Habitat use by juvenile salmon, other migratory fish, and resident fish species underscores the importance of estuarine habitat mosaics

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ABSTRACT: Interfacing with land and sea, estuaries support a mosaic of habitats that underpin the production of many coastal fisheries. These ecosystems are threatened by multiple stressors, including habitat loss and climate change, but the relative importance of estuarine habitat types for different fish species remains poorly understood since direct habitat comparisons are rare. This knowledge gap is exemplified in temperate estuaries by salmon — ecologically and commercially important species that use estuaries during their migrations to and from the ocean. Here, we tested for species-specific habitat use by sampling fishes in 3 interconnected estuarine habitats (brackish marsh, eelgrass, and sand flat), across seasons and temperature regimes. We quantified fish species richness, community distinctness, and catches (of Chinook and chum salmon, other migratory fishes, and resident fishes) in the Pacific Northwest's heavily urbanized Fraser River estuary, the terminus of what was once the world's most productive salmon basin. Overall, eelgrass habitat supported the greatest fish species richness (n = 37) and catches (37 402 fish), exceeding that of both the marsh (19 species, 7154 fish) and sand flat (22 species, 6697 fish). However, the majority of salmon were caught in the marsh (61 %). These differences, coupled with our finding that at least one unique fish species inhabited each habitat (eelgrass = 15, marsh = 8, sand flat = 1), demonstrate species-specific habitat use and underscore the importance of connected seascapes for biodiversity conservation.

KEY WORDS: Salmon · Coastal habitats · Seagrass · Brackish marsh · Seasonality · Biodiversity · Seascape

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1. INTRODUCTION

Estuaries provide vital ecosystem services including nutrient cycling and fish production (Barbier et al. 2011, McDevitt-Irwin et al. 2016, Mahoney & Bishop 2017), but coastal development threatens these ecosystems globally, through habitat degradation and shoreline modification, alteration of hydrology, nutrient and waste runoff, and noise pollution (Lotze et al. 2006, Mahoney & Bishop 2017). These important ecosystems encompass a mosaic of interconnected habitat patches, including seagrass, marsh, and sand flats, which together form a 'seascape' and may each support a different composition and biomass of fish species (Boström et al. 2011). Seagrass meadows are highly productive, offering invertebrate food resources (Kennedy et al. 2018, Unsworth et al. 2018) and providing structural shelter that appears to be particularly important for small or juvenile fishes (Jackson et al. 2001). Estuarine marsh

vegetation also provides shelter when inundated and increases food availability in the surrounding water column relative to unvegetated habitats, making it another important nursery habitat for resident fishes and migratory species, including Pacific salmon (Levings et al. 1991, Baltz et al. 1993). For some fishes, particularly in subadult and adult phases, unvegetated habitats such as sand and mud flats have proven equally or more important (Hindell & Jenkins 2004). Use of these habitats varies by species, but understanding their relative importance is challenging given habitat spatial variability and patchiness, and as such, direct comparisons between multiple vegetated habitats are rare (McDevitt-Irwin et al. 2016, Whitfield 2017). Although a recent meta-analysis found that half of studies (n = 25/51) did compare seagrass fish communities to fish in other structured habitats, very few of these comparisons (n = 6) were for temperate estuaries, and of these, only 2 directly compared seagrass and marsh habitat in the same system (McDevitt-Irwin et al. 2016). Importantly, we found no studies comparing the use of seagrass and marsh habitat by salmonids, which is a critical gap in our understanding and management of imperiled salmon stocks.

The temporal dynamism of estuaries, which arises from seasonal shifts in temperature and hydrology, species-specific life-cycle patterns, and other factors (Jackson et al. 2001), adds to the complexity of determining the relative importance of estuarine habitat types. Many migratory fish and bird species, for example, use estuarine habitats seasonally for reproduction and feeding (Baltz et al. 1993, Bond et al. 2008). Seasonal variation in water temperature and flow in temperate marine systems stimulates plankton blooms and vegetation growth, providing increased food availability to fishes during summer (Chandler et al. 2017). This temporal variation can result in under- or over-estimation of the importance of each habitat type for fish communities if repeat surveys that span across seasons are not conducted. Sampling over a range of conditions and seasons may be necessary to accurately quantify fish habitat use in these dynamic systems, which is critical for accurate impact assessment of development proposals and for informing management (Cohen 2012, Shaffer et al. 2017).

Of the commercially important fish species inhabiting temperate estuarine ecosystems, salmon arguably have the broadest ecological, economic, and cultural footprint, but many populations are threatened (Northcote & Atagi 1997, Cohen 2012). In British Columbia, overall abundance and commercial catch of the 5 major Pacific salmon species have declined precipitously over the last several decades (BC Wild Salmon Advisory Council 2019), and despite interest and effort, several depressed populations have failed to recover for reasons that remain unclear (Beamish et al. 1995, Zimmerman et al. 2015). In particular, Chinook salmon *Oncorhynchus tshawytscha* in British Columbia's Salish Sea have not recovered despite tighter catch restrictions and increased hatchery production (Ruff et al. 2017). A critical bottleneck for salmon survival is believed to occur shortly after emigration from rivers, when different species spend varying amounts of time in estuarine habitats, before moving out to the ocean (Zimmerman et al. 2015). One hypothesis for survival during this period is that mortality is size-dependent, with smaller fish unable to outpace their predators in growth and less likely to survive their first winter before reaching size refugia (Beamish & Mahnken 2001). The productivity and relative shelter offered by the habitats experienced during this period are therefore believed to be highly important for survival (Rubin et al. 2018).

All Pacific salmon species feed in estuaries and many will reside for days to months during their downstream migrations (Weitkamp et al. 2014, Moore et al. 2016). Of these, subyearling (migrating to sea within the first year after hatching) Chinook and chum (*O. keta*) salmon spend the greatest length of time in estuaries (Levings et al. 1989, Volk et al. 2010, Carr-Harris et al. 2015), but the extent to which they rely on estuaries for survival, and which estuarine habitats they use most during this critical period, remains poorly understood (Weitkamp et al. 2014). For example, although 2 recent studies provided evidence that juvenile Chinook and chum salmon use eelgrass habitat during their emigration, because neither study considered other estuarine habitats, such as marsh, it is unclear if juveniles of these species require eelgrass specifically or simply some vegetated habitat (Kennedy et al. 2018, Rubin et al. 2018). Understanding these distinctions is critical, especially in urban estuaries, where localized impacts may mean different habitat types are being lost at different rates, and conservation efforts need to prioritize habitat recovery. This challenge is exemplified by the heavily urbanized Fraser River estuary. The Fraser River estuary was once the world's most productive salmon basin, and still produces more salmon than any other river in British Columbia (Northcote & Atagi 1997), while also being the site of one of Canada's largest cities (Vancouver) and most active port (Fig. 1). Historical use of the Fraser estu-

ary by Chinook, chum, and pink salmon (*O. gorbuscha*) has been documented (Levy et al. 1979, Greer et al. 1980). Today, much of the estuarine habitat in the Fraser River estuary has been lost or degraded, with uncertain implications for salmon.

Our objective here was to advance the understanding of the relative importance of temperate estuarine habitat types for resident and migratory fish populations, including juvenile salmon. To achieve this, we tested for species-specific habitat use by sampling fishes in 3 interconnected estuarine habitats (brackish marsh, eelgrass, and sand flat), across seasons (spring, summer, and fall), and over 2 years with distinct temperature regimes (an El Niño year [2016] and more typical year [2017]). We examined the influence of habitat type, as well as season and temperature regime, on estuarine fish species richness, community distinctness, and catch of 4 distinct fish species groups: Chinook salmon, chum salmon, other migratory fishes (other salmonids and forage fish), and resident fishes (e.g. shiner surfperch *Cymatogaster aggregata*, three-spined stickleback *Gasterosteus aculeatus*, and others) (Nightingale & Simenstad 2001). In doing so, we tested 3 hypotheses: (1) estuarine fish preferentially inhabit eelgrass meadows, such that fish species richness and catch will be highest within this habitat; (2) within each habitat, salmon and migratory fish species richness and catch will peak in summer (May–August), owing to migration patterns and to seasonal increases in food availability and vegetation growth (marsh and eelgrass); and (3) resident species richness will be consistent across seasons, but relative abundance will peak in summer as these species take advantage of optimal conditions for reproduction (i.e. seasonal increases in food availability and vegetation growth).

