler in marine reaches during the summer (Figure 3.1). For example, in April 2018 the lower estuary (Reach 1) was 2.20°C warmer than the upper estuary (Reach 6), but in August 2018 the upper estuary was 4.80°C warmer than the lower estuary. Salinity and water temperature gradients then returned to spring-like conditions in the fall (Figure 3.1).

The 2018 sampling season was much dryer (30% less total precipitation) than 2017, with associated major differences in both estuarine aquatic conditions and river flow characteristics (Figure 3.1; Table 3.1 and 3.2). Kruskal-Wallis tests showed significant differences between sampling years in both salinity ($p = 0.0002$) and river elevation ($p = 0.003$) (Appendix B: Tables B.1. and B.2.). The middle estuary reaches were particularly variable in salinity (Figure 3.1; Table 3.2). Using the Conover-Iman test we found that the salinities in Reaches 2, 3, and 4 were all significantly higher in 2018 than in 2017 ($p = 0.042$, $p = 0.001$, and $p = 0.0379$ respectively) and Reach 5 was only slightly non-significant ($p = 0.053$) (Appendix B: Table B.1.). River elevation was significantly lower in both May ($p = 0.0003$) and August ($p = 0.0000$) of 2018 (Appendix B: Table B.2.). August of 2018 was especially dry, 104.6 mm less rain than 2017,

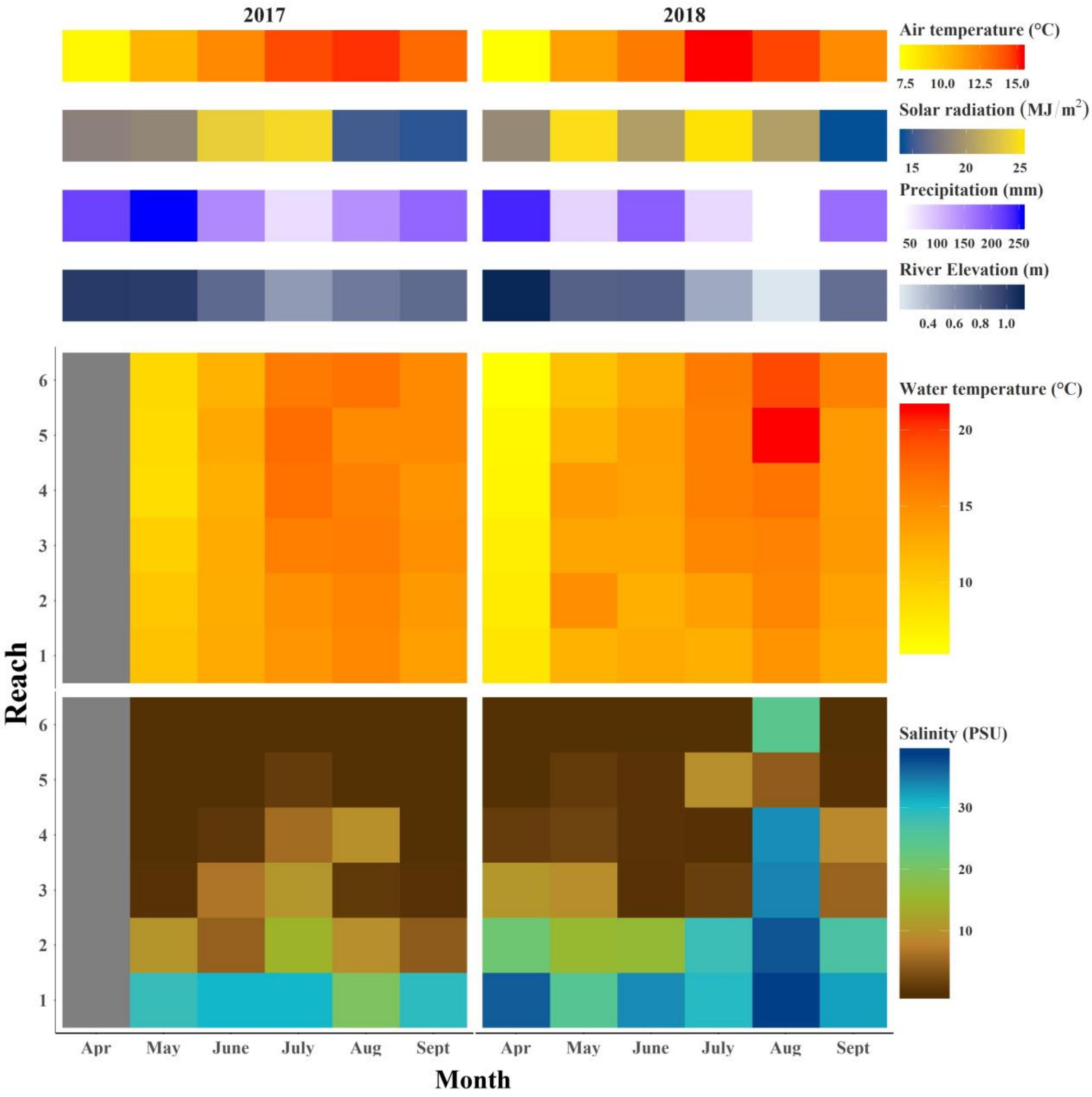

Figure 3.1 Heat maps of monthly median air temperature, median solar radiation, total precipitation and median river elevation, as well as median monthly water temperatures and salinities found in each reach during the 2017 and 2018 sampling seasons. Median values for air temperatures and river elevations were calculated from average daily measurements. Median values for solar radiation were calculated from maximum daily measurements. Monthly precipitation values are the sum of daily precipitation measurements. Median values for water conditions were calculated from measurements taken at multiple sites within each reach throughout each month.

Table 3.3 Yearly totals and ranges of monthly values found in each reach and the full estuary, as well as the overall study values, for species richness, catch abundance, Shannon-wiener diversity index, and Pielou's evenness index.

Reach	Species richness			Catch abundance[1]			Shannon-wiener diversity index			Pielou's evenness index		
	2017	2018	Overall	2017	2018	Overall	2017	2018	Overall	2017	2018	Overall
1	24 (8 – 17)	24 (2 – 16)	32	29,933 (191 – 25,751)	362,146 (4 – 283,913)	392,0179	0.61 (0.17 – 1.91)	0.06 (0.03 – 1.73)	0.12	0.19 (0.07 – 0.83)	0.02 (0.01 – 0.81)	0.04
2	15 (6 – 13)	21 (6 – 14)	22	11,711 (223 – 5,345)	15,359 (18 – 9,901)	27,070	0.85 (0.23 – 1.26)	0.91 (0.26 – 1.52)	0.93	0.32 (0.10 – 0.65)	0.30 (0.10 – 0.86)	0.30
3	16 (7 – 10)	19 (6 – 12)	21	24,174 (384 – 9,686)	17,666 (176 – 6,998)	41,840	1.53 (0.79 – 1.45)	0.97 (0.36 – 1.51)	1.39	0.55 (0.38 – 0.66)	0.33 (0.15 – 0.84)	0.46
4	12 (5 – 9)	10 (4 – 7)	13	3,255 (197 – 1,282)	3,086 (58 – 796)	6,341	1.33 (0.49 – 1.42)	1.07 (0.40 – 1.15)	1.22	0.53 (0.30 – 0.73)	0.46 (0.29 – 0.64)	0.48
5	9 (3 – 6)	12 (3 – 10)	13	5,205 (58 – 2,573)	4,133 (44 – 1,750)	9,338	0.59 (0.15 – 1.39)	1.00 (0.15 – 1.26)	0.85	0.27 (0.13 – 0.87)	0.40 (0.09 – 0.70)	0.33
6	10 (4 – 6)	10 (3 – 8)	12	1,664 (74 - 530)	2,030 (24 – 680)	3,694	0.84 (0.35 – 1.08)	0.85 (0.17 – 0.96)	0.93	0.37 (0.19 – 0.78)	0.37 (0.13 – 0.59)	0.37
Full estuary	27 (14 – 20)	30 (9 – 23)	36	75,942 (4,759 – 34,744)	404,420 (324 – 290,815)	480,362	1.49 (0.79 – 1.47)	0.39 (0.14 – 1.81)	0.64	0.45 (0.27 – 0.54)	0.11 (0.05 – 0.82)	0.18

[1]corrected catch abundances based on net size

Table 3.4 Catch species' characteristics; codes, common names, scientific names, and classifying assemblage. ('Marine' are only known to inhabit fully saline waters; 'brackish' are known to inhabit fully saline to brackish waters but not freshwater; 'freshwater' are euryhaline; 'outmigrant salmonids' are transient smolt outmigrants.)

Code	Common Name	Scientific Name	Assemblage
ANC	northern anchovy	*Engraulis mordax*	marine
BLRF	black rockfish	*Sebastes melanops*	marine
BYPF	bay pipefish	*Syngnathus leptorhynchus*	brackish
CHMK	chub mackerel	*Scomber japonicus*	marine
CM	chum salmon	*Oncorhynchus keta*	outmigrant salmonid
CO/COFR	coho smolt/coho fry	*Oncorhynchus kisutch*	outmigrant salmonid/ freshwater
CPRF	copper rockfish	*Sebastes caurinus*	marine
CUTT	cutthroat trout	*Oncorhynchus clarkii*	freshwater
DV	Dolly Varden	*Salvelinus malma*	freshwater
ENG	English sole	*Parophrys vetulus*	marine
FWSC	freshwater sculpin	*Cottus asper / Cottus aleuticus*	freshwater
GN	gunnel	*Pholis laeta / Pholis ornata*	marine
GRSC	great sculpin	*Myoxocephalus polyacanthocephalus*	marine
HR	Pacific herring	*Clupea pallasii*	freshwater
KPGL	kelp greenling	*Hexagrammos decagrammus*	marine
LGCD	lingcod	*Ophiodon elongatus*	marine
PDSC	padded sculpin	*Artedius fenestralis*	marine
PK	pink salmon	*Oncorhynchus gorbuscha*	outmigrant salmonid
SDSO	sand sole	*Psettichthys melanostictus*	marine
SFSM	surf smelt	*Hypomesus pretiosus*	brackish
SHPR	shiner perch	*Cymatogaster aggregata*	brackish
SHSC	smooth headed sculpin	*Artedius lateralis*	marine
SK	sockeye salmon	*Oncorhynchus nerka*	outmigrant salmonid
SL	Pacific sand lance	*Ammodytes hexapterus*	brackish
SMSH	salmon shark	*Lamna ditropis*	marine
SNDB	Pacific sanddab	*Citharichthys sordidus*	marine
SNSC	snubnose sculpin	*Orthonopias triacis*	marine
SPSN	spotted snailfish	*Liparis callyodon*	marine
SSSC	silverspotted sculpin	*Blepsias cirrhosus*	marine
STEEL	steelhead trout	*Oncorhynchus mykiss*	outmigrant salmonid
STFL	starry flounder	*Platichthys stellatus*	freshwater
STSC	staghorn sculpin	*Leptocottus armatus*	brackish
TBSN	tubesnout	*Aulorhynchus flavidus*	marine
TMCD	tomcod	*Microgadus proximus*	brackish
TPSC	tidepool sculpin	*Oligocottus maculosus*	brackish
TSSB	three-spined stickleback	*Gasterosteus aculeatus*	freshwater

