Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 10:435–451, 2018
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ISSN: 1942-5120 online
DOI: 10.1002/mcf2.10035

ARTICLE

Juvenile Chinook Salmon and Forage Fish Use of Eelgrass Habitats in a Diked and Channelized Puget Sound River Delta

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Abstract

Eelgrass *Zostera marina* can form extensive meadows on Puget Sound river deltas. The extent to which these meadows provide critical rearing habitat for local estuarine fishes, especially out-migrating juvenile salmon, is not well understood. Further, delta eelgrass has been impacted by diking and river channelization with unknown consequences for fish. We sampled fish in the Skagit River delta, Washington, during April–September with a lampara net, which is well suited to capturing fish in eelgrass. We compared abundance and body size of Chinook Salmon *Oncorhynchus tshawytscha* and three forage fish species between eelgrass and nearby unvegetated habitat. We also assessed combined effects of eelgrass characteristics (meadow size and morphology) and oceanographic conditions (temperature and salinity), which covaried according to proximity and orientation to channelized distributary outlets, diked shorelines, and a jetty. Chinook Salmon were more abundant in eelgrass than in unvegetated habitat in June–July and were relatively more abundant in eelgrass compared with unvegetated habitat in regions with intact eelgrass than offshore from a channelized distributary outlet. Abundances of Pacific Herring *Clupea pallasii* and Shiner Perch *Cymatogaster aggregata* were consistently severalfold higher in eelgrass than in unvegetated habitat. Surf Smelt *Hypomesus pretiosus* were more abundant in eelgrass than in unvegetated habitat at some locations, but never less abundant in eelgrass. Our results suggest that conservation and restoration of delta eelgrass would benefit these species and help to identify the settings in which these actions would be most beneficial.

Seagrasses form structurally complex habitats that support other aquatic organisms by providing attachment substrate, food, refuge from predation, and nursery areas (i.e., food and cover for juveniles) (Heck et al. 2003). There is concern over seagrass losses worldwide (Orth et al. 2006). The dominant native seagrass in the northeastern Pacific Ocean is *Zostera marina*, referred to hereafter as eelgrass. For the past 40 years, eelgrass abundance in Puget Sound, Washington, has been stable at the scale of the entire region, but there have been losses in several localities (Christiaen et al. 2016; Shelton et al. 2017). Eelgrass was recently established as an indicator of

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Subject editor: Milo Adkison, University of Alaska–Fairbanks, Juneau

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Received October 20, 2017; accepted May 15, 2018

the health of Puget Sound, and in 2011 a goal was set to increase eelgrass extent in Puget Sound by 20% by 2020 (Goehring et al. 2015). There is considerable interest in further defining whether eelgrass constitutes essential estuarine habitat for fish and shellfish species of management concern (Levin and Stunz 2005; Rehr et al. 2014).

Estuarine habitats in populated areas have often been extensively altered for agricultural, industrial, and residential purposes, resulting in losses of habitat and species (Lotze et al. 2006). River deltas in particular have been diked to prevent riverine and tidal intrusion, and major distributaries have been channelized to route water past the diked areas (Nichols et al. 1986; Hood 2004). A consequence of channelization is to also route river-born sediments past the diked areas and farther offshore than has occurred historically (Hood et al. 2016). Such flow and sediment rerouting can impact eelgrass growing on river deltas because the depth range occupied by eelgrass is offshore from the complex of dikes and channelized distributaries. Eelgrass directly offshore from distributary mouths can be degraded and fragmented by burial and abrasion associated with increased sediment delivery, whereas eelgrass offshore from dikes may be more protected from such sediment disturbance. In recent years, dike removal and/or breaching have been implemented on several Puget Sound deltas to restore tidal marsh habitat and associated ecosystem services, especially rearing capacity for juvenile salmon (Ellings et al. 2016). There is evidence that dike removal also benefits eelgrass on the outer delta, perhaps by reestablishing more dispersed sediment delivery, and for this reason it is thought that large river deltas show potential for increasing eelgrass extent in conjunction with reduced diking (Goehring et al. 2015; Christiaen et al. 2016). Thus, it is of interest to know how diking and river channelization affect the functionality of eelgrass as rearing habitat for fish.