2. MATERIALS AND METHODS

2.1. Study system

The Fraser River estuary extends from the tidal wedge at Mission, British Columbia, Canada, to a steep drop-off into the Strait of Georgia, where the river enters the Salish Sea (Fig. 1). Between the mouth of the river and this drop-off are the tidal flats known as Sturgeon Bank and Robert's Bank, which are characterized by shallow slopes and moderate salinity (Levy et al. 1979). The Fraser River is the largest contributor of freshwater into the surrounding marine environment, providing terrestrial nutrients to fish communities, influencing the migration pathways of emigrating salmon, and dictating the nutrient cycling processes of the sur-
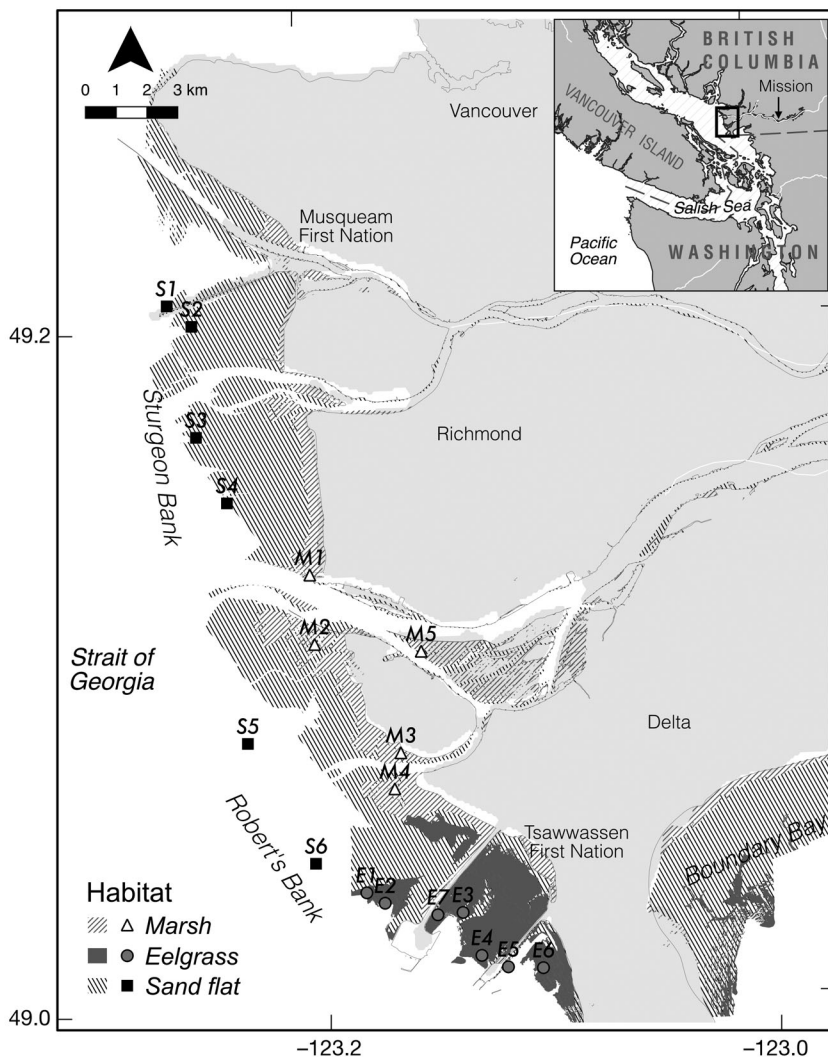

Fig. 1. Sites sampled in 2016 and 2017 within the Fraser River estuary, British Columbia, Canada: 5 marsh sites (white triangles; M1–M5), 6 sand flat sites (black squares; S1–S6), and 6 eelgrass sites (grey circles; E1–E6). All sites were sampled each year, with the exception of E6, which was replaced by E7 in 2017. Habitat polygons are approximations from the 2002/2003 Fraser River Estuary Management Program Habitat Inventory of the Lower Fraser River Estuary, and boundaries may vary. Sand flat habitat extends seaward beyond the shown polygons to a drop-off between 5 and 6 km from shore

rounding Salish Sea (Barraclough & Phillips 1978, Riche et al. 2014). The lower reaches of the estuary provide important habitat for freshwater, estuarine, and marine fish communities, comprising over 50 fish species (Greer et al. 1980, Conlin et al. 1982); the main (southern) river mouth hosts small islets and channels that represent some of the last intact brackish marsh habitat in the estuary. More than 70% of the estuary has been permanently converted or altered by industrial, agricultural, and urban development, resulting in decreased connectivity between habitat patches (Waldichuk 1985, Sutherland et al. 2013). The majority of the remaining marsh habitat is near the mouth of the south (main) arm of the river, and the eelgrass is limited to Robert's Bank, which is segregated by 2 large causeways (Fig. 1).

2.2. Fish sampling

We quantified fish communities in 3 distinct estuarine habitat types: brackish marsh (dominant species *Carex lyngbyei*), eelgrass (*Zostera marina*) meadows, and sand flats (unvegetated), by sampling at 17 sites spanning Sturgeon and Robert's Bank and around the Fraser River mouth (Fig. 1). We surveyed each site approximately every 2 wk between March and July in both 2016 and 2017 to capture seasonal shifts in fish distribution and abundance. Two additional sampling rounds (i.e. sampling all sites) were conducted in the fall (September and October) of 2016, and one round of marsh sites only was conducted in August 2017.

Our survey design followed previous surveys in the estuary (Greer et al. 1980, Levings 1985, Archipelago Marine Research Ltd 2014a,b), with sites a minimum of 500 m apart. Sites were selected non-randomly, to be relatively evenly distributed across the estuary, within habitat types. We attempted to ensure that all habitats were equally accessible to fish and under similar environmental conditions at the time of sampling by selecting sites that were relatively consistent in depth (2.0–4.3 m during sampling), and by surveying at high tide (minimum 2.9 m above Chart Datum at Tsawwassen tidal station 7590) and during daylight hours (minimum 1 h from sunrise or sunset). A few of the marsh channels experienced delayed tidal shifts, resulting in a small number of sampling events at depths less than 2 m. However, for small fish such as salmonids, which may remain in marsh channels at depths less than 0.5 m (Hering et al. 2010), we do not believe that this made a significant difference in detectability.

Each sampling event at a site consisted of 3 non-overlapping, round-haul seine sets; after each set, we identified all fish to species. We used a custom purse seine (40 m long × 4 m wide bunt [4 mm mesh] and 3 m wide cod end [6 mm mesh]) to survey outer (eelgrass and sand flat) sites, and a beach seine (20 m long × 3 m wide, 1.5 × 1.5 m bag [3 mm mesh]) to survey the inner (marsh) sites. Past surveys in the Fraser estuary typically employed beach or purse seines (e.g. Greer et al. 1980, Levings 1985, Archipelago Marine Research Ltd 2014a), and habitat constraints necessitated the use of both gear types to adequately sample all 3 habitat types. In the marsh channels, we used a small beach seine, the most commonly used method historically in this area and ideal as the channels are quite narrow and relatively shallow. In contrast, for safety on the flats (eelgrass and sand flat sites), which can experience rapid tidal shifts and have unconsolidated mud that personnel can sink into (Sutherland et al. 2013), and to sample at high tide, we designed the small purse seine that could be easily deployed without disembarking the vessel. Both seines reached the bottom substrate during sampling and successfully caught motile pelagic and epibenthic fishes. The difference in size between the purse and beach seine resulted in approximately half the area swept for each marsh sampling event relative to the eelgrass and sand flat sampling events. We did not conduct efficiency tests for the gear, but it is likely that the catch efficiency was lowest in the marsh habitat for this reason (Franco et al. 2012).

2.3. Abiotic variables

At each site, we measured a suite of water-quality and habitat characteristics that can influence fish communities. Water-quality parameters, including temperature, salinity, pH, and dissolved oxygen, were measured at each site 0.5 m from the water surface once per sampling round (i.e. approximately every 2 wk) each year using a Hanna Instruments 9829 Multiparameter Meter. Turbidity was measured in the same way but only in 2016. In some cases, one or more water quality values could not be recorded at a site. We estimated these missing values (7% total; n = 72/624 measurements in 2016, 18/647 in 2017) from cubic spline interpolations of the existing field data, separating measured values by habitat type and ordering by Julian day (na.spline, 'zoo' package in R; Zeileis & Grothendieck 2005). We assessed the effect of year, habitat, and month on each continuous abiotic environmental variable using general linear

mixed models with site as a random effect (lmer, 'lme4' package in R; Bates et al. 2015).

We also quantified the following habitat characteristics at each marsh site: marsh tidal channel width, because this directly influences water levels and dictates the accessibility of the channel to fish (Levy et al. 1979), and vegetation elevation (i.e. the height from the channel bottom to the nearest marsh vegetation, as a measure of the relative extent of submerged/overhanging vegetation, which can affect water quality by providing shade, facilitating nutrient cycling, and reducing turbidity by stabilizing sediments; Seliskar & Gallagher 1983). Vegetation has also been linked to increased food availability to fish via increased invertebrate abundance in the water column (Seliskar & Gallagher 1983, Levings et al. 1991). Although we measured several other habitat characteristics (e.g. eelgrass shoot density, leaf area index, marsh channel bank slope, and elevation), we did not include these in our final catch models because of collinearity with other abiotic variables (Fig. A1 in the Appendix).