[1] as reported in FishBase.se species summaries

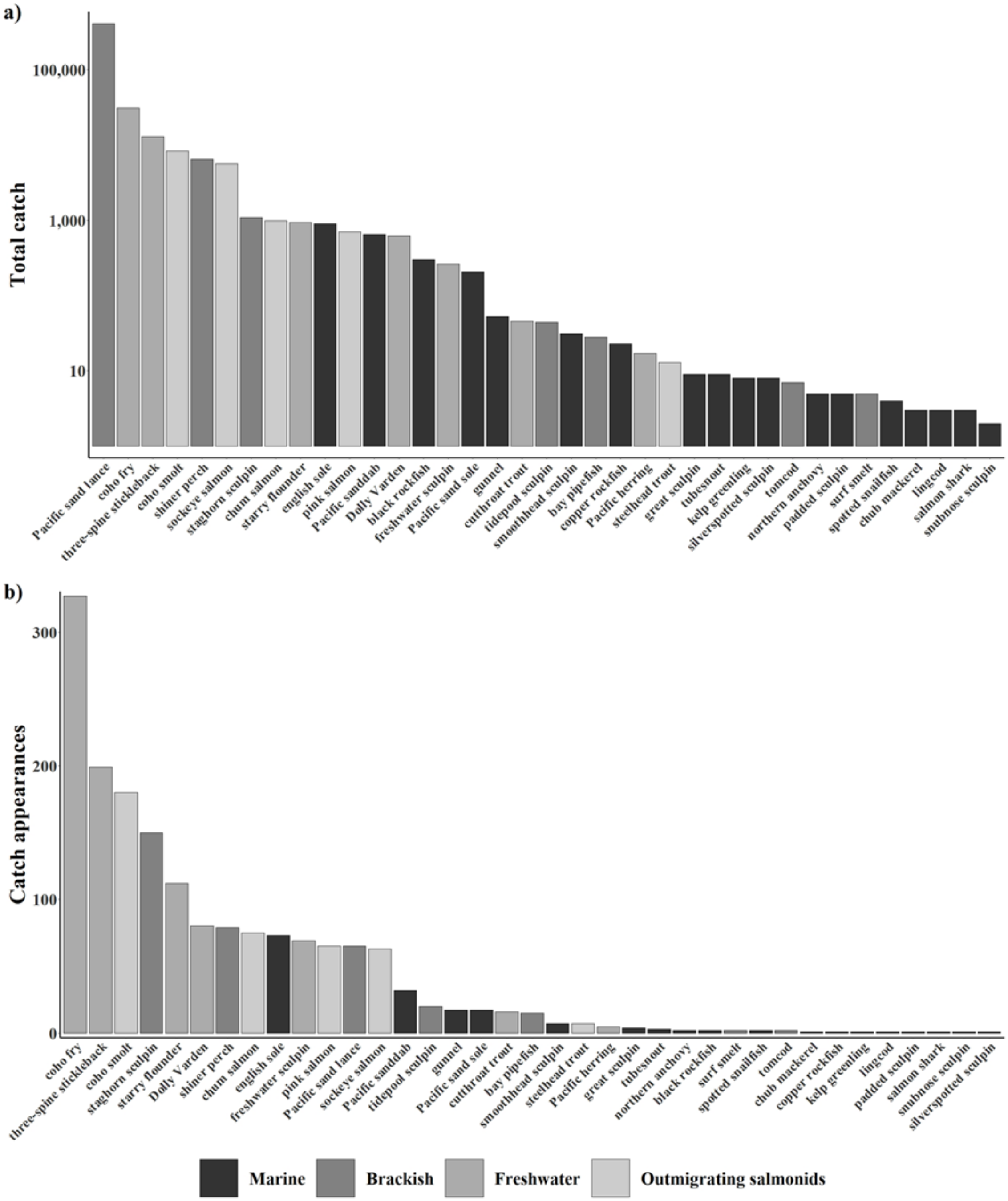

Figure 3.2 **Total catch abundance (a) and total number of appearances in the catch (b) of each species across the entire estuary during both years. Colors represent the known aquatic environments inhabited by each species.**

resulting in near fully marine conditions in the upper estuary during high tides (median salinity in Reach 6 = 24.17 PSU) and water temperatures exceeding 20°C (max water temperature in Reach 6 = 21.0°C) (Figure 3.1; Tables 3.1 and 3.2). Thus, the dry summer of 2018 resulted in notable saltwater intrusion up the estuary.

3.4.2. Fish community dynamics

The estuary fish community was strongly organized by the overarching salinity gradient. Similar to that of other transitional waters, species richness and catch abundance were both significantly correlated with and tended to increase along the salinity gradient from freshwater to marine ($\tau = 0.268$ and $p = 1.88e\text{-}14$ for richness; $\tau = 0.096$ and $p = 0.004$ for abundance) (Table 3.3; Appendix B: Table B.9.). While richness and abundance were highest in the lower marine reaches at Koeye, diversity and evenness peaked in the middle-estuary (Table 3.3). Richness in most reaches showed a slight increase in 2018, while diversity and evenness both showed declines in the middle and lower estuary but slightly increased in the upper estuary (Table 3.3).

In total, 36 different species were identified and over 480,000 individuals were captured during the course of sampling. Of the 36 species, 18 were classified as ‘marine’, 7 as ‘brackish’, 7 as ‘freshwater’, and 5 as ‘outmigrant salmonid’ (Table 3.4) (Froese and Pauly 2018). Sand lance were the most numerically abundant species caught, while coho salmon (*Oncorhynchus kisutch*) were the most frequently caught and most ubiquitous species across the estuary (Figure 3.2). Overall, ‘marine’ and ‘brackish’ fish species tended to be numerically abundant in individual catches, while ‘freshwater’ fishes had a tendency to be caught more often (Figure 3.2).

Fish community structure of each habitat type, based on the relative abundance of the 14 most abundant and frequently caught species in multi-dimensional space, was organized by temperature and salinity but also differed between study years. In multi-dimensional space, fish communities were organized by salinity levels (blue contours, Figure 3.3) and water temperatures (yellow/red contours, Figure 3.3). The loadings of specific species in this multidimensional space corresponded to the salinity and temperature regimes they were most commonly found in (Figure 3.3). For example, marine flatfish species (SDSO, SNDB, ENG; Table 3.4) were situated where salinities were highest and water temperatures were near oceanic averages (upper left of Figure

3.3), whereas outmigrant salmon (PK, CM, SK; Table 3.4) were situated where salinities and temperature were low as would be expected during spring freshet flows (lower middle of Figure 3.3). The

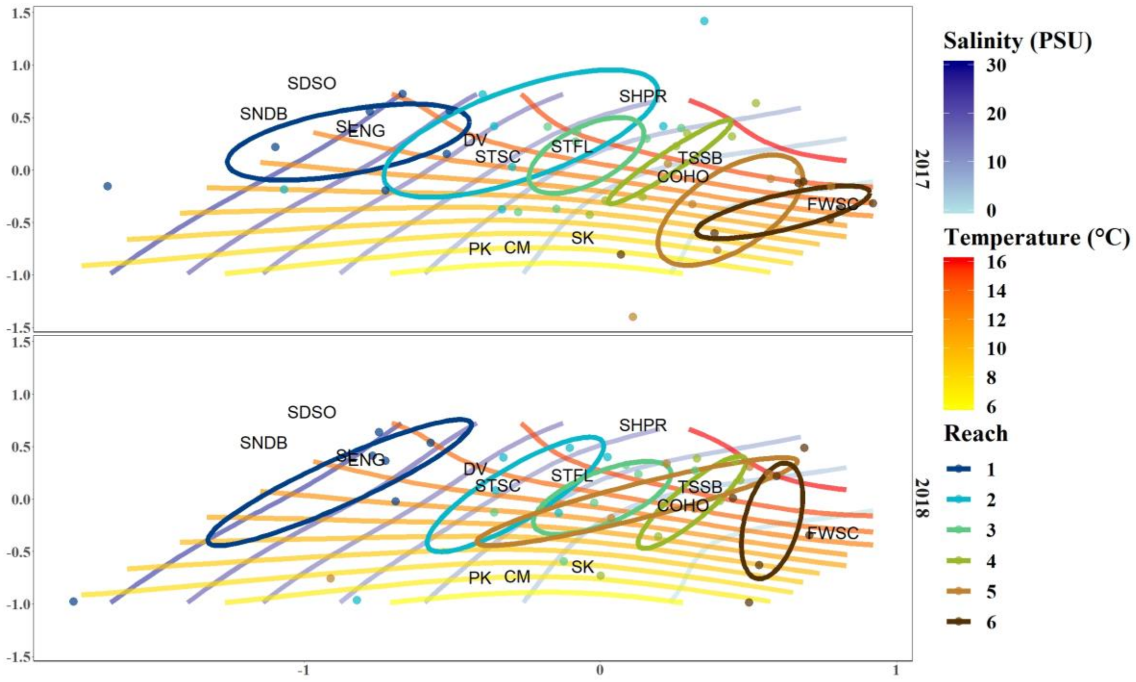

Figure 3.3 **NMDS plots of the Koeye fish communities in 2017 and 2018 with water temperature and salinity grid overlays. Species were limited to the 14 most abundant and frequently caught species to facilitate convergence. Analysis was performed in the 'vegan' package for R using Bray-Curtis dissimilarity, was constrained to two dimensions, utilized log10 transformed net-area corrected monthly total abundances for each species in each reach and monthly average water temperature and salinity measurements for each reach, and reached two solutions after 20 attempts with a final stress of 0.164. Both panels are based on the analysis of both sampling years combined, but reach ellipses were produced for each year by using only the points associated with that year.**

fish communities of the static habitats (points and ellipses) aligned closely with the salinity gradient and clearly showed a gradual community shift from upper to lower estuary reaches (right to left on Figure 3.3). Community structure varied slightly between study years, likely due to increased saltwater intrusion during 2018 (Figure 3.3).

3.4.3. Saltwater intrusion and fish response

Fish distribution patterns across the estuary habitats were dependent on species' environmental tolerances and the level of saltwater intrusion into the upper estuary reaches. Of those species caught in multiple sampling events in both years, over half were found to have different distributions across the estuary from year to year (Figure 3.4). Nine out of the 14 species with varying distributions showed expanded ranges in the drier 2018, mostly in the up-estuary direction (7 of 9) (Figure 3.4). For example, bay pipefish were only found in the lowermost Reach 1 in 2017, but in the dry 2018 summer they were found all the way up into the middle Reach 3 (Figure 3.4). Of those species which shifted their distributions up-estuary, all but 1 were from the marine or brackish assemblages (Figure 3.4).