Our study was conducted in the Skagit River delta in Puget Sound (Figure 1) during April–September, when juvenile salmon were out-migrating (Zimmerman et al. 2015), juvenile forage fish were resident in the area and growing (Reum et al. 2011, 2013), and eelgrass standing crop was at its seasonal maximum (Thom and Albright 1990; Thom et al. 2008). We focused analyses on the four fish species occurring most frequently in our catch: Chinook Salmon *Oncorhynchus tshawytscha*, Pacific Herring *Clupea pallasii*, Surf Smelt *Hypomesus pretiosus*, and Shiner Perch *Cymatogaster aggregata*. Here we briefly review eelgrass use by these species at this time of year. Semmens (2008) found that in a large estuarine enclosure, Chinook Salmon spent more time in eelgrass than in other structured habitats (oyster *Crassostrea gigas* beds, nonnative eelgrass *Z. japonica*, and smooth cordgrass *Spartina alterniflora*) or bare sand–mud flats, apparently in response to high avian predation risk. In contrast, Murphy et al. (2000), Johnson et al. (2003), Hosack et al. (2006), and Dumbauld et al. (2015) did not find Chinook Salmon to be more abundant in net catches from eelgrass than from other habitats. Kennedy et al. (2018) demonstrated that eelgrass-associated invertebrates, primarily harpacticoid copepods, dominated juvenile Chinook Salmon diets in May. In contrast, Dumbauld et al. (2015) found that juvenile Chinook Salmon diets during June–August were dominated by terrestrial insects and pelagic zooplankton rather than prey associated with benthic habitats. Eelgrass growing on the outer margins of large river deltas may be particularly important to salmon because it forms extensive meadows in this setting (Mumford 2007) and is the first eelgrass encountered by out-migrating juveniles. Hodgson et al. (2016) found that such eelgrass continued to support high abundances of juvenile Chinook Salmon in July and August, after they had mostly vacated other nearshore habitats.

The importance of eelgrass (and other submerged vegetation) as spawning substrate for Pacific Herring in late winter is well known (Hay 1985; Penttila 2007; Shelton et al. 2014), but the extent to which other life stages of herring or other forage fish species rely on eelgrass is less well established. Abundances of herring and Surf Smelt during April–July appeared higher in eelgrass than in oyster beds or mud flats in a study by Hosack et al. (2006). Other studies have found herring and/or Surf Smelt to be abundant in eelgrass but not more so than in other habitat types (Miller et al. 1976; Murphy et al. 2000; Johnson et al. 2003; Dumbauld et al. 2015). In northern Puget Sound, Pacific Herring typically eat pelagic zooplankton, whereas Surf Smelt feed on both pelagic and epibenthic invertebrates (Miller et al. 1980; Simenstad et al. 1988). Shiner Perch, in contrast to Pacific Herring and Surf Smelt, are often strongly associated with eelgrass (Murphy et al. 2000; Johnson et al. 2003; Dumbauld et al. 2015). Shiner Perch feed on epibenthic invertebrates that can be abundant in eelgrass (Miller et al. 1976), for example, caprellid amphipods (Caine 1991), and release their live-born young in eelgrass (Love 2011).

Our primary objective was to investigate the use of eelgrass on a Puget Sound river delta by juvenile Chinook Salmon and forage fish. Our approach was to compare fish abundance and body size between eelgrass and nearby unvegetated habitat. A secondary objective was to examine combined effects of eelgrass characteristics (meadow size and morphology) and oceanographic conditions (temperature and salinity), which covaried according to location on the delta with respect to channelized distributary outlets, diked shorelines, and a jetty. This examination led to some insights concerning how diking and river channelization interacted with hydrodynamic processes to influence use of delta eelgrass by the target fish species. Our