2.4. Species richness

We compared fish species richness across habitats and seasons using sample-based rarefaction curves (999 bootstrapped replications) as implemented for incidence-based data ('iNEXT' in R; Hsieh et al. 2016). We estimated rarified species richness to account for the effects of bias associated with unequal sampling effort (i.e. number of sampling events among habitats, or among the seasons within each habitat compared) and fish abundance per seine haul. We performed sample-based rarefaction rather than individual-based rarefaction because the independent sample is at the level of the sample unit (seine) rather than at the level of the individual fish. Rarefying the data allowed us to accurately compare richness across habitats, despite differences in sample size (Chao et al. 2014). We defined seasons as spring (sampling events in March–April), summer (May–August), and fall (September–October). Year did not have a strong effect on richness in preliminary analyses, so we pooled sampling events across years.

2.5. Community composition

We visualized community distinctness across habitats using an Euler diagram ('eulerr' in R; Larsson 2018) and non-metric multidimensional scaling

(NMDS; 'vegan' in R; Oksanen et al. 2018). The Euler diagram shows area-proportional relationships between the number of species captured in each habitat over all seasons and all years. We used presence–absence data for each species and habitat, and calculated the number of intersections, unions, and disjoints, representing the number of species in common or unique to each habitat type. The NMDS ordination plot depicts variation in fish communities by site. The ordination uses Bray-Curtis dissimilarity index and the data were subjected to Wisconsin double standardization, which standardizes species first by their count maxima and then by their sample totals, improving the quality of the ordination (Oksanen 2015).

2.6. Catch

To determine which factors contributed to observed catch patterns, we modeled the catch of each of 4 species groups (see Table 1) in the estuary, with separate models for beach-seined sites (marsh) and purse-seined sites (eelgrass and sand flat) (8 total models) because of inherent differences in the catch efficiency of these 2 gear types (Franco et al. 2012). We classified species other than Chinook and chum salmon as either resident or migratory, following Nightingale & Simenstad's (2001) categories, but simplifying by aggregating their resident and seasonal resident species into a single 'resident' group. For the marsh habitat data, we implemented generalized linear models (GLMs) with a negative binomial error structure to account for large counts at the tail of the distribution (glm.nb, 'MASS' package in R; Venables & Ripley 2002) and included the fixed-effects of year, Julian day, temperature, salinity, pH, dissolved oxygen, mean turbidity, channel width, and vegetation elevation. Based on an apparent non-linear seasonal effect on abundance, which was strongly evident for some fish species groups, Julian day was modeled as a quadratic term (Julian day + Julian day squared) in the full models. We did not include 'site' as a random effect because there were only 5 marsh sites (which is at the lower threshold of capacity for mixed-effects models to provide accurate estimates of among-population variance; Harrison et al. 2018) nor did we include site as a fixed effect in the models because it was highly collinear with the site-level habitat variables. For the eelgrass/sand flat models, we implemented generalized linear mixed-effects models (GLMMs) with a

negative binomial error structure and site as a random effect to account for repeat measures within 13 sites (glmer, 'lme4' package in R; Bates et al. 2015). We included the fixed effects of year, Julian day (as a quadratic term, as above), temperature, salinity, pH, dissolved oxygen, mean turbidity, and habitat type (eelgrass and sand flat only). All continuous variables were standardized and centered on the mean prior to analysis ('robustHD' package in R; Alfons 2016). A summary of covariates included in the 8 global catch models is provided in Table S1 in the Supplement at www.int-res.com/articles/suppl/m625p145_supp.pdf.

For each fish group and gear type, we examined the collinearity of the variables using variance inflation factors (VIF) in the context of model stability (O'Brien 2007). Several variables had very high collinearity within the data sets (Fig. A1), and these were removed one by one, following a hypothesis-based approach and VIF scores, from each full model until the model converged and collinearity was sufficiently addressed. VIF for all variables retained in our reduced global models were below 3.50, with the exception of the marsh Chinook model (6.18, Julian day). We then performed model selection on these 8 reduced global models for each fish group and data type. Model selection was carried out using Akaike's information criterion for small sample sizes (AICc) following an examination of all possible subsets of explanatory variables (dredge, 'MuMIn' package in R; Bartoń 2018). In complex biological systems, model averaging can provide more robust conclusions by incorporating the uncertainty inherent in the model using the model's Akaike weight (Harrison et al. 2018). Due to the low weights of our top models, we averaged all models with an AICc score within 4 of that of the top-ranked model to ensure the best estimates of the top coefficients (Harrison et al. 2018). Including models with a ΔAIC up to 4–7 in the model set can help to minimize Kullback-Leibler information loss and incorporate plausible hypotheses for estimating the response variable, particularly when model weights are low (Burnham et al. 2011, Harrison et al. 2018). In our case, a ΔAIC of 4 included the majority of the expected model variability while also reducing the model set to a reasonable number for multimodel inference, given our sample sizes (Burnham et al. 2011). We report pseudo r-squared values for each model following the methods detailed in Nakagawa & Schielzeth (2013), using the 'MuMIn' package in R. All statistical analyses were computed using R version 3.4.1 (R Core Team 2017).

3. RESULTS

3.1. Species richness

We identified 46 fish species (39 in 2016, 36 in 2017), of which 35 were classified as resident and 11 were classified as migratory species (including Chinook and chum salmon) (Table 1). Resident fishes included 2 introduced species that are invasive in coastal British Columbia (pumpkinseed *Lepomis gibbosus*, white crappie *Pomoxis annularis*; Table 1). Of the 3 sampled estuarine habitats, eelgrass had significantly higher fish species richness (37) than either the marsh (19) or sand flats (22), which were similar to each other (rarefied comparison; Fig. 2A). An influx of fish species in the summer resulted in significantly greater richness in summer than in fall in eelgrass, with a similar (though not significant) trend in sand flat (Fig. 2C,D). No other significant trends between seasons were detected (Fig. 2).

3.2. Catch and community composition

Overall, in 288 sampling events over 2 years (Table S2), we caught 51143 fish, the majority of which were in eelgrass (37385 fish; mean ± SD = 378 ± 546 fish per sampling event, where one sampling event is 3 seine sets taken per site per day) followed by marsh (7126; 85 ± 131 fish per sampling event) and sand flat (6632; 63 ± 135 fish per sampling event). The 3 habitats differed considerably in their most abundant species (Fig. 3), and each habitat supported distinct species that were not found in the other sampled habitats (Fig. 4, Fig. S1). Resident fishes comprised the majority of all those caught (46141; 90% of total), and of these, 2 species accounted for the vast majority: shiner surfperch (49% of all fish caught) and three-spined stickleback (26% of all fish; Fig. 3). In total, we caught 1193 Chinook and 1088 chum salmon (Fig. 3). The remaining fish were other migratory species (2347 individuals) and 374 unclassified fish (Fig. 3).

Marsh habitat supported the highest and most consistent salmonid catches in the estuary (1514 salmonids total, mean ± SD = 18 ± 37 fish per sampling event, 6 species, 61% of overall salmonid catch; Fig. 3A). Marsh sites had more freshwater-tolerant resident fishes, 8 of which were only found in this habitat type, including peamouth chub *Mylocheilus caurinus* and northern pikeminnow *Ptychocheilus oregonensis* (Fig. 4). The marsh was also the source of a high catch of juvenile flatfish in 2017 (1366

Species group/ common name	Latin name	Unique habitat	Year
Chinook			
Chinook salmon	*Oncorhynchus tshawytscha*		
Chum			
Chum salmon	*Oncorhynchus keta*		
Resident			
Arrow goby	*Clevelandia ios*		
Bay pipefish	*Syngnathus leptorhynchus*		
Big skate	*Raja binoculata*	E	2016
Buffalo sculpin	*Enophrys bison*	E	2017
Crescent gunnel	*Pholis laeta*		
English sole	*Parophrys vetulus*		
Kelp greenling	*Hexagrammos decagrammus*		2017
Kelp perch	*Brachyistius frenatus*	E	2016
Kelp poacher	*Agonomalus mozinoi*	E	2017
Largescale sucker	*Catostomus macrocheilus*	M	
Pacific herring	*Clupea pallasii*		
Pacific sanddab	*Citharichthys sordidus*	E	2017
Pacific tomcod	*Microgadus proximus*	E	2016
Peamouth chub	*Mylocheilus caurinus*	M	
Penpoint gunnel	*Apodichthys flavidus*	E	
Northern pikeminnow	*Ptychocheilus oregonensis*	M	
Pile perch	*Rhacochilus vacca*	E	
Plainfin midshipman	*Porichthys notatus*	E	
Prickly sculpin	*Cottus asper*	M	
Pumpkinseed[a]	*Lepomis gibbosus*	M	2017
Redside shiner	*Richardsonius balteatus*	M	2017
River lamprey	*Lampetra ayresi*		
Saddleback gunnel	*Pholis ornata*	E	
Sand sole	*Psettichthys melanostictus*		2016
Shiner surfperch	*Cymatogaster aggregata*		
Snake prickleback	*Lumpenus sagitta*		
Speckled sanddab	*Citharichthys stigmaeus*		
Staghorn sculpin	*Leptocottus armatus*		
Starry flounder	*Platichthys stellatus*		
Three-spined stickleback	*Gasterosteus aculeatus*		
Tidepool sculpin	*Oligocottus maculosus*		
Tubesnout	*Aulorhynchus flavidus*	E	
Walleye pollock	*Gadus chalcogrammus*	E	2016
White crappie[a]	*Pomoxis annularis*	M	2016
Whitespotted greenling	*Hexagrammos stelleri*	E	2016
Migratory			
Coho salmon	*Oncorhynchus kisutch*	M	2016
Longfin smelt	*Spirinchus thaleichthys*	SF	2016
Northern anchovy	*Engraulis mordax*		
Pacific sand lance	*Ammodytes hexapterus*		
Pink salmon	*Oncorhynchus gorbuscha*		2016
Sockeye salmon	*Oncorhynchus nerka*		
Steelhead	*Oncorhynchus mykiss*	E	2017
Surf smelt	*Hypomesus pretiosus*		
Tiger rockfish	*Sebastes nigrocinctus*	E	2017
[a]Invasive species			