Modelling the probability of presence (POP) of species across the estuary, using a binomial generalized linear mixed effects model, revealed that species distributions and variations in those distributions differed between assemblages of fish based on known aquatic environments (Figure 3.5 and 3.7; Appendix B: Table B.10.). Species in the 'freshwater' assemblage showed higher POP in upper estuary reaches and hardly any change in distribution between years (Figure 3.5 and 3.6; Appendix B: Table B.10.). Species in the 'brackish' assemblage were generally less likely to occur up-estuary but showed an increase in POP across the estuary in the dryer, more saline 2018 (Figure 3.5; Appendix B: Table B.10.). 'Brackish' assemblage distribution showed an expansion of range into upper estuary reaches during summer months when saltwater intrusion was highest, and this trend was exacerbated during the drier 2018 year (Figure 3.6). Species in the 'marine' assemblage showed a steep decline in POP in the up-estuary direction, becoming nearly zero by Reach 4 (Figure 3.5; Appendix B: Table B.10.). 'Marine' species showed a small increase in POP during the dry year and there was some expansion of range into the upper estuary reaches in 2018 compared to 2017, but there was no clear seasonal trend (Figure 3.5 and 3.6; Appendix B: Table B.10.). 'Outmigrant salmonid' species had slightly lower POP in the upper estuary than in the lower estuary and this trend was exaggerated during the dry year (Figure 3.7a; Appendix B: Table B.10.). 'Outmigrant salmonid' distribution across the estuary was relatively stable between months and only slightly different between years (Figure 3.7b).

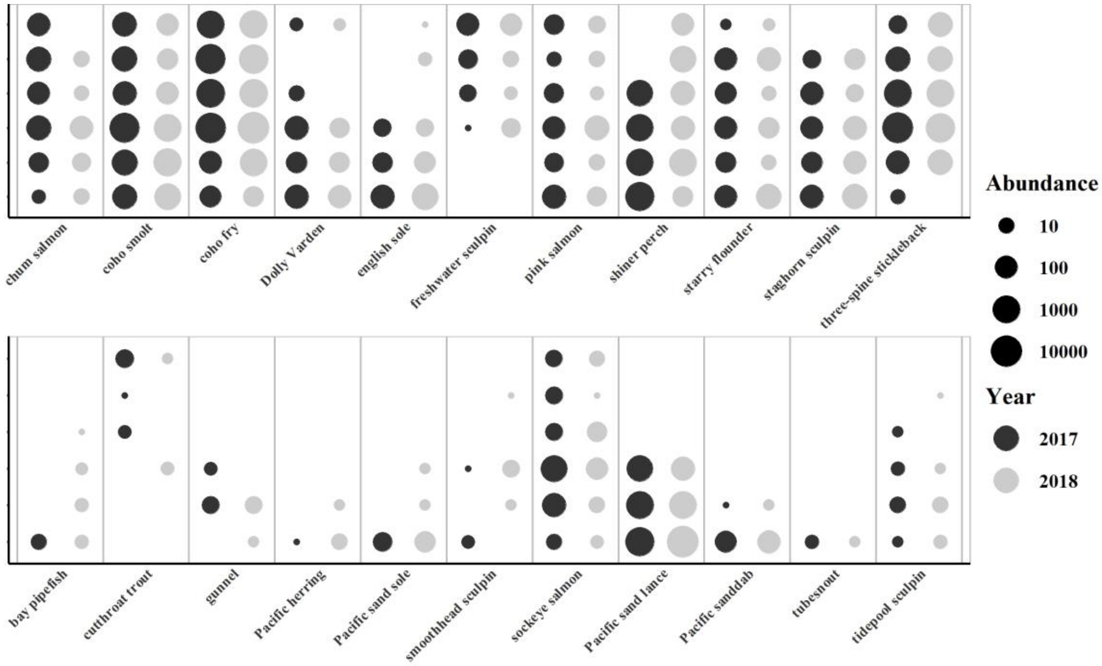

Figure 3.4 **Yearly catch abundances in each reach for species caught in both sampling years. Point areas are representative of the log10(catch abundance).**

3.5. Discussion

Estuaries are highly dynamic landscapes where shifting environmental conditions are a key determinant of community composition across the habitat mosaic (Harrison and Whitfield 2006; Selleslagh and Amara 2008; Sheaves 2016). Here, we observed shifts in species' distributions and fish community structure associated with seasonal patterns in environmental conditions and biological events, which were then exaggerated as a result of inter-year differences in climatic conditions. The primary difference between the sampling years was significantly reduced precipitation in 2018 resulting in significantly reduced river flow allowing seawater to intrude farther up the estuary (Figure 3.1). This increased saltwater intrusion led to 'marine' and 'brackish' species expanding their range up the estuary, while 'freshwater' species tended to retain their range (Figure 3.4, 3.5, and 3.6).

The estuary habitat mosaic is composed of both static (vegetation, bathymetry, etc.) and dynamic (salinity, temperature, flow, etc.) elements (Fulford et al. 2011). The perception of these combined elements presumably underpins the spatial movements of fishes, and movement between stationary habitat types is often dictated

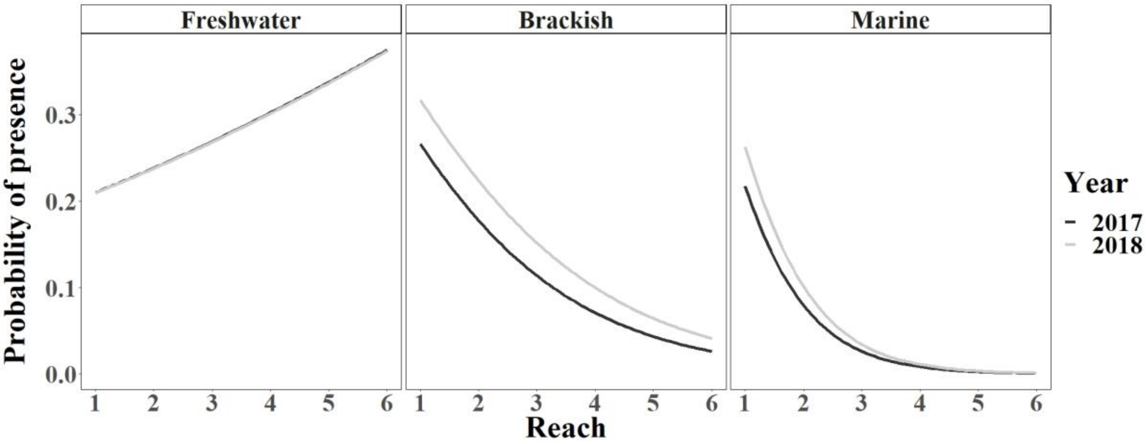

Figure 3.5 **Modeled probability of presence each year across the estuary reaches for the three non-migrant fish classes. Only species caught on more than two occasions during both sampling years were used. Outmigrant salmonids (sockeye, pink, chum, coho, and steelhead smolts) were included in the model as a fourth fish class, but their results can be found in Fig. 8. Non-migrant fish classes are based on known inhabited environments (marine, brackish, and freshwater) taken from FishBase. Model used was a binomial generalized linear mixed effects model with a logit link (presence/absence of individual species ~ (fish class * median salinity) + (1 | species) + (month | species) + (month^2 | species) + (fish class * reach)). Model results can be found in Appendix S1: Table S10.**

by an individual's tolerance of the various dynamic elements (Fulford et al. 2011; Fulford et al. 2014). Juvenile fish utilizing the estuary as nursery habitat often have shifting needs as they grow, necessitating movement between static habitat elements in order to optimize foraging and predation risk (Pope et al. 1994; Peterson 2003; Nagelkerken et al. 2015; Sheaves et al. 2015; Seitz et al. in review). Variability in the dynamic habitat elements could either limit or increase an individual's movement potential among static patches which could in turn affect growth, survival, and overall population production (Peterson 2003; Fulford et al. 2011; Nagelkerken et al. 2015; Sheaves et al. 2015).

Fish community structures in the Koeye reflect the general findings of many previous studies in that shifts in community composition are primarily aligned with the salinity and temperature gradients of the estuary (Harrison and Whitfield 2006; Selleslagh and Amara 2008; Sheaves 2016). In Koeye, it appeared that salinity was a more important driver of community structure than temperature as evidenced by the relatively similar thermal regimes occupied by the various static habitat communities (Figure 3.3) and the overall weak correlations between abundance and richness with temperature. While richness and abundance were highest in the marine reaches, diversity and evenness were highest in the middle estuary reaches (Table 3.3). As has been seen in other studies, estuary-wide diversity and evenness were reduced in the dry year, corresponding with increased saltwater intrusion (Table 3.3) (Gillanders et al. 2011).

We documented two years with contrasting environmental conditions, which enabled us to examine how different fish assemblages respond to different levels of saltwater intrusion. Reduced precipitation and river flow in 2018 led to increased saltwater intrusion up the estuary (Figure 3.1; Tables 3.1 and 3.2), allowing ‘marine’ and ‘brackish’ fishes to exploit habitat patches that were typically outside their physiological tolerance range (Figure 3.5 and 3.6). For example, the ‘marine’ English sole (Parophrys vetulus) and the ‘brackish’ shiner perch (Cymatogaster aggregata) were found all the way up into the typically freshwater Reach 6 during the dry year but were found only as far as Reaches 3 and 4 in the wet year. Interestingly, ‘freshwater’ fishes tend to conserve their distributions across the static habitat despite changing environmental conditions (Figure 3.1 and 3.6).

These results suggest that saltwater intrusion, such as that associated with climate change, will have disparate impacts on different assemblages of estuarine fishes. For example, in an analysis of the potential impacts of sea level rise on fish production in Southern United States estuaries, Fulford et al. (2014) suggests that rising sea levels and increased saltwater intrusion may increase nursery production of ‘brackish’ fish (spot; Leiostomus xanthurus). Rising sea levels are likely to cause inundation, fragmentation, and increased salinization of estuarine wetlands which could increase the local available habitat for marine and brackish water fishes but could reduce suitable habitat for freshwater species (Love et al. 2008; Fulford et al. 2014). Love et al. (2008) found that fish communities in upper estuary reaches had reduced numbers of freshwater-dependent species in drainages where saltwater intrusion was higher. Increased saltwater intrusion has also been shown to reduce species richness and diversity in Australian estuaries, primarily due to decreased abundances of freshwater and diadromous species (Gillanders et al. 2011). Salinity levels alone cannot explain all the variation in freshwater species distributions, indicating that other factors