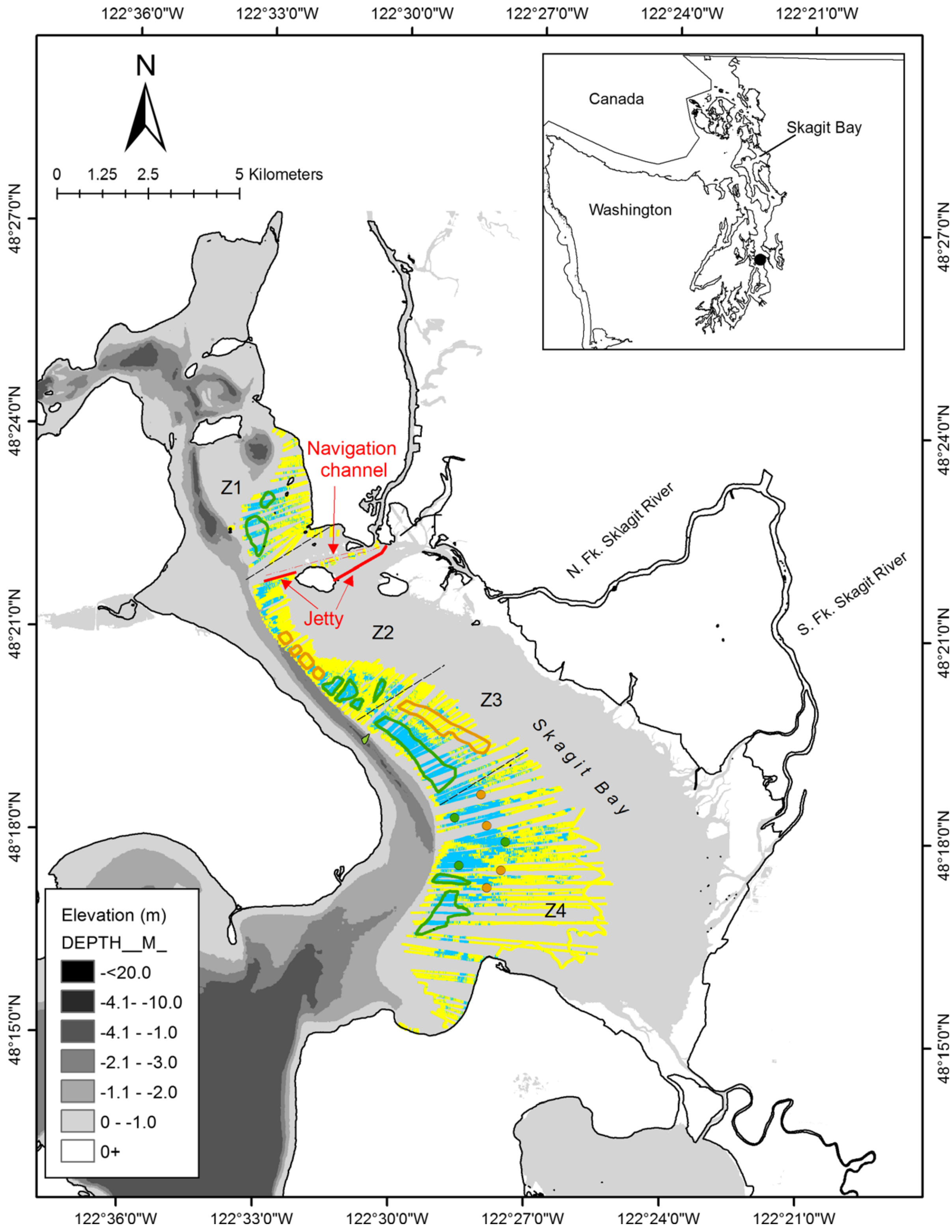

FIGURE 1. Skagit Bay study area with borders of the four sampling zones (Z1, Z2, Z3, and Z4) indicated by dashed lines. Irregularly shaped polygons outlined in green (eelgrass) and orange (unvegetated) are areas within which fish-netting sites were randomly selected, and correspondingly colored small circular dots in zone 4 are permanent netting sites. Blue indicates eelgrass presence and yellow indicates eelgrass absence along transects surveyed during 2006–2011 (Washington Department of Natural Resources Nearshore Habitat Program 2017). The jetty and navigation channel between zones 1 and 2 are shown in red. Gray shading indicates bottom elevation (m) relative to mean lower low water level.

results are relevant to incorporating benefits for fish into decisions concerning conservation and restoration of eelgrass on river deltas.

METHODS

Study area.— The Skagit River is the largest river entering Puget Sound, accounting for 35% of the freshwater and 40% of the sediment entering the sound (Czuba et al. 2011). This river retains important salmon populations including Chinook Salmon runs that are relatively healthy compared with other Puget Sound populations (NFSC 2015). Puget Sound Chinook Salmon are currently listed as threatened under the U.S. Endangered Species Act (NOAA 1999). Skagit Bay has abundant populations of all forage fish species (Greene et al. 2015).

The Skagit River delta has been extensively diked and the river channelized to develop farmland and protect it from flooding and saltwater intrusion, and a jetty was constructed to maintain a navigation channel (Figure 1). Diking and river channelization began in the late 1800s and the jetty was constructed in the 1930s and 1940s (Grossman et al. 2011). Previous work documented large changes in delta tidal flat sediments resulting from these modifications (Grossman et al. 2011). Sediments coarsened offshore from the confined river channels due to focused flow that delivered sand but transported finer sediments farther away. Sand deposition offshore from the North Fork Skagit River outlet resulted in the delta front prograding 0.5 km seaward since the late 1800s (E. E. Grossman, U.S. Geological Survey, unpublished data). In contrast, delta sediments north of the jetty are now finer than in the past. The jetty blocks northward river flow and disrupts tidal currents with the net effect of creating a fine sediment deposition zone north of it. Delta tidal flats seaward of the dike complex range in width from 4 km offshore from of the North Fork to 7 km off the South Fork Skagit River and range in elevation from +1 to −2 m mean lower low water level (Figure 1). The range of mixed semidiurnal tides in Skagit Bay is nearly 4 m (Grossman et al. 2011).