Table 1. Fish species caught in marsh, eelgrass, and sand flat habitats in the Fraser River estuary in 2016 and 2017. Species are listed alphabetically by common name within each of 4 species groups: Chinook salmon, chum salmon, resident, and migratory (i.e. all migratory species other than Chinook and chum salmon). Species that were only found in a single habitat (M: marsh; E: eelgrass; SF: sand flat) are noted under Unique habitat. Species that were caught in only 1 of the 2 years are noted under Year. Eight types of juvenile fish were identified to genus or family only and classified as resident (6: unidentified flatfish, unidentified gadid, unidentified gunnel, unidentified greenling, unidentified sanddab, unidentified sculpin) or migratory (2: unidentified salmonid, unidentified smelt). Because these juveniles were assumed to represent one of the previously identified species, they were not included in the richness totals. Additionally, 2 larval taxa that could not be classed as resident or migratory were excluded from analyses

2016, and was also the primary habitat for Pacific herring *Clupea pallasii*, surf smelt *Hypomesus pretiosus*, and bay pipefish *Syngnathus leptorhynchus* (Fig. 3B). Over one-third of species caught in the study were only found in eelgrass habitat (Table 1, Fig. 4). Eelgrass-specific species were commonly demersal fishes with high site fidelity (e.g. penpoint gunnel *Apodichthys flavidus*, buffalo sculpin *Enophrys bison*, plainfin midshipman *Porichthys notatus*) or deep dwellers that were found in the shallows as juveniles (e.g. big skate *Raja binoculata* and walleye pollock *Gadus chalcogrammus*).

Sand flat habitat included a variety of migratory species, such as northern anchovy *Engraulis mordax* in 2016 and Pacific sand lance *Ammodytes hexapterus* in 2017, but resident fishes such as arrow goby *Clevelandia ios*, snake prickleback *Lumpenus sagitta*, and flatfish species were also abundant (Fig. 3C). Sand flat sites had the highest incidents of empty nets. The only species that was uniquely found in sand flat was a single longfin smelt *Spirinchus thaleichthys* (Fig. 4).

We observed substantial differences in environmental conditions, fish catches, and community composition between years, potentially due to the El

unidentified flatfish total; Fig. 3A). Invasive fishes were only caught in marsh habitat and in low abundance (1 fish each year; Table 1).

Eelgrass habitat supported a high catch of shiner surfperch and three-spined stickleback, particularly in
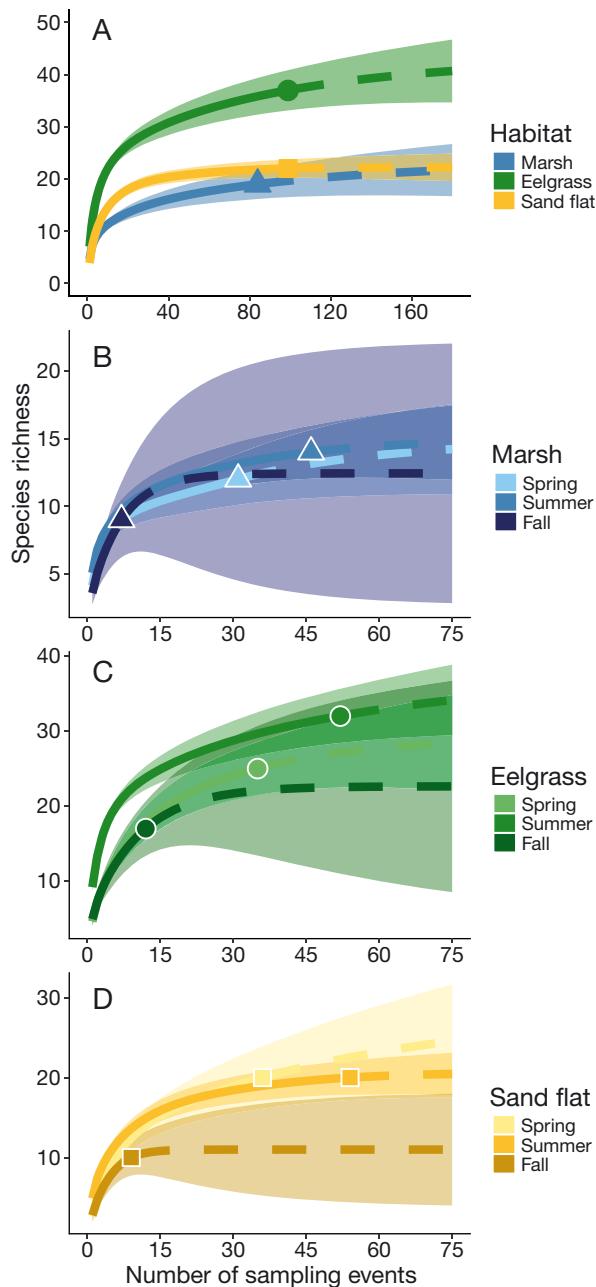
Fig. 2. (A) Rarefied species richness curves for marsh (blue triangles), eelgrass (green circles), and sand flat (yellow squares) habitats, combining data across seasons and years, and (B–D) species richness curves by season for marsh (B), eelgrass (C), and sand flat (D) habitats. Symbols reflect observed species richness, solid lines represent interpolated values, and dashed lines represent extrapolated values. Shading represents 95% confidence intervals