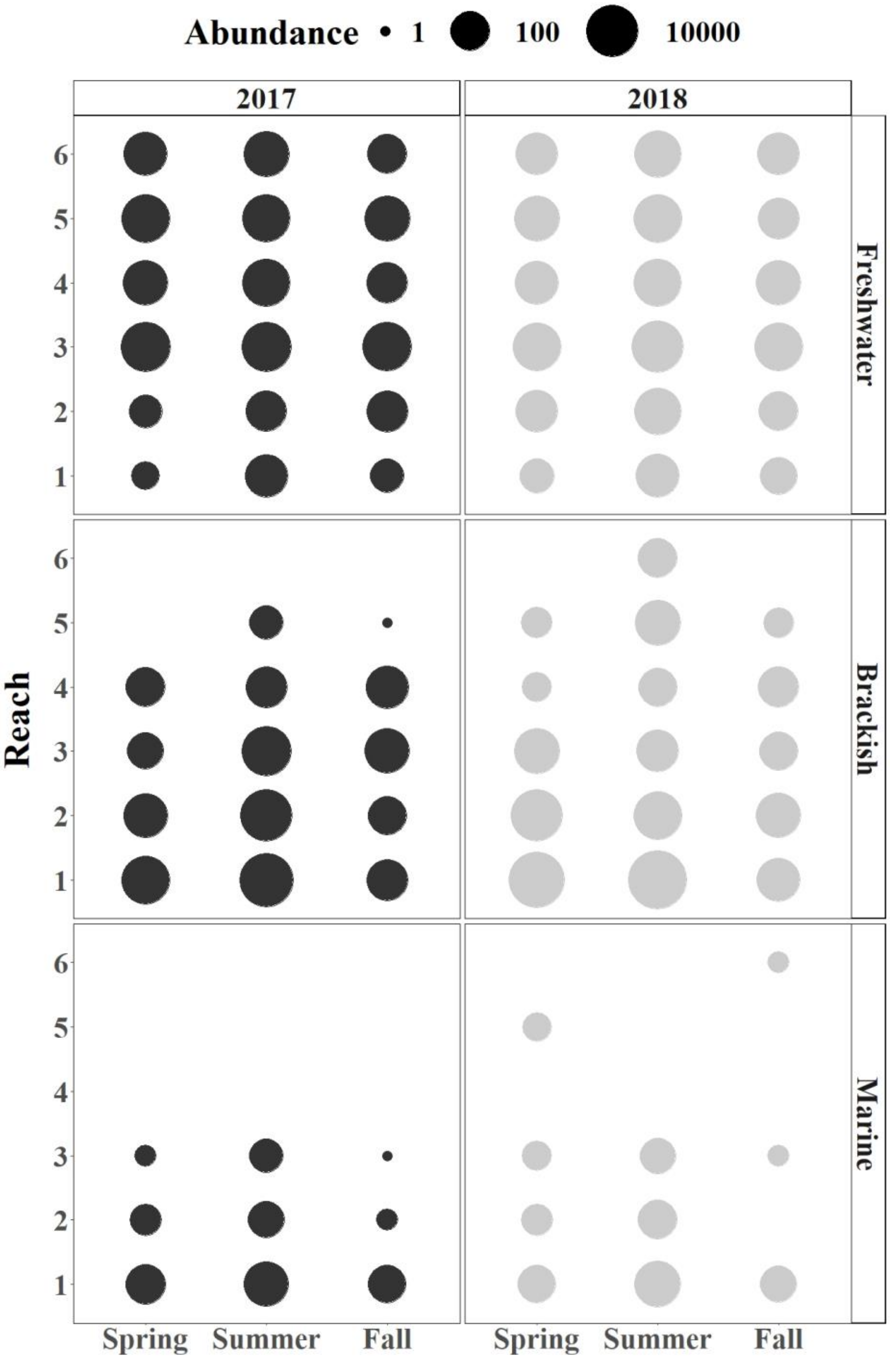

Figure 3.6 Yearly seasonal catch abundances in each reach for the three non-migrant classes of fish in the estuary. All species catches were included except outmigrant salmonids (sockeye, pink, chum, coho, and steelhead smolts) which were removed due to their highly transient nature and can be found in Fig. 8. Non-migrant fish classes are based on known inhabited environments (marine, brackish, and freshwater) taken from FishBase. Point areas are representative of the log10(catch abundance). Spring = April and May, Summer = June, July, and August, Fall = September and October.

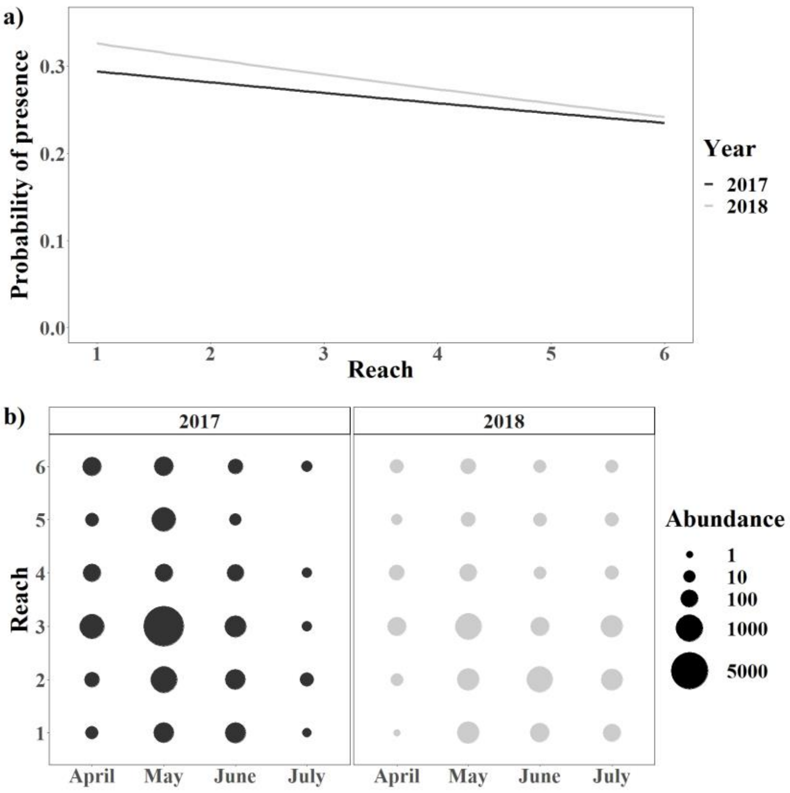

Figure 3.7 **a) Modeled probability of presence each year across the estuary reaches for outmigrant salmonids. These are from the results of the model used in Fig. 7. Model results can be found in Appendix S1: Table S10. b) Monthly catch abundances in each reach for outmigrant salmonids (sockeye, pink, chum, coho, and steelhead smolts) during each sampling year. Point areas are representative of the sqrt(catch abundance).**

such as food type and availability, competition, and predation may also be influencing their habitat use (Love et al. 2008; Gillanders et al. 2011; Whitfield 2015).

The Koeye estuary was not home to any purely freshwater fish, instead our ‘freshwater’ assemblage was composed of the most euryhaline fish species. The ‘freshwater’ assemblage has a stable distribution across the estuary throughout the season and between years, with almost no change in probability of presence between the wet and dry years. This suggests that ‘freshwater’ species have high tolerances to variable environmental conditions, have a high affinity for static habitat types, and the benefits of living in such a harsh environment must outweigh the difficulties. Even if the fish in this assemblage are apparently physiologically tolerant of a wide range of salinities, highly variable salinity regimes may increase osmoregulatory costs which could in turn impact growth and other aspects of performance. In addition, if as saltwater intrusion increases, ‘freshwater’ species retain their range while ‘marine’ and ‘brackish’ species expand theirs, ‘freshwater’ fishes will likely experience increased competition for resources in their upper estuary habitats and potentially experience increased predation pressure from newly immigrating marine species (Love et al. 2008; Gillanders et al. 2011; Whitfield 2015).

The most ubiquitous and abundant species in the ‘freshwater’ assemblage was young of year coho salmon (Figure 3.2). Though the phenomenon is still poorly understood, it has been hypothesized that estuary rearing of coho provides resilience to their populations, buffering against reduced survival in stream habitats during years of poor freshwater conditions (Koski 2009; Craig et al. 2014; Jones et al. 2014). Climate variability may influence the capacity of estuaries to support such estuary rearing. The estimated upper thermal tolerance for coho salmon in some systems is 23.4°C, but juveniles are rarely found in streams exceeding 18.0°C (Eaton et al. 1995; Welsh et al. 2001). Yet, we observed coho fry rearing in reaches of the Koeye estuary even when they exceed 20°C (max ~23°C) (Table 3.2). Thus, estuary rearing coho fry are being exposed to potentially excessively hot temperatures. As atmospheric temperatures continue to rise, summer river flows will likely continue to decrease and water temperatures increase in estuaries, which may have negative impacts on coho estuary rearing (BC Ministry of Environment 2016). Coho salmon stocks in BC have been in decline or at persistently low abundances for decades (Walters and Korman 1999). Other ‘freshwater’ fishes, such as three-spine stickleback (*Gasterosteus aculeatus*), could be similarly at risk as estuary conditions become more extreme and variable, being pushed to the margins of their habitat range in order to remain in optimal conditions or at least avoid those beyond their survival limits (Gillanders et al. 2011).

Estuaries are used by many of the Pacific salmon species as stopover habitats during seaward migration where they feed and grow, increasing their chances of survival as they transition to ocean life (Quinn 2005; Munsch et al. 2019). ‘Outmigrant salmonids’ were considered separately from ‘freshwater’ species because of the fundamental transient nature of their use of estuaries. Munsch et al. (2019) found that cooler, higher springtime flows in California systems allowed juvenile salmon to remain in estuary habitats longer and achieve larger sizes before migrating out to sea; whereas reduced flows and earlier onset of the freshet can lead to early departures from estuarine environments, causing potential mismatches in timing with food availability and disrupting trade-offs related to predation risk. Climate change has led to reduced winter snowpack which fuels river flows through the spring and early summer and has shifted spring freshets earlier in the year, decreasing smolt utilization of the estuary (BC Ministry of Environment 2016; Munsch et al. 2019). In our study, we saw higher smolt abundance in the middle estuary during the wetter, higher flow year (Reach 3 abundance/percent of total population 2017 = 8518/73.8%, 2018 = 1649/39.3%), indicating their utilization of estuarine habitats (Figure 3.7b). Smolt abundance across the estuary decreased substantially (96.1%) when river flow dropped and temperatures and salinities jumped in July 2017, suggesting that they may leave the estuary if conditions become challenging (Figures 3.1 and 3.7b). Probability of presence was higher in the lower estuary reaches for the drier, lower flow 2018 year potentially indicating reduced use of upper estuary habitats and faster transition through the mosaic (Figure 3.7a). These observations lend support to the idea that river flow, temperature, and salinity can influence residence times of migrating salmon smolts in the estuary.

Our study was based on two years of intensive study across the full extent of an estuary. Our study was performed in an estuary on the remote Central Coast of British Columbia that has never experienced major industrial activities and thus represents a rare reference system that can provide insight into the dynamics of undeveloped estuaries. Further, we contrasted two years that differed in weather to reveal how saltwater intrusion can shift fish communities. But two years is limited, and caution should be taken with inference, as there could have been other unknown differences between these years. In addition, longer-term impacts of climate change will shift the distribution of habitats that appear static on shorter time horizons. For example, saltwater intrusion and sea level rise over longer time frames could lead to shifts in habitats such as marshes (Fulford et al. 2014; Alizad et al. 2018). Thus, our study provides a step forward towards understanding the dynamics of these complicated ecosystems.

Here we provide rare evidence of the linked dynamics of estuary environmental conditions and fish communities in an era of rapid climatic change. In an undeveloped estuary in remote British Columbia, we found strong signals of shifting environmental conditions on fish community dynamics. Saltwater intrusion, associated with sea-level rise and changing hydrology signals of climate change, led to up-estuary expansion of ‘marine’ and ‘brackish’ fishes, with a lack of response of ‘freshwater’ species. Thus, not only will estuary climate change drive different responses of different fish assemblages, but also may lead to new species interactions.