Niño in 2016. Surface temperature was greater in 2016 (14.82 ± 1.81°C, mean ± SD) than 2017 (13.87 ± 2.53°C; Fig. 5), with a significant effect of year (p < 0.001; Table S3). These differences were larger for marsh and sand flat habitats (Fig. 5), which are more
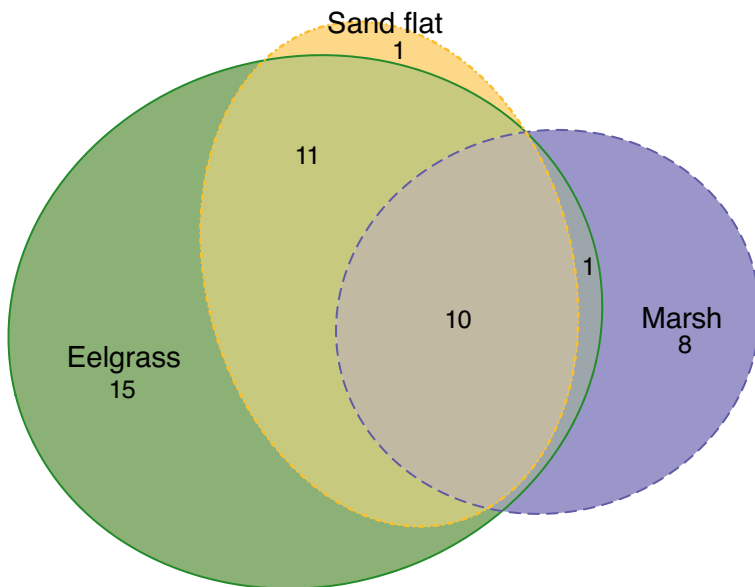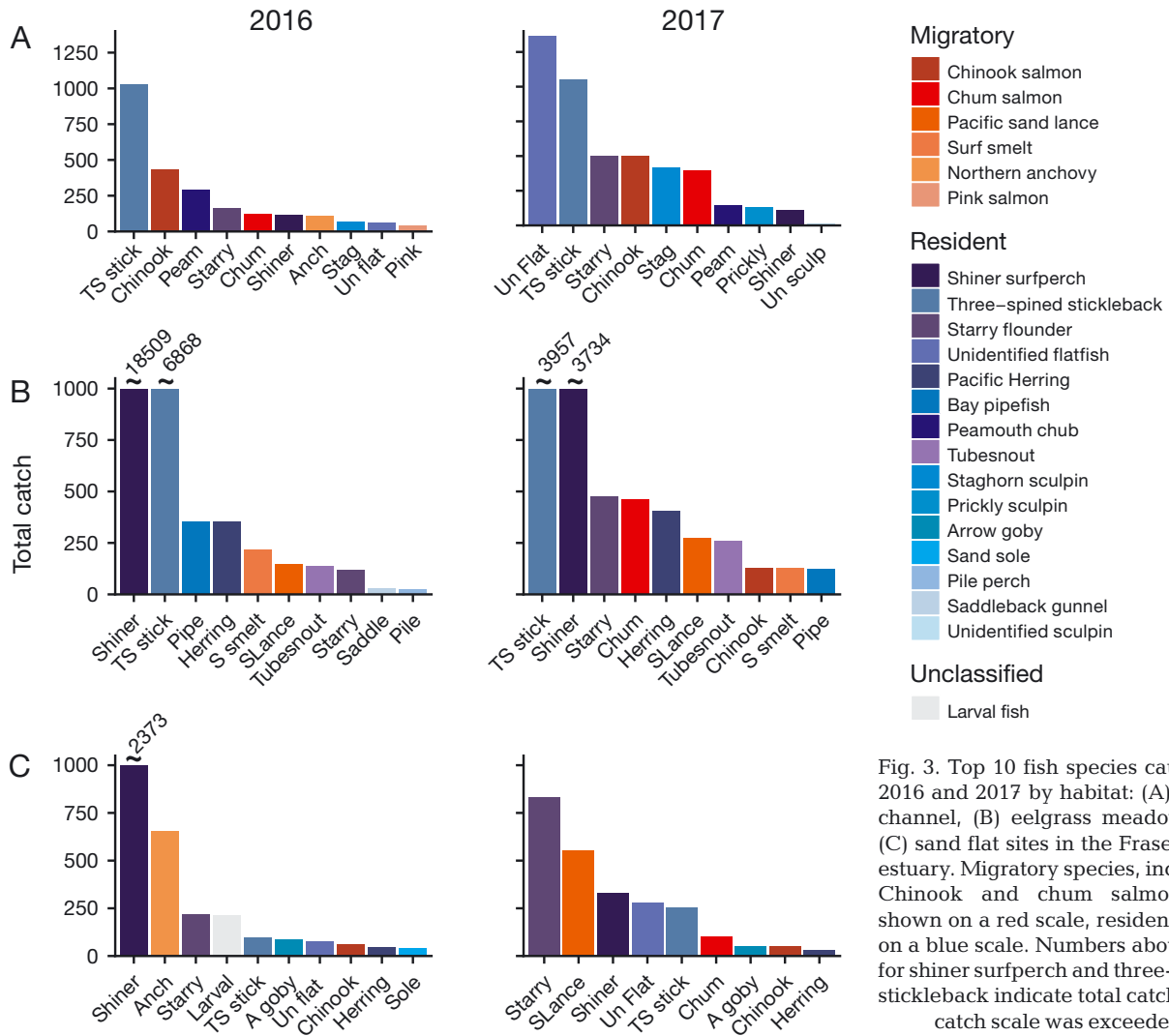
strongly influenced by the Fraser River outflow than the eelgrass sites (Fig. 1). Dissolved oxygen was also higher in 2016 (10.47 ± 0.96 versus 10.42 ± 1.43 mg l^{-1}, p < 0.001; Table S3), except during the month of May (10.46 ± 0.74 versus 11.06 ± 0.78 mg l^{-1}). Both salinity and pH were significantly higher in 2016, with elevated salinity reflecting low river flows, particularly during the freshet months (Table S3, Fig. 5). Nearly two-thirds of the total fish catch occurred in the El Niño year (2016; 33435 fish), despite having only 53% of the total sampling effort (Table S2), and fish community composition differed considerably between years (Fig. 3). This difference in total catch between years was primarily a result of a more than 400% higher catch of shiner surfperch in 2016 (20999 [mean ± SD = 136 ± 373 fish per sampling event] in 2016 versus 4177 [31 ± 133 fish per sampling event] in 2017) (Fig. 3). Three-spined stickleback were also 34% more abundant during the El Niño year (7995 versus 5260). A notable difference in estuarine fish species composition was the large schools of Northern anchovy of various life stages we caught in 2016, particularly in the sand flat, which shifted to greater abundances of starry flounder and Pacific sand lance in 2017 (Fig. 3C).

3.3. Chinook salmon catch

The majority of Chinook salmon occurred in the marsh habitat in both years (78%). Within the marsh, Chinook catch was best explained by year, Julian day, water temperature, pH, and marsh channel width (pseudo R^2 = 51%, df = 7, w = 0.21; Table S4). Chinook catch was slightly higher in the marsh in 2017 at 500 (mean ± SD = 13 ± 21 fish per sampling event) than in 2016 at 435 (10 ± 25 fish per sampling event), when water temperatures were higher, earlier in the season, and in wider marsh channels (Fig. 6A, Fig. A2). Although Chinook catch was also greater in 2017 than 2016 in eelgrass habitat, neither water temperature nor pH were important predictors of abundance in the eelgrass and sandflat model. Instead, dissolved oxygen had a positive effect on Chinook catch, and more were caught in eelgrass than on the sand flats (conditional R^2 = 50%, df = 6, w = 0.27; Fig. 6E, Table S5).

3.4. Chum salmon catch

Chum salmon were caught in far greater numbers in 2017 than in 2016 (total 959 [mean ± SD = 7 ± 25 fish per sampling event] versus 129 [1 ± 4
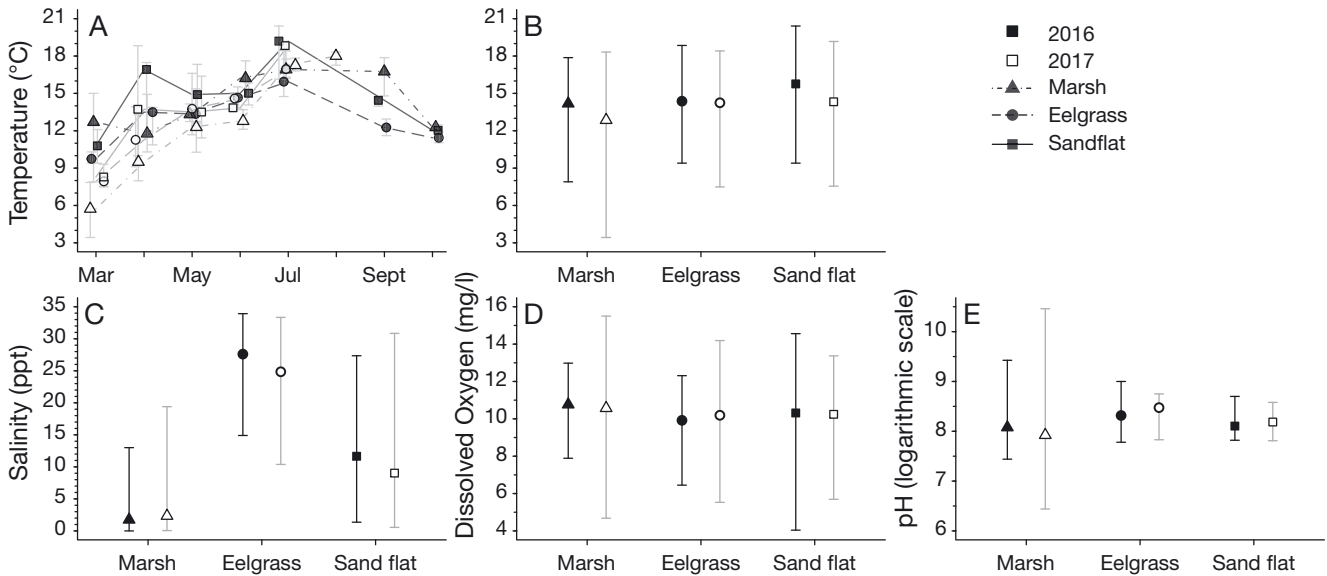
Fig. 3. Top 10 fish species caught in 2016 and 2017 by habitat: (A) marsh channel, (B) eelgrass meadow, and (C) sand flat sites in the Fraser River estuary. Migratory species, including Chinook and chum salmon, are shown on a red scale, resident fishes on a blue scale. Numbers above bars for shiner surfperch and three-spined stickleback indicate total catch when catch scale was exceeded

Fig. 4. Euler diagram showing area-proportional representation of fish community composition among habitats in the Fraser River estuary in 2016 and 2017. There are 8 unique and 11 shared species in marsh (blue ellipse, dashed outline), 15 unique and 22 shared species in eelgrass (green ellipse, solid line), and 1 unique and 21 shared species in sand flat (yellow ellipse, dash-dot line) habitat. Numbers within each segment represent the number of species either shared between habitats (unions) or distinct within each habitat (disjoints)

Fig. 5. Mean (A,B) surface temperature, (C) salinity, (D) dissolved oxygen, and (E) pH over time for marsh, eelgrass, and sand flat in 2016 and 2017 in the Fraser River estuary. Error bars show minimum and maximum measured values. Values were averaged across all sites for each sampling month (A) and year (B–E) in each habitat
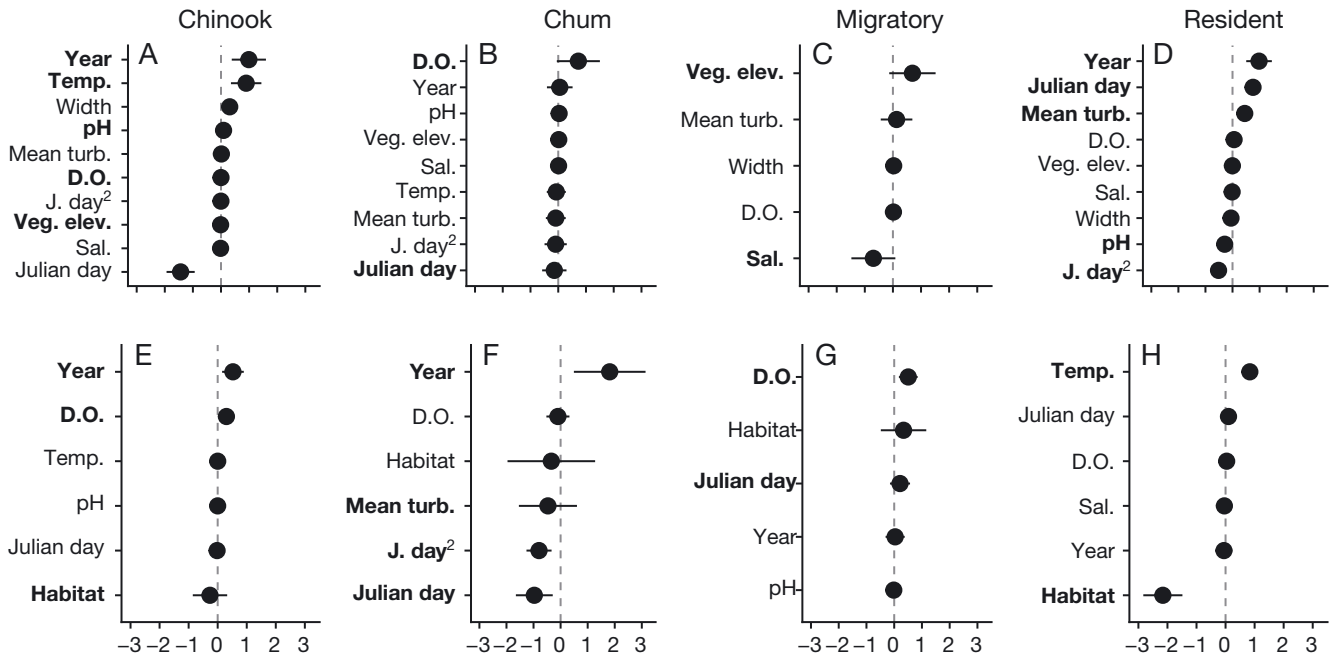

Fig. 6. Multimodel-averaged model coefficients for (A–D) marsh and (E–H) eelgrass/sand flat catch models for each species group (A,E: Chinook; B,F: chum; C,G: other migratory; D,H: resident). Data included sampling from 2016 and 2017 in the Fraser River estuary. Temp.: temperature; DO: dissolved oxygen; J day^2: Julian day squared; Sal.: salinity; Width: marsh channel width; Mean turb.: mean turbidity in 2016; Veg. elev.: vegetation elevation. Within each panel, coefficients are ordered from most to least positive effects; coefficients with relative variable importance (cumulative Akaike weight) >0.5 are in **bold** on each *y*-axis. Error bars represent 95% confidence intervals

fish per sampling event] fish, respectively), and were distributed across habitats differently between years. In 2016, almost all (93%) chum were caught in marsh sites, whereas less than half (41%) were caught there in 2017. In 2017, almost

half (48%) of chum salmon were caught in large schools in the eelgrass habitat. Within the marsh habitat, however, year was not identified as a significant explanatory variable for chum (R^2 = 33%, df = 4, *w* = 0.08; Table S4, Fig. 6B); instead, chum

were most abundant when dissolved oxygen levels were high, which occurred earlier in the season. In the eelgrass and sand flat model, year and turbidity were significant, reflecting the high chum catch in 2017 in eelgrass sites with low turbidity relative to the sand flats (R^2 = 95%, df = 7, w = 0.35; Fig. 6F, Table S5). Within these habitats, more chum were caught early in the season, with a quadratic relationship for day of year, due to an increase in catch in April–May followed by a sharp decline (Fig. 6F).

3.5. Other migratory fish catch

Migratory fishes consisted of other salmonid species, including sockeye salmon *O. nerka* (147 over both years), as well as forage fishes, such as surf and longfin smelts (368 combined), and Pacific sand lance (990). Some species were only seen in 2016, including pink salmon (43), which display an alternating year life history pattern (Beamish et al. 1994), and anchovy (788), which respond to changing temperature and current regimes in the Salish Sea (Duguid et al. 2019). In the marsh, vegetation elevation was the most significant parameter for these species, indicating greater catch within the marsh for sites with steeper or taller banks (R^2 = 54%, df = 7, w = 0.38; Fig. 6C, Table S4). Migratory fishes were also caught in higher numbers when marsh sites had lower salinity. Migratory fishes in the eelgrass and sand flat habitats were more abundant later in the season and when dissolved oxygen was high, with slightly higher abundance in sand flat habitat (R^2 = 91%, df = 5, w = 0.20; Fig. 6G, Table S5).

3.6. Resident fish catch

Within the marsh habitat, resident fish catch peaked bimodally in May and July (Fig. A2), which was represented by significant Julian day and Julian day squared parameter estimates (Fig. 6D). In the marsh, resident fish catch was higher in 2017, in more turbid sites and at lower pH levels, indicating the effect of a stronger freshet in 2017 and higher river input to the marsh (R^2 = 54%, df = 7, w = 0.22; Fig. 6D, Table S4). In the eelgrass/sand flat, resident fish catch peaked in July (Fig. A2). Resident fishes were far more abundant in eelgrass compared to sand flat (35779 versus 4868 total catch) and were strongly positively affected by water temperature, reflecting the high catches of shiner surfperch and

three-spined stickleback during the El Niño conditions of 2016 (R^2 = 100%, df = 5, w = 0.16; Fig. 6H, Table S5). Year was not significant, despite the considerably higher catches of these 2 species in 2016.

4. DISCUSSION

Our study found unique roles of different habitat types and multiple environmental influences on total biodiversity and catch of fishes in an urbanized estuary. The spatiotemporal variation among habitat types within this continuous seascape supports the theory that connectivity of nearshore habitats is integral to the maintenance of diverse and productive nearshore ecosystems (Bishop et al. 2017). As predicted, eelgrass provided the largest contribution and had the greatest seasonal variation in both estuarine fish species richness and abundance. Though marsh supported the fewest species, this habitat had more unique species than sand flat and notably was the most used habitat for juveniles of 5 species of commercially important salmon. This study employed 2 seine nets, which are highly efficient methods to capture small resident coastal fishes and migrant marine fishes, but which inherently vary in efficiency between habitat types and species (Franco et al. 2012). Gear efficiency is difficult to quantify, but we assume that the presence of vegetation (eelgrass and marsh) decreased catch efficiency. The mesh size was very close between nets and targeted demersal and motile juvenile fishes successfully. The marsh net was smaller in size, and so we assume that it had decreased catch efficiency relative to the purse seine (eelgrass and sand flat). While the differences in gear type prevent a direct quantitative comparison of catches between the 2 vegetated habitats, such a dramatic difference in catch (73% of all fish in eelgrass, and 61% of all salmonids in marsh) suggests that there is a true difference between habitats and is noteworthy, given that these habitats presumably had lower catch efficiency. Although this study did not attempt to elucidate true population abundances in the estuary, by comparing catches across habitat types we were able to estimate the relative abundances of fishes across temporal and spatial scales within this system. Comparing these vegetated habitats yielded important results that would have been missed had we assessed only a single vegetated habitat, as in the majority of estuarine studies (McDevitt-Irwin et al. 2016). Habitat use is still seldom incorporated into fisheries stock assessments, an oversight that may be leading to over- or under-

exploitation of stocks (Brown et al. 2019). Our results underscore the importance of understanding fish use of multiple nearshore habitats and conserving or restoring a mix of critical habitats for maintenance of these populations. Finally, we show that a warmer water regime coincided with novel migratory species, increases in select hardy species (i.e. tolerant to high temperature, low oxygen, varying salinity, and/ or high nutrient input conditions; Wiebe 1968, Healey 1997, Moran et al. 2010, Taugbøl et al. 2014, Christensen et al. 2018), and declines in abundance of the majority of resident species.