Chapter 4. General Discussion

This thesis broadly examined how fishes distribute themselves among the interconnected habitats of the estuary mosaic and what factors, both biotic and abiotic, are influencing those distributions. Chapter 2 investigated nursery function across the estuary using size-spectra analysis as a way to infer the biotic factors of predation risk and productivity in different habitat types. Chapter 3 explored the effects of shifting abiotic conditions on estuarine fish community structure and species distributions. By comparing climatically divergent sampling seasons, this chapter also explored the potential responses of different species assemblages to climate change. In this concluding chapter, I provide an overview of the key findings of these studies, their implications, some associated caveats, and future directions this research could take.

Nursery habitats should provide rearing juvenile fish with favorable conditions for both growth and survival, which leads to their successful recruitment to the adult population (Beck et al. 2001; Dahlgren et al. 2006). To determine the relative nursery function of different habitat types within the Koeye River estuary, I compared the slope (λ) and intercept (Γ_H) values of the size-spectra found in each habitat, interpreted respectively as measures of predation risk and production. It was predicted that predation risk and production would both increase from the upper to lower estuary habitats, but that a habitat exhibiting particularly high nursery function might break this trade-off and show both low predation risk and high production. I found that the middle estuary mudflat habitat had the lowest median predation risk and the highest median production of all of the habitats, suggesting this habitat was exhibiting the highest overall nursery function. Intriguingly, mudflats often receive less attention as fish rearing habitats than adjacent seagrass beds and salt marshes, especially in Pacific salmon bearing watersheds (Simenstad et al. 1982; Carr-Harris et al. 2015; Levings 2016; Sharpe et al. 2019).

Size-spectra have been found to reflect changes in environmental conditions as well as shifts in the predator-prey size and abundance ratios (Blumenshine et al. 2000; Maury et al. 2007; Guiet et al. 2016; Law et al. 2009). Since sampling was done on two-week intervals throughout the growing season, I was able to track changes in the size-spectra through time for each of the habitats. I found that spectra slopes (λ) varied synchronously across all of the habitats through time, suggesting that while the magnitude of predation risk across the estuary may change through the season, the relative risk between the different habitats remains the same. Spectra intercepts (Γ_H), however, varied independently for each habitat, suggesting that production is much more closely linked to habitat and environmental conditions, being higher and more variable in the lower, marine habitats than in the upper, freshwater habitats. Shifting size-spectra across the habitat mosaic suggests that juvenile fish could track changes in productivity and predation risk between habitats, maximizing their growth potential while maintaining high survival probability throughout their ontogeny (Pope et al. 1994). This emphasizes the idea that habitat diversity and connectivity within estuaries is essential for the maintenance of optimal nursery function (Peterson 2003; Nagelkerken et al. 2015).

Size-spectra analysis is an attractive method of studying aquatic ecosystems because it is a simple two parameter system which by its nature incorporates a host of physiological and ecological processes and is purely functional, eliminating any taxonomic complexities (Giacomini et al 2016). In the context of estuary nursery function, the use of size-spectra analysis allows one to determine habitats most likely to be of value to juvenile fish of any taxa based upon a set of easily understandable criteria. The relative simplicity of the sampling and computation needed for this method make it well suited for the initial assessment of ecosystem structure and function, as well as continued monitoring of ecosystem health. As many estuaries are faced with ongoing anthropogenic change, both degenerative and restorative, size-spectra analysis could provide a quick and informative base from which further management decisions could be made. Since many estuary studies already incorporate some form of size and abundance sampling, size-spectra could be constructed from past datasets and used to augment previous findings or make cross-system comparisons. This method is also highly adaptable and can be modified in numerous ways to suit research objectives.

Estuaries are ecosystems in constant flux, necessitating that the organisms that live there be either extremely tolerant of a wide range of conditions or possess the ability to seek out conditions favorable to their existence (Stanford et al. 2005; Sheaves 2016; Teichert 2017; Brennan et al. 2019). In Chapter 3, I investigated how dynamic environmental elements, combined with static habitat structures, shaped the fish communities of the Koeye River estuary. I found that, like most estuaries, temperature and salinity were the primary abiotic determinants of species distributions and community structure within the Koeye (Harrison and Whitfield 2006; Selleslagh and Amara 2008; Sheaves 2016). Of those two, salinity appeared to be the strongest driver, having significant positive correlations with both richness and abundance. These correlations were mirrored in the habitat gradient, increasing richness and abundance from freshwater to marine habitats, emphasizing the importance of the salinity driver. Temperature also had a significant positive relationship with abundance, likely representing increased estuary use during summer, but was not correlated with richness. Diversity and evenness indices were highest in the middle estuary, indicating that these habitats are valuable to a wide variety of species, giving support to the findings in Chapter 2 regarding their nursery function.

Global climate change is predicted to effect the structure and dynamics of estuary environments in a variety of ways, but two major impacts will be through the alteration of river flow regimes and sea level rise leading to increased saltwater intrusion into the estuary (Roessig et al. 2004; Fulford et al. 2014; BC Ministry of Environment 2016; Munsch et al. 2019). The 2018 sampling year was significantly drier than 2017, which resulted in increased salinities in the upper estuary. This allowed me to examine how the distributions of estuarine fish assemblages might be altered as a result of climate change. I found that in 2018, ‘marine’ and ‘brackish’ fishes were able to exploit the increased up-estuary salinities and expand their range into habitats from which they were absent in 2017. ‘Freshwater’ fishes, however, maintained the same distribution in 2018 as they had in 2017, suggesting these species may have high affinity for static habitat types. This suggests that as saltwater intrusion into estuaries increases due to the effects of global warming, ‘marine’ and ‘brackish’ fishes will benefit from increased habitat availability and new foraging opportunities, while ‘freshwater’ fishes may locally have to contend with new competition for resources and increased osmotic stress. Studies have already observed that estuaries with increased salinity levels have decreased richness and diversity, primarily from reduced abundances of ‘freshwater’ and ‘diadromous’ fishes (Love et al. 2008; Gillanders et al. 2011). Modelling the effects of sea level rise, Fulford et al. (2014) also noted that inundation, fragmentation, and salinization of estuary wetlands was associated with increases in available habitat and nursery production for ‘marine’ and ‘brackish’ species.

Pacific salmon (*Oncorhynchus* spp.) are a foundational component of coastal ecosystems and culture of the Pacific Northwest of North America. Young of year coho salmon (*Oncorhynchus kisutch*) are the most ubiquitous and the second most abundant fish found in the Koeye estuary. This estuary rearing strategy is thought to provide resilience to coho populations by buffering against reduced survival of their stream rearing counterparts during years of poor freshwater conditions (Koski 2009; Craig et al. 2014; Jones et al. 2014). Reduced flows, rising temperatures and salinities, and the introduction of marine species into middle and upper estuary reaches could reduce the capacity of estuaries to support viable coho fry populations. The loss of this buffering system would leave coho populations, which have already been in decline, much more vulnerable to collapse (Walters and Korman 1999).

Many species of Pacific salmon use estuaries as stopover habitats during their seaward migration in order to feed, grow, and increase their chances of survival in the ocean (Quinn 2005; Munsch et al. 2019). 'Outmigrant salmon' were treated as a separate species assemblage, rather than as part of the 'freshwater' group, in Chapter 3's analysis because of their fundamental transient nature in estuaries. I found that during the wet year, 2017, salmon smolts were much more abundant in the middle estuary than the rest of the habitat areas, likely indicating their utilization of this area as stopover habitat. This usage pattern was not observed during the dry year, 2018, instead smolts had a higher probability of presence in the lower estuary, suggesting reduced utilization of estuarine rearing habitats. I also saw that smolt abundance in the estuary decreased substantially when river flow dropped and water temperatures and salinities spiked in 2017, suggesting salmon may leave the estuary abruptly if conditions become adverse. Munsch et al. (2019) found that reduced springtime river flows and warmer water temperatures led to early departures of salmon smolts from estuary rearing habitats. Early departure from estuary habitats has the potential to cause mismatches in timing with oceanic food availability and increase predation risk (Munsch et al. 2019).

My analyses were based off of two consecutive years of intensive field sampling across the full extent of the Koeye River estuary. While the sampling effort was exhaustive, two years of data is limited, and caution should be taken with inferences as there may have been other factors at play which are not presently apparent. The true effects of climate change will also be more far-reaching than what could be examined with this dataset, including, but not limited to, the gradual shifting of apparently static habitat types as environmental regimes change.

As sampling efforts are ongoing on the Koeye River estuary, new data will be incorporated into these, and further, analyses as they become available. Additional data will help to expand upon and validate the findings presented in this thesis, as well as, allow for the integration of the two chapters, investigating how size-spectra relate to environmental variables. Future research will look more closely at juvenile salmon estuary use, in particular coho fry and smolts. Work is already being done to examine juvenile coho growth rates, residence times, diets, and movements, and I hope to dovetail my thesis research with these efforts.

4.1. Final thoughts

“You can’t protect a place unless you understand it.”

– Kristine Tompkins[3]

Estuaries are one of the most heavily impacted ecosystems on Earth and continue to face threats from anthropogenic activities, despite increasing recognition of their critical ecological role (Kennish 2002; Robb 2014). Many organizations have put forth great efforts to protect and restore estuaries around the globe, but the ecological processes underlying estuary functionality are still poorly understood (Kennish 2002). Attempts to study underlying estuary processes are often hindered by the fact that most estuaries being studied have already been degraded and teasing apart natural stresses from anthropogenic ones is difficult, if not impossible (Elliott and Quintino 2007). The environmental shifts caused by climate change occur slowly, with conditions oscillating between normal and slightly aberrant but trending ever farther from the baseline as time goes by. Climate change also causes a multitude of responses within an ecosystem, making the monitoring and understanding of its effects challenging under the best circumstances (Adrian et al. 2009). The difficulties of detecting subtle shifts in community structure and ecosystem function in such a dynamic environment emphasizes the need for quality data from intact systems with little human footprints. My

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[3] Former CEO of Patagonia, Inc., President and Cofounder of Tompkins Conservation, UN Environment Patron of Protected Areas (Planet unplugged speaker series, UN Environment Programme).

work on the Koeye River estuary provides just that; rare insights into the workings of a nearly pristine estuary system. It is my hope that this thesis has contributed to the understanding of how static and dynamic habitat elements interact to shape estuarine fish community structure without the added influence of anthropogenic impacts. I hope my limited insights into the potential effects of climate change on different estuary fish species assemblages will be useful to those attempting to untangle climate signals in systems with additional human complications. And I hope I have provided a new and useful analytical tool for the estuary scientist's toolbox through my application of size-spectra analysis.

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Appendix A. Supplemental information for Chapter 2

Table A.1. Water chemistry parameters and habitat characteristics found in each sampling reach.