4.1. Species richness and composition within habitats

Our study supports a growing body of evidence that eelgrass meadows provide integral habitat for migratory and resident fish species (Unsworth et al. 2018). The higher species richness in eelgrass than in marsh or sand flat habitat is potentially due to its greater productivity and provision of shelter. Eelgrass meadows support complex food webs, linking nutrients from primary productivity to higher trophic levels (Duffy et al. 2015). The diet of juvenile chum salmon, for instance, may be predominantly composed of eelgrass-associated zooplankton and benthic invertebrates (Kennedy et al. 2018). Aquatic vegetation can also provide shelter from predators for juvenile fishes (Magnhagen 1988, Semmens 2008), and spawning habitat (e.g. Pacific herring) (Fox et al. 2018). Species richness and abundance have previously been shown to fluctuate in synchrony with eelgrass shoot density and blade length (Xu et al. 2016), and indeed we found fish species richness in eelgrass to be significantly greater during summer months, when the vegetation had reached maximum growth, and lowest in fall months as the vegetation died back.

Each habitat reflected unique species communities, likely based on a combination of selectivity, life history traits, and abiotic tolerances. Increasingly, the connectivity between habitats has been emphasized as a foundation for functioning estuarine ecosystems (Boström et al. 2011, Whitfield 2017). It is imperative, then, that we understand the integrated use of connected estuarine habitats and their combined role in supporting nearshore fish communities. The combination of habitat types available and the connectivity and structure of the estuary may greatly influence the use of habitats across systems (Litvin et al. 2018, Schrandt et al. 2018). For salmon, which were caught in surprisingly low numbers in the eelgrass, the use of eelgrass

versus marsh may depend more on the estuary conditions that are present than the vegetation itself.

Vegetated habitats are influenced by water conditions: brackish marsh plants typically grow in turbid, low-salinity (0.5–15 ppt) waters (Balke 2017), whereas eelgrass thrives in clear, saline (10–30 ppt) water (Durance 2002). In the Fraser estuary, coal port and ferry terminal causeways block the flow of river water to Robert's Bank, resulting in clearer, more saline water, and leading to the expansion of the eelgrass meadows (Sutherland et al. 2013). These causeways also significantly lengthen the distance from the river mouth to the densest eelgrass habitat for emigrating salmon (Fig. 1). Meanwhile, the severe reduction and ongoing recession of brackish marsh owing to human activities and development in the Fraser River estuary is especially concerning for salmon in this system (Balke 2017). Restoration of tidal inundation to these habitats would increase connectivity and likely increase the use of these habitats by sub-yearling salmon migrants (Weitkamp et al. 2014).

For juvenile salmon, precise habitat use appears to vary between estuaries, depending on local conditions (Sibert & Kask 1978, Levings et al. 1986), interspecific competition (Fraser et al. 1982, Levings & Kotyk 1983), and hatchery–wild intraspecific competition (Taylor 1990, Korman et al. 1997). In this system, marsh appears to be the most used habitat by emigrating salmon. Despite using a smaller net for marsh sampling, we consistently caught salmon in substantially higher numbers in marsh sites than eelgrass or sand flat sites throughout the emigration period. Brackish marsh is the first estuarine habitat encountered by emigrating salmon, as it is situated around the mouth of the river and the shoreline (Fig. 1). The Chinook salmon population in the Fraser River consists of both larger yearling migrants (growing in freshwater for the first year) and very small sub-yearling migrants, the latter of which include fish that may enter the estuary as newly emerged fry. Chum and sub-yearling Chinook salmon rear in the estuary for extended periods (Levy & Northcote 1982), and the marsh offers less osmotically stressful and more sheltered habitat than the outer flats (Taylor 1990, Gregory & Levings 1998). Chum are adapted to osmotic changes at an earlier life stage (Björnsson et al. 2011) and were found to use eelgrass habitat more extensively than Chinook in the present study. Fraser River chum salmon populations had particularly high escapement in 2016 (Fisheries and Oceans Canada 2018), resulting in much higher densities of juveniles migrating through the estuary in 2017. During years of high abundance, juvenile salmon

may leave freshwater habitats early due to density-dependent effects (Freshwater et al. 2017), which could explain the large schools of chum salmon we captured in eelgrass in 2017.

Differences in species composition between habitats diminished during peaks in abundance. For example, shiner surfperch were most abundant in eelgrass habitat, but were also caught in high numbers in marsh and sand flat habitats during their peak abundance in July. The sand flats physically connect the 2 vegetated habitats in the Fraser River estuary, which was reflected in the greatest species overlap between this habitat with the other two. The single unique fish found in the sand flats (longfin smelt) has previously been found in the eelgrass (Archipelago Marine Research Ltd 2014a) and marsh (Levy et al. 1979) in the Fraser River estuary and likely would have been caught across all habitats in this study had it been more abundant. However, sand flat supported high abundances of arrow goby and flatfish in the estuary. The overarching compositional differences between habitats are consistent with results from a tropical estuarine system (Bloomfield & Gillanders 2005) and with a recent meta-analysis (McDevitt-Irwin et al. 2016), with seagrass supporting the most species and other vegetated habitats ranking higher than unvegetated sand, suggesting a broad pattern for similar coastal habitats. Spatiotemporal variation in community composition among habitats further highlights the importance of maintaining an intact seascape to allow migration and movement of fishes across seasons and changing life history needs (Duffy 2006).

4.2. Seasonal shifts in catch

As predicted, we found temporal variation in the peak catch of different migratory fish species that was indicative of their unique life-history strategies. Juvenile salmon peaked in spring as they entered the estuary and in the following months migrated out to the ocean (Fig. A2). Conversely, other migratory fishes had multiple peaks in catch and were virtually absent from the marsh during summer (Fig. A2), a pattern that was driven by northern anchovy and Pacific sand lance. Anchovy are continuous spawners, and indeed, we observed adults in the estuary followed by high catches of juveniles. This pattern occurred multiple times, with hundreds of anchovy caught in April, July, and September 2016, interspersed with near-0 catches outside of those times. Similarly, sand lance were virtually absent from the estuary until April, then were numerous until July,

when they disappeared again. Resident fishes, however, had a consistent presence in the estuary and experienced much higher peaks in catch during warmer months (Fig. A2D,H), as predicted. Specifically, we noted increases in the catch of adult resident fishes in the spring, followed by large numbers of juveniles in the summer, indicating reproduction during peak productivity in the estuary. Seasonal variation in productivity is common in temperate systems, with changes in flow, light, and temperature regimes leading to plankton blooms, vegetation growth, and subsequent increases in food availability for fishes during summer months (El-Sabaawi et al. 2012, Chandler et al. 2017). Smaller-scale effects of localized temperature, salinity, pH, and dissolved oxygen may have a greater impact on resident species, which remain in the nearshore environment, as opposed to migratory species, which pass through over periods of days to weeks. Temperature can impact metabolic rates and affect food web interactions and fish growth (Attrill & Power 2004, O'Connor et al. 2011), or cause physiological stress near the thermal limit of a fish (Teffer et al. 2018), salinity and pH are physiologically limiting to fish and influence species composition in many systems (Martino & Able 2003), and dissolved oxygen is important for fish respiration and can be detrimental to fish at low levels (Schein et al. 2012, Scott et al. 2016). These environmental conditions vary by habitat and by season, both of which were found to have strong effects on resident species abundances. Temperature and year in particular played an important role in resident fish abundance, highlighting the effects of the 2016 El Niño.

4.3. El Niño effects

The climate-change-amplified 2016 El Niño consistently broke global records for highest sea surface temperatures, with a persistent warm-water 'blob' remaining in North Pacific coastal waters, and the US National Oceanic Atmospheric Administration recorded 2016 as the warmest year in their 137-yr time series (Chandler et al. 2017). These effects were apparent in our study, with increased water temperatures, a decreased freshet leading to higher and more stable salinity, increased pH, and increased dissolved oxygen content relative to 2017. Changes in sea surface temperature and hydrologic regimes lead to shifts in the migratory patterns of many fish species (Kortsch et al. 2015), including northern anchovy, which are currently at the northern extent of their range in British Columbia (Duguid et al. 2019). Dur-

ing the 2016 El Niño, we caught a high number of anchovy at a variety of life stages, compared to a single adult anchovy in 2017, supporting the idea that El Niño effects cause range shifts in migratory species. This influx of biomass can potentially alter the food web by providing increased prey for piscivorous fishes and increased competition among planktivores (Duguid et al. 2019). We also observed large increases of shiner surfperch and three-spined stickleback in 2016, hardy species that have been associated with anthropogenic disturbance (Iacarella et al. 2018), and which are known to have overlapping diets with juvenile Pacific salmon (Weitkamp et al. 2014). This coincided with lower catches of several other species, particularly Pacific sand lance and flatfishes, which may be more sensitive to changes in temperature and hydrology. Earlier and weaker freshets may also lead to earlier spring blooms, potentially creating mismatches for fish food web interactions (Riche et al. 2014, Sato et al. 2018). While interannual variation is expected in such a dynamic system, we encourage ongoing monitoring of the community composition in this system to detect potential climate impacts on the coastal food web.