	Water chemistry parameters[1]				Habitat characteristics		
Reach	Temperature (°C)	Salinity (PSU[a])	O_2 (mg/L)	pH	Tide height (m)[2]	Substrate[3]	Vegetation[4]
1	12.7 (7.7 - 15.4)	30.1 (20.48 - 46.78)	10.09 (8.66 - 11.03)	8.13 (7.86 - 8.31)	1.8 (0.9 - 3.1)	SD	-
2	13.3 (6.7 - 15.9)	26.8 (0.06 - 37.49)	10.67 (8.48 - 12.15)	8.08 (6.51 - 8.34)	2.4 (1.2 - 3.6)	GV, SD, CB	EG, RW
3	14.2 (6.8 - 19.0)	9.45 (0.02 - 37.00)	10.47 (7.88 - 12.27)	7.85 (6.36 - 8.28)	2.8 (1.3 - 4.1)	MD, GV, CB	RW, MG, EG
4	14.7 (6.0 - 18.5)	1.82 (0.01 - 33.60)	10.39 (8.33 - 13.05)	7.69 (6.04 - 8.29)	3.4 (2.7 - 4.1)	GV, CB	MG
5	15.2 (6.1 - 21.6)	0.71 (0.01 - 23.19)	10.33 (8.28 - 12.74)	7.32 (6.03 - 8.44)	3.2 (1.6 - 4.1)	GV, MD	MG
6	14.5 (5.1 - 21.0)	0.01 (0.00 - 28.11)	10.34 (8.63 - 12.67)	6.51 (6.09 - 8.00)	3.6 (2.6 - 4.1)	GV, CB	MG

[1] Median and range values of water chemistry parameters. [a] Practical Salinity Unit. [2] Median and range values of tide height at time of sampling. [3] Substrates observed at sampling sites. (SD = sand, GV = gravel, CB = cobble, MD = mud). [4] Aquatic and shoreline vegetation observed at sampling sites. (EG = eelgrass, RW = rockweed, MG = marsh grass).

Table A.2. Yearly totals and ranges of monthly values found in each reach and the for the full estuary, as well as the overall study values, for species richness, catch abundance, Shannon-wiener diversity index, and Pielou's evenness index.

Reach	Species richness	Catch abundance[1]	Shannon-wiener diversity index	Pielou's evenness index
1	24 (2 – 16)	194,568 (4 – 152,538)	0.06 (0.03 – 1.73)	0.02 (0.01 – 0.81)
2	21 (6 – 14)	8,261 (18 – 5,322)	0.91 (0.26 – 1.52)	0.30 (0.10 – 0.86)
3	19 (6 – 12)	7,007 (176 – 2,402)	0.97 (0.36 – 1.51)	0.33 (0.15 – 0.84)
4	10 (4 – 7)	3,086 (58 – 796)	1.07 (0.40 – 1.15)	0.46 (0.29 – 0.64)
5	12 (3 – 10)	1,755 (9 – 546)	1.00 (0.15 – 1.26)	0.40 (0.09 – 0.70)
6	10 (3 – 8)	2,040 (24 – 680)	0.85 (0.17 – 0.96)	0.37 (0.13 – 0.59)
Full estuary	30 (9 – 23)	216,717 (289 – 162,284)	0.39 (0.14 – 1.81)	0.11 (0.05 – 0.82)

[1] corrected catch abundances based on net size

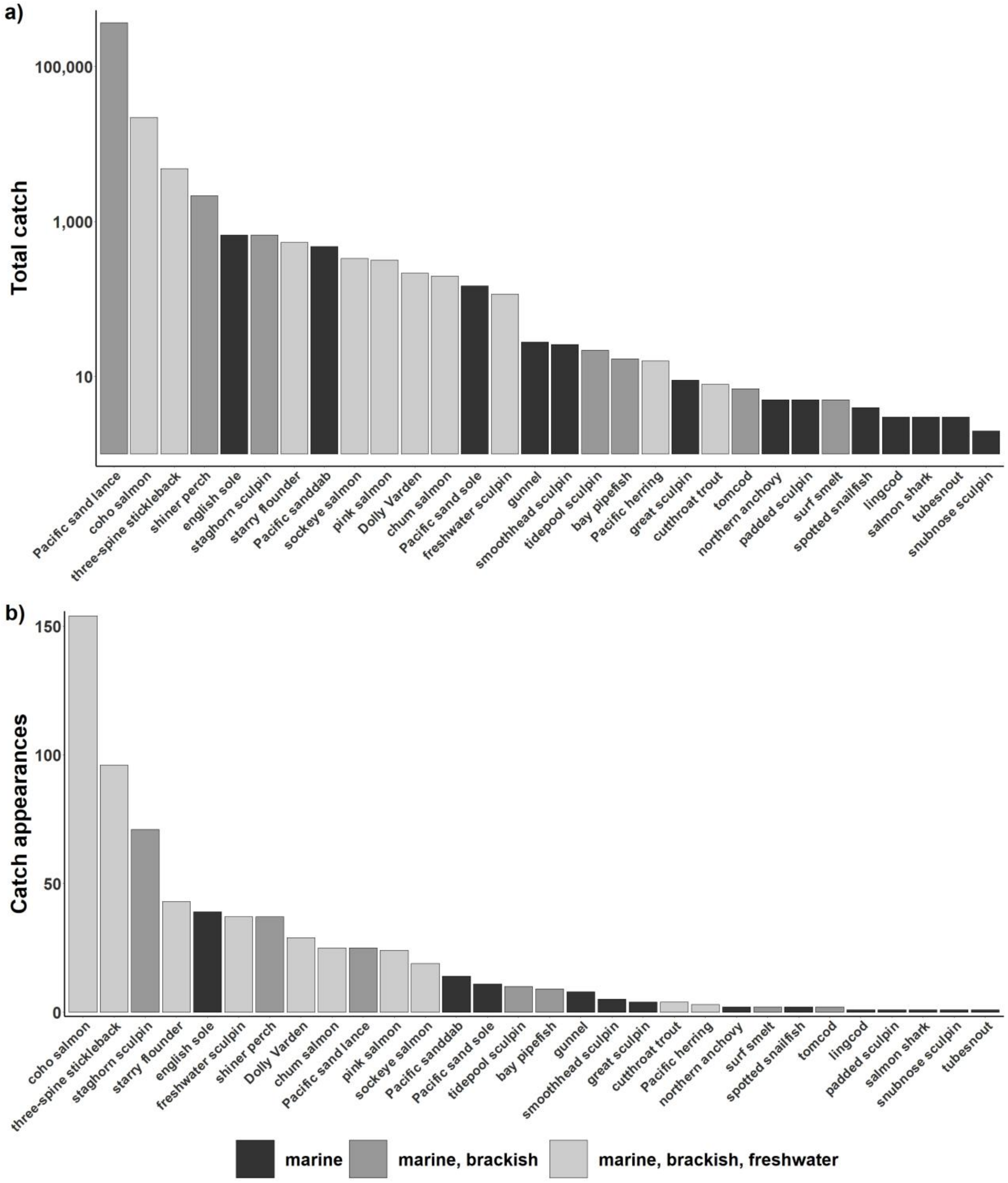

Figure A.1. Total corrected catch abundance (a) and total number of appearances in the catch (b) of each species across the entire estuary. Colors represent the known aquatic environments inhabited by each species.

Appendix B. Supplemental information for Chapter 3

Table B.1. Kruskal-Wallis and Conover-Iman pairwise comparison results for salinity. Conover-Iman test result *p*-values adjusted using the Holm method.

a. Full estuary salinity differences between years.

Salinity ~ Year - Kruskal-Wallis chi-squared = 13.631, df = 1, p-value = 0.0002225*

b. Monthly whole estuary differences in salinity, both years combined.

Salinity ~ Month - Kruskal-Wallis chi-squared = 16.3753, df = 5, p-value = 0.01*

Month	**April**	**May**	**June**	**July**	**August**
May	T = 0.288649 *p* = 1.0000				
June	T = -0.316133 *p* = 1.0000	T = -1.027512 *p* = 1.0000			
July	T = -1.474073 *p* = 1.0000	T = -3.023497 *p* = 0.0372*	T = -1.906989 *p* = 0.5721		
August	T = -1.671425 *p* = 0.8585	T = -3.134264 *p* = 0.0277*	T = -2.125209 *p* = 0.3758	T = -0.392106 *p* = 1.0000	
September	T = -0.038017 *p* = 0.9697	T = -0.571672 *p* = 1.0000	T = 0.473152 *p* = 1.0000	T = 2.450329 *p* = 0.1762	T = 2.617233 *p* = 0.1195

c. Differences in salinities of each month between years.

Salinity ~ Year + Month - Kruskal-Wallis chi-squared = 27.122, df = 10, p-value = 0.002491*

Month Year	**May 2017**	**June 2017**	**July 2017**	**August 2017**	**September 2017**
May 2018	T = -2.687627 p = 0.2921				
June 2018		T = 0.408280 p = 1.0000			
July 2018			T = 0.583379 p = 1.0000		
August 2018				T = -5.349912 p = 0.0000*	
September 2018					T = -3.185346 p = 0.0654

d. Differences in salinity between reaches, both years combined.

Salinity ~ Reach - Kruskal-Wallis chi-squared = 228.06, df = 5, p-value < 2.2e-16*

Reach	**1**	**2**	**3**	**4**	**5**
2	T = 4.991990 *p* = 0.0000*				
3	T = 9.978008 *p* = 0.0000*	T = 4.883337 *p* = 0.0000*			
4	T = 12.06793 *p* = 0.0000*	T = 7.420812 *p* = 0.0000*	T = 3.086468 *p* = 0.0022*		
5	T = 15.15753 *p* = 0.0000*	T = 10.59869 *p* = 0.0000*	T = 6.431196 *p* = 0.0000*	T = 3.089595 *p* = 0.0043*	
6	T = 19.24636 *p* = 0.0000*	T = 14.88799 *p* = 0.0000*	T = 11.02143 *p* = 0.0000*	T = 7.422255 *p* = 0.0000*	T = 4.395082 *p* = 0.0000*

e. Differences in salinity of each reach between years.

Salinity ~ Year + Reach - Kruskal-Wallis chi-squared = 248.22, df = 11, p-value < 2.2e-16*

Year-Reach	**2017-1**	**2017-2**	**2017-3**	**2017-4**	**2017-5**	**2017-6**
2018-1	T = -1.478656 *p* = 1.0000					
2018-2		T = -3.060866 *p* = 0.0424*				
2018-3			T = -4.059939 *p* = 0.0012*			
2018-4				T = -3.110844 *p* = 0.0379*		
2018-5					T = -2.957166 *p* = 0.0526	
2018-6						T = -1.303136 *p* = 0.9663

f. Differences in monthly salinities of each reach between years. Significant results only.

Salinity ~ Year + Month + Reach Significant Between Year Conover-Iman Results				
Reach 1 – August	**Reach 2 – September**	**Reach 3 – May**	**Reach 3 – August**	**Reach 3 - September**
T = -3.830726 *p* = 0.0184*	T = -3.772288 *p* = 0.0196*	T = -4.352480 *p* = 0.0021*	T = -3.800849 *p* = 0.0136*	T = -3.446562 *p* = 0.0406*

Table B.2. Kruskal-Wallis and Conover-Iman pairwise comparison results for river elevation. Conover-Iman test result p-values adjusted using the Holm method.

a. Mean daily river elevation differences between years.

River elevation ~ Year - Kruskal-Wallis chi-squared = 8.8186, df = 1, p-value = 0.002982*

b. Monthly differences in mean daily river elevation, both years combined.

River elevation ~ Month - Kruskal-Wallis chi-squared = 155.95, df = 5, p-value < 2.2e-16*

Month	April	May	June	July	August
May	T = 4.553503 *p* = 0.0000*				
June	T = 6.332612 *p* = 0.0000*	T = 1.869298 *p* = 0.1872			
July	T = 12.59783 *p* = 0.0000*	T = 8.111095 *p* = 0.0000*	T = 6.105466 *p* = 0.0000*		
August	T = 14.08040 *p* = 0.0000*	T = 9.605961 *p* = 0.0000*	T = 7.575206 *p* = 0.0000*	T = 1.494865 *p* = 0.2717	
September	T = 7.281345 *p* = 0.0000*	T = 2.845441 *p* = 0.0188*	T = 0.968688 *p* = 0.3334	T = -5.093424 *p* = 0.0000*	T = -6.556548 *p* = 0.0000*

c. Differences in mean daily river elevation for each month between years.

River elevation ~ Year + Month - Kruskal-Wallis chi-squared = 197.77, df = 11, p-value < 2.2e-16*

Month Year	**April 2017**	**May 2017**	**June 2017**	**July 2017**	**August 2017**	**September 2017**
April 2018	T = -1.803588 *p* = 1.0000					
May 2018		T = 4.519542 *p* = 0.0003*				
June 2018			T = 0.141232 *p* = 1.0000			
July 2018				T = -1.395845 *p* = 1.0000		
August 2018					T = 7.930618 *p* = 0.0000*	
September 2018						T = 1.191515 *p* = 1.0000

Table B.3. **Kruskal-Wallis and Conover-Iman pairwise comparison results for water temperature. Conover-Iman test result *p*-values adjusted using the Holm method.**

a. Full estuary temperature differences between years.

Water temperature ~ Year - Kruskal-Wallis chi-squared = 0.18741, df = 1, *p*-value = 0.6651

b. Monthly whole estuary differences in water temperature, both years combined.

Water temperature ~ Month - Kruskal-Wallis chi-squared = 223.49, df = 5, *p*-value < 2.2e-16*

Month	**April**	**May**	**June**	**July**	**August**
May	T = -4.659140 *p* = 0.0000*				
June	T = -6.541965 *p* = 0.0000*	T = -3.340741 *p* = 0.0018*			
July	T = -12.85823 *p* = 0.0000*	T = -14.19395 *p* = 0.0000*	T = -10.38389 *p* = 0.0000*		
August	T = -14.07689 *p* = 0.0000*	T = -15.53082 *p* = 0.0000*	T = -12.06842 *p* = 0.0000*	T = -2.633956 *p* = 0.0088*	
September	T = -10.67449 *p* = 0.0000*	T = -10.57311 *p* = 0.0000*	T = -6.795590 *p* = 0.0000*	T = 3.907932 *p* = 0.0003*	T = 6.229919 *p* = 0.0000*

c. Differences in water temperatures of each month between years.

Water temp ~ Year + Month - Kruskal-Wallis chi-squared = 43.517, df = 10, p-value = 4.018e-06*

Month Year	**May 2017**	**June 2017**	**July 2017**	**August 2017**	**September 2017**
May 2018	T = -6.208189 *p* = 0.0000*				
June 2018		T = -1.620815 *p* = 0.6350			
July 2018			T = 2.161772 *p* = 0.3122		
August 2018				T = -1.156854 *p* = 0.9920	
September 2018					T = 0.991649 *p* = 0.9659

d. Differences in water temperatures between reaches, both years combined.

Water temperature ~ Reach - Kruskal-Wallis chi-squared = 18.081, df = 5, p-value = 0.002847*

Reach	**1**	**2**	**3**	**4**	**5**
2	T = -1.139902 *p* = 1.0000				
3	T = -2.872764 *p* = 0.0513	T = -1.729469 *p* = 0.6758			
4	T = -3.058442 *p* = 0.0308*	T = -2.005941 *p* = 0.4096	T = -0.438237 *p* = 1.0000		
5	T = -3.077532 *p* = 0.0312*	T = -2.025577 *p* = 0.4345	T = -0.458903 *p* = 1.0000	T = -0.019090 *p* = 0.9848	
6	T = -3.344448 *p* = 0.0135*	T = -2.320462 *p* = 0.2288	T = -0.803144 *p* = 1.0000	T = -0.347798 *p* = 1.0000	T = -0.329094 *p* = 1.0000

e. Differences in water temperatures of each reach between years.

Water temperature ~ Year + Reach - Kruskal-Wallis chi-squared = 20.8023, df = 11, p-value = 0.04*						
Year-Reach	**2017-1**	**2017-2**	**2017-3**	**2017-4**	**2017-5**	**2017-6**
2018-1	T = 1.334610 *p* = 1.0000					
2018-2		T = 0.686361 *p* = 1.0000				
2018-3			T = 0.157628 *p* = 1.0000			
2018-4				T = -0.230211 *p* = 1.0000		
2018-5					T = -0.676324 *p* = 1.0000	
2018-6						T = 0.035420 *p* = 0.9718

f. Differences in monthly water temperatures of each reach between years. Significant results only.

Water temperature ~ Year + Month + Reach Significant Between Year Conover-Iman Results		
Reach 1 – July	**Reach 2 – May**	**Reach 4 – May**
T = 3.450692 *p* = 0.0492*	T = -4.021572 *p* = 0.0072*	T = -3.830421 *p* = 0.0141*

Table B.4. Kruskal-Wallis and Conover-Iman pairwise comparison results for catch abundance. Conover-Iman test result *p*-values adjusted using the Holm method.

a. Full estuary catch abundance differences between years.

Catch abundance ~ Year - Kruskal-Wallis chi-squared = 23.586, df = 1, p-value = 1.194e-06*

b. Monthly whole estuary differences in catch abundance, both years combined.

Catch abundance ~ Month - Kruskal-Wallis chi-squared = 48.488, df = 5, p-value = 2.824e-09*

Month	April	May	June	July	August
May	T = -4.926754 *p* = 0.0000*				
June	T = -5.933955 *p* = 0.0000*	T = -1.459607 *p* = 0.5802			
July	T = -4.899381 *p* = 0.0000*	T = -0.206501 *p* = 0.8365	T = 1.195248 *p* = 0.6977		
August	T = -5.929348 *p* = 0.0000*	T = -1.839819 *p* = 0.3985	T = -0.501621 *p* = 1.0000	T = -1.591291 *p* = 0.5610	
September	T = -2.833826 *p* = 0.0431*	T = 2.255706 *p* = 0.1718	T = 3.515818 *p* = 0.0048*	T = 2.337625 *p* = 0.1585	T = 3.692467 *p* = 0.0027*

c. Differences in catch abundance of each month between years.

Catch abundance ~ Year + Month - Kruskal-Wallis chi-squared = 84.226, df = 11, p-value = 2.236e-13*

Month Year	April 2017	May 2017	June 2017	July 2017	August 2017	September 2017
April 2018	T = 1.835868 *p* = 1.0000					
May 2018		T = -1.208471 *p* = 1.0000				
June 2018			T = -4.083413 *p* = 0.0027*			
July 2018				T = -3.224464 *p* = 0.0580		
August 2018					T = -1.841779 *p* = 1.0000	
September 2018						T = -2.643737 *p* = 0.3050

d. Differences in catch abundance between reaches, both years combined.

Catch abundance ~ Reach - Kruskal-Wallis chi-squared = 38.288, df = 5, p-value = 3.303e-07*

Reach	**1**	**2**	**3**	**4**	**5**
2	T = 1.819547 *p* = 0.5556				
3	T = -2.858984 *p* = 0.0488*	T = -4.952094 *p* = 0.0000*			
4	T = 1.375396 *p* = 1.0000	T = -0.427345 *p* = 1.0000	T = 4.404259 *p* = 0.0002*		
5	T = 1.849577 *p* = 0.5849	T = 0.099115 *p* = 0.9211	T = 4.845841 *p* = 0.0000*	T = 0.508789 *p* = 1.0000	
6	T = 1.931867 *p* = 0.5397	T = 0.203283 *p* = 1.0000	T = 4.895879 *p* = 0.0000*	T = 0.606746 *p* = 1.0000	T = 0.101587 *p* = 1.0000

e. Differences in catch abundance of each reach between years.

Catch abundance ~ Year + Reach - Kruskal-Wallis chi-squared = 68.371, df = 11, p-value = 2.489e-10*

Year-Reach	2017-1	2017-2	2017-3	2017-4	2017-5	2017-6
2018-1	T = -3.734932 *p* = 0.0112*					
2018-2		T = -2.400485 *p* = 0.7206				
2018-3			T = -1.011764 *p* = 1.0000			
2018-4				T = -2.735768 *p* = 0.3035		
2018-5					T = -2.206759 *p* = 1.0000	
2018-6						T = -1.070458 *p* = 1.0000

f. Differences in monthly catch abundance of each reach between years. Significant results only.

Catch abundance ~ Year + Month + Reach
Significant Between Year Conover-Iman Results

Reach 1 – July - T = -4.363162, *p* = 0.0032*

Table B.5. Kruskal-Wallis and Conover-Iman pairwise comparison results for species richness. Conover-Iman test result *p*-values adjusted using the Holm method.

a. Full estuary species richness differences between years.

Species richness ~ Year - Kruskal-Wallis chi-squared = 16.02, df = 1, p-value = 6.269e-05*

b. Monthly whole estuary differences in species richness, both years combined.

Species richness ~ Month - Kruskal-Wallis chi-squared = 32.535, df = 5, p-value = 4.653e-06*

Month	April	May	June	July	August
May	T = -3.581179 *p* = 0.0045*				
June	T = -3.438061 *p* = 0.0070*	T = -0.058173 *p* = 0.9536			
July	T = -4.312931 *p* = 0.0003*	T = -1.014798 *p* = 1.0000	T = -0.893848 *p* = 0.7437		
August	T = -4.750637 *p* = 0.0000*	T = -1.830485 *p* = 0.4746	T = -1.686639 *p* = 0.5539	T = -0.896957 *p* = 1.0000	
September	T = -1.493150 *p* = 0.6803	T = 2.294564 *p* = 0.1997	T = 2.197418 *p* = 0.2277	T = 3.154903 *p* = 0.0171*	T = 3.716163 *p* = 0.0029*

c. Differences in species richness of each month between years.

Species richness ~ Year + Month - Kruskal-Wallis chi-squared = 51.239, df = 11, p-value = 3.744e-07*						
Month Year	**April 2017**	**May 2017**	**June 2017**	**July 2017**	**August 2017**	**September 2017**
April 2018	T = 0.205463 *p* = 1.0000					
May 2018		T = -1.917394 *p* = 1.0000				
June 2018			T = -0.956705 *p* = 1.0000			
July 2018				T = -2.092522 *p* = 1.0000		
August 2018					T = -2.577272 *p* = 0.4822	
September 2018						T = -2.188030 *p* = 1.0000

d. Differences in species richness between reaches, both years combined.