4.4. Conclusions

Estuarine fish communities exhibit complex spatiotemporal variation in habitat use, and multiple habitat types are required to conserve overall fish species richness and abundance. Focusing on a single habitat or species risks underestimating the value brought to the system by each component — in the case of the Fraser River estuary, focusing habitat remediation efforts solely on eelgrass could lead to further declines in salmon populations with the loss of remaining marsh. This supports the premise that connected seascapes of different habitat types maintain greater biodiversity and productivity, and we suggest that estuaries be managed as such.

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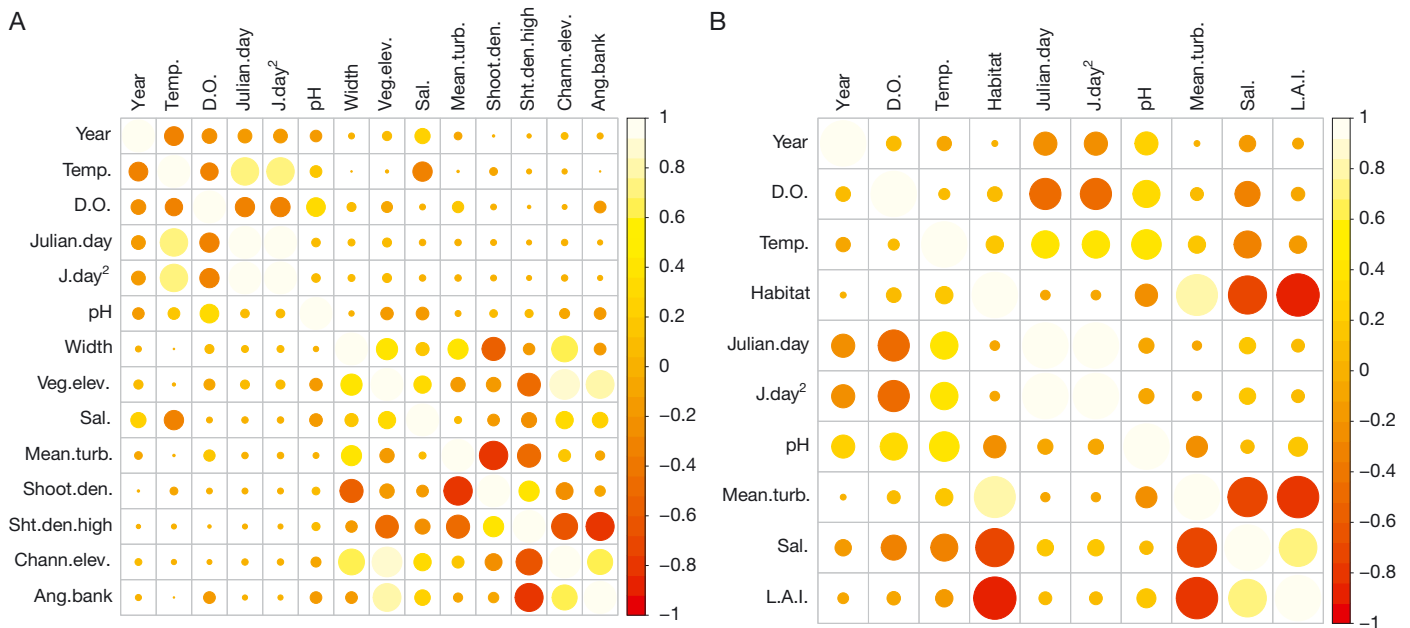
Appendix. Additional information

Fig. A1. Correlation plots for all variables considered in (A) global marsh and (B) eelgrass/sand flat catch models for the Fraser River estuary. Pale yellow indicates positive 1:1 correlation, red indicates negative 1:1 correlation, size indicates strength of correlation in either direction. Year: year of surveys (2016 and 2017); Temp.: surface water temperature; DO: dissolved oxygen; J day: Julian day; J day^2: quadratic modifier of Julian day (Julian day squared); Width: marsh channel width; Veg. elev.: mean elevation of lowest marsh; Sal.: salinity; Mean turb.: mean turbidity measured over all sampling events in 2016; Shoot den.: mean density of lowest marsh vegetation; Sht. den. high: mean density of upper marsh vegetation; Channel elev.: elevation of channel bed relative to chart datum; Ang. Bank: mean bank slope; Habitat: eelgrass or sand flat; LAI: leaf area index of eelgrass. All variables were standardized and centered on the mean. Correlation scores varied slightly for each species group subset
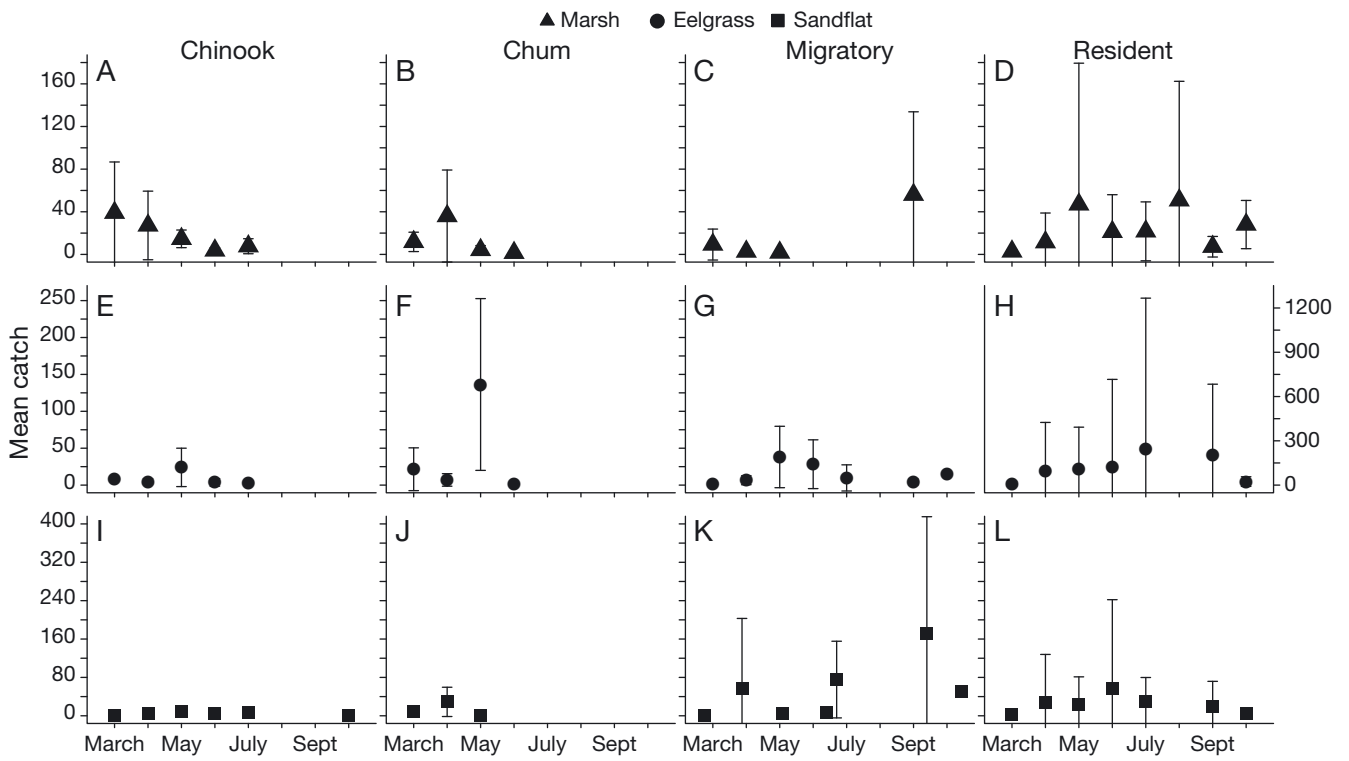
Fig. A2. Trends in catch over time in (A–D) marsh, (E–H) eelgrass, and (I–L) sand flat for Chinook salmon (A,E,I), chum salmon (B,F,J), other migratory fish (C,G,K), and resident fish (D,H,L). Mean catch is shown for each sampling month with standard deviation (error bars). Note the changing *y*-axis to match varying scales of abundance among groups and the unique y-axis for eelgrass resident fish catch in H (right). Data includes both sampling years (2016 and 2017) in the Fraser River estuary