Species richness ~ Reach - Kruskal-Wallis chi-squared = 85.824, df = 5, p-value < 2.2e-16*

Reach	**1**	**2**	**3**	**4**	**5**
2	T = 3.197781 *p* = 0.0118*				
3	T = 0.320267 *p* = 0.7489	T = -3.143992 *p* = 0.0124*			
4	T = 4.848534 *p* = 0.0000*	T = 1.765830 *p* = 0.3122	T = 4.929352 *p* = 0.0000*		
5	T = 7.655366 *p* = 0.0000*	T = 4.727748 *p* = 0.0000*	T = 7.951641 *p* = 0.0000*	T = 2.947106 *p* = 0.0202*	
6	T = 5.901953 *p* = 0.0000*	T = 2.946810 *p* = 0.0168*	T = 6.050019 *p* = 0.0000*	T = 1.216344 *p* = 0.4489	T = -1.666605 *p* = 0.2887

e. Differences in species richness of each reach between years.

Species richness ~ Year + Reach - Kruskal-Wallis chi-squared = 107.45, df = 11, p-value < 2.2e-16*

Year-Reach	**2017-1**	**2017-2**	**2017-3**	**2017-4**	**2017-5**	**2017-6**
2018-1	T = -3.064669 *p* = 0.0921					
2018-2		T = -1.769466 *p* = 1.0000				
2018-3			T = -1.732697 *p* = 1.0000			
2018-4				T = -0.940082 *p* = 1.0000		
2018-5					T = -3.120349 *p* = 0.0786	
2018-6						T = -1.010166 *p* = 1.0000

f. Differences in monthly species richness of each reach between years. Significant results only.

Species richness ~ Year + Month + Reach **Significant Between Year Conover-Iman Results**
Reach 1 – July - T = -3.679008, p = 0.0290*

Table B.6. Kruskal-Wallis and Conover-Iman pairwise comparison results for precipitation. Conover-Iman test result p-values adjusted using the Holm method.

a. Daily precipitation differences between years.

Precipitation ~ Year - Kruskal-Wallis chi-squared = 2.4155, df = 1, p-value = 0.1201

b. Monthly differences in daily precipitation, both years combined.

Precipitation ~ Month - Kruskal-Wallis chi-squared = 23.191, df = 5, p-value = 0.0003104*

Month	**April**	**May**	**June**	**July**	**August**
May	T = 2.688830 *p* = 0.0900				
June	T = 1.807712 *p* = 0.5719	T = -0.866360 *p* = 1.0000			
July	T = 4.485906 *p* = 0.0001*	T = 1.811990 *p* = 0.6374	T = 2.663437 *p* = 0.0889		
August	T = 3.341861 *p* = 0.0129*	T = 0.658450 *p* = 1.0000	T = 1.519391 *p* = 0.9068	T = -1.153539 *p* = 0.9978	
September	T = 1.462174 *p* = 0.8674	T = -1.214719 *p* = 1.0000	T = -0.345537 *p* = 0.7299	T = -3.011795 *p* = 0.0361*	T = -1.867750 *p* = 0.6261

c. Differences in daily precipitation for each month between years.

Precipitation ~ Year + Month - Kruskal-Wallis chi-squared = 36.945, df = 11, p-value = 0.0001177*

Month Year	April 2017	May 2017	June 2017	July 2017	August 2017	September 2017
April 2018	T = 0.491980 *p* = 1.0000					
May 2018		T = 2.412084 *p* = 0.7857				
June 2018			T = -2.159284 *p* = 1.0000			
July 2018				T = 0.526971 *p* = 1.0000		
August 2018					T = 1.744413 *p* = 1.0000	
September 2018						T = 0.893907 *p* = 1.0000

Table B.7. Kruskal-Wallis and Conover-Iman pairwise comparison results for air temperature. Conover-Iman test result p-values adjusted using the Holm method.

a. Mean daily air temperature differences between years.

Air temperature ~ Year - Kruskal-Wallis chi-squared = 0.0071375, df = 1, p-value = 0.9327

b. Monthly differences in mean daily air temperatures, both years combined.

Air temperature ~ Month - Kruskal-Wallis chi-squared = 253.33, df = 5, p-value < 2.2e-16*

Month	April	May	June	July	August
May	T = -6.671199 *p* = 0.0000*				
June	T = -13.41482 *p* = 0.0000*	T = -6.853133 *p* = 0.0000*			
July	T = -22.66436 *p* = 0.0000*	T = -16.12589 *p* = 0.0000*	T = -9.140030 *p* = 0.0000*		
August	T = -23.18885 *p* = 0.0000*	T = -16.65473 *p* = 0.0000*	T = -9.664520 *p* = 0.0000*	T = -0.528842 *p* = 0.5972	
September	T = -14.29633 *p* = 0.0000*	T = -7.741844 *p* = 0.0000*	T = -0.881514 *p* = 0.7573	T = 8.251320 *p* = 0.0000*	T = 8.775810 *p* = 0.0000*

c. Differences in mean daily air temperatures for each month between years.

Air temperature ~ Year + Month - Kruskal-Wallis chi-squared = 259.05, df = 11, p-value < 2.2e-16*

Month Year	April 2017	May 2017	June 2017	July 2017	August 2017	September 2017
April 2018	T = -0.176204 *p* = 1.0000					
May 2018		T = -2.317041 *p* = 0.2529				
June 2018			T = -0.352409 *p* = 1.0000			
July 2018				T = -1.586383 *p* = 1.0000		
August 2018					T = 0.899609 *p* = 1.0000	
September 2018						T = 3.200678 *p* = 0.0224*

Table B.8. Kruskal-Wallis and Conover-Iman pairwise comparison results for solar radiation. Conover-Iman test result p-values adjusted using the Holm method.

a. Daily maximum solar radiation differences between years.

Solar radiation ~ Year - Kruskal-Wallis chi-squared = 2.1633, df = 1, p-value = 0.1413

b. Monthly differences in daily maximum solar radiation, both years combined.

Solar radiation ~ Month - Kruskal-Wallis chi-squared = 85.864, df = 5, p-value < 2.2e-16*

Month	April	May	June	July	August
May	T = -3.398278 *p* = 0.0045*				
June	T = -3.435433 *p* = 0.0046*	T = -0.065199 *p* = 0.9481			
July	T = -5.662097 *p* = 0.0000*	T = -2.282606 *p* = 0.0921	T = -2.198619 *p* = 0.0856		
August	T = 0.325360 *p* = 1.0000	T = 3.754540 *p* = 0.0018*	T = 3.788838 *p* = 0.0018*	T = 6.037147 *p* = 0.0000*	
September	T = 3.482466 *p* = 0.0045*	T = 6.909174 *p* = 0.0000*	T = 6.917900 *p* = 0.0000*	T = 9.172993 *p* = 0.0000*	T = 3.185535 *p* = 0.0079*

c. Differences in daily maximum solar radiation for each month between years.

Solar radiation ~ Year + Month - Kruskal-Wallis chi-squared = 94.226, df = 11, p-value = 2.465e-15*

Month Year	April 2017	May 2017	June 2017	July 2017	August 2017	September 2017
April 2018	T = -0.315317 *p* = 1.0000					
May 2018		T = -1.899571 *p* = 1.0000				
June 2018			T = 1.261270 *p* = 1.0000			
July 2018				T = -0.765867 *p* = 1.0000		
August 2018					T = -2.244074 *p* = 0.7379	
September 2018						T = -0.108826 *p* = 0.9134

Table B.9. **Correlations between static (reach) and dynamic (salinity, water temperature) habitat variables and community attributes (catch abundance, species richness) using Kendall's Tau (τ).**

Year	Correlation	*p*-value	τ
Combined	Salinity ~ Abundance	0.003524*	0.095649 (0.036, 0.155)
Combined	Salinity ~ Richness	1.89e-14*	0.268474 (0.202, 0.335)
Combined	Temperature ~ Abundance	0.03577*	0.068923 (0.003, 0.139)
Combined	Temperature ~ Richness	0.6725	0.014843 (-0.052, 0.081)
Combined	Reach ~ Abundance	0.02063*	-0.07625 (-0.14, -0.013)
Combined	Reach ~ Richness	8.94e-15*	-0.27305 (-0.341, -0.206)
2017	Salinity ~ Abundance	0.5289	0.027897 (-0.057, 0.11)
2017	Salinity ~ Richness	3.83e-06*	0.219302 (0.126, 0.31)
2017	Temperature ~ Abundance	0.7917	0.011704 (-0.08, 0.093)
2017	Temperature ~ Richness	0.0921	0.0047 (-0.093, 0.099)
2017	Reach ~ Abundance	0.3489	-0.03957 (-0.114, 0.039)
2017	Reach ~ Richness	1.85e-08*	-0.25446 (-0.345, -0.169)
2018	Salinity ~ Abundance	0.003893*	0.141978 (0.055, 0.224)
2018	Salinity ~ Richness	6.66e-09*	0.304541 (0.221, 0.388)
2018	Temperature ~ Abundance	0.009848*	0.127576 (0.003, 0.239)
2018	Temperature ~ Richness	0.608	0.027075 (-0.076, 0.127)
2018	Reach ~ Abundance	0.001667*	-0.1666 (-0.27, -0.062)
2018	Reach ~ Richness	4.35e-09*	-0.3322 (-0.426, -0.225)

Table B.10. Probability of presence model output.

Probability of presence ~ (Assemblage * Salinity) + (1 | Species) + (Month | Species) + (Month^2 | Species) + (Assemblage * Reach), Family = Binomial

AIC	BIC	log-Likelihood	Deviance	DF Residual
5649.8	6039.5	-2769.9	5539.8	8765

Scaled residuals

Min	1st quartile	Median	3rd quartile	Max
-2.898	-0.369	-0.156	-0.043	42.13

Random effects

Groups	Name	Variance	Standard deviation
1 | Species	Intercept	1.155e-06	0.001075
Month | Species	Intercept	1.265	1.124502
Month | Species	May	0.1570	0.396229
Month | Species	June	0.2502	0.500225
Month | Species	July	1.772	1.331113
Month | Species	August	5.539	2.353497
Month | Species	September	4.135	2.033390
Month^2 | Species	Intercept	0.1819	0.426501
Month^2 | Species	May	0.8111	0.900628
Month^2 | Species	June	2.260	1.503469
Month^2 | Species	July	2.950	1.717567
Month^2 | Species	August	4.797	2.190136
Month^2 | Species	September	3.068	1.751592

Fixed Effects

	Estimate	Standard error	z-value	*p*-value
Intercept	-1.999156	1.432385	-1.396	0.1628
Freshwater	-0.948371	1.651731	-0.574	0.5659
Brackish	0.894079	1.559655	0.573	0.5665
Marine	0.961713	1.536992	0.626	0.5315
Salinity	0.040916	0.019326	2.117	0.0342*
Reach	-0.104163	0.046348	-2.247	0.0246*
Freshwater:Salinity	-0.028699	0.020656	-1.389	0.1647
Brackish:Salinity	0.003634	0.021283	0.171	0.8644
Marine:Salinity	-0.004535	0.022766	-0.199	0.8421
Freshwater:Reach	0.331592	0.056061	5.915	3.32e-9*
Brackish:Reach	-0.496100	0.069566	-7.131	9.94e-13*
Marine:Reach	-1.152726	0.121114	-9.518	<2e-16*