Eelgrass is present along much of the outer edge of the Skagit River delta (Figure 1); however, bed morphology is variable and has been shaped by the above-mentioned alterations in flow and sedimentation. Eelgrass offshore from the North Fork outlet comprises several relatively small beds (Figure 1), which are likely more fragmented than in the past. Eelgrass offshore from the South Fork also comprises multiple beds, but the beds may be less affected than those off the North Fork. The beds are larger off the South Fork than off the North Fork (Figure 1). Further, water and sediment discharges are usually lower in the South Fork than in the North Fork (Curran et al. 2016), and distance between the river fork outlet and eelgrass is greater off the South Fork than off the North Fork (Figure 1). Eelgrass between the North and South forks and offshore from diked-off farmland forms a single large continuous bed, and eelgrass north of the jetty also forms a relatively continuous bed (Figure 1). Sediments underlying eelgrass are primarily mud north of the jetty and primarily sand south of the jetty (Grossman et al. 2011).

Sampling.— We selected four zones for examining fish use of eelgrass (Figure 1) based on proximity to Skagit River outlets, eelgrass meadow morphology, and grain size of underlying sediments as described above. We netted fish at sites in eelgrass meadows and unvegetated habitat within each zone. Using a digital mapping program (Esri ArcMap 10.4.1.5686), we drew a polygon around each eelgrass meadow and unvegetated area to be sampled (Figure 1). Polygon boundaries were based on information obtained from aerial photos, hydro-acoustic surveys (Stevens et al. 2008), and underwater video. Unvegetated areas sometimes included small amounts of macroalgae, usually filamentous green algae. In zone 1, sampling in unvegetated habitat was precluded by the absence of unvegetated habitat with depths similar to the eelgrass meadows.

We sampled during the daylight hours (range, 0830–1944 hours) on two consecutive days, once per month during neap tides from April to September, 2008–2010. Site locations were selected randomly within each polygon each month, except for seven sites in zone 4 that were sampled every trip (Figure 1) because we lacked enough information to delineate eelgrass and unvegetated habitat boundaries. To ensure that sites occurred inside our eelgrass or unvegetated polygons and did not overlap, random site selection included forcing sites to be at least 50 m from the polygon edge and at least 100 m from each other. We sampled from four to eight sites in each habitat (eelgrass or unvegetated) in each zone each month, except that in 2008 we did not sample unvegetated habitat (Table S1-1 in Supplement 1 available separately online).

We captured fish using a lampara net (Hayes et al. 1996) that was 48.8 m long and 4.9 m deep, with a 0.6-m-deep bag. The net was made of black knotless nylon netting, and stretched mesh size graded from 102 mm on the outer wings to 25 mm on the outer bag and 12.7 mm on the inner bag. The net was deployed in a circle between two boats and retrieved into one of the boats. Captured fish were identified to the lowest possible taxon and counted. Hatchery Chinook Salmon were identified by the presence of a clipped adipose fin and/or a wire tag detected with a hand-held wand (Blue Wand, Northwest Marine Technologies). Up to 25 fish per species per net deployment were measured for TL (2008) or FL (2009 and 2010). Total lengths were converted to fork lengths using literature conversion factors (Karpov and Kwiecien 1988; Ramseyer 1995).

In 2008–2010 we measured depth, and in 2009–2010 we measured surface (0.3 m below the water surface) and bottom (0.3 m above the substrate) temperature and salinity, water clarity, and presence or absence of eelgrass at each site before deploying the net. Water clarity was determined with a Secchi disk, and eelgrass presence was assessed with an underwater video camera connected to an onboard monitor (Harbor Freight Tools underwater camera with monitor, model 91309; camera angle of view: 83° horizontal, 60° vertical). Mean values of surface and bottom temperatures and salinities were used in analyses.

We used underwater video transects, with the camera deployed just above the eelgrass (camera described above), to quantify percentage cover of eelgrass inside our eelgrass meadow polygons. Video was recorded while drifting with the current from a polygon border to the opposite border. Percent cover was estimated as the percent of total transect time that eelgrass was visible in the video.

Data from surveys of Skagit Delta eelgrass during 2006–2011 (Washington Department of Natural Resources Nearshore Habitat Program 2017) were used to describe where eelgrass occurred during our study (Figure 1) and to estimate total cover of eelgrass for comparison with cover in our sampling area. A range of years wider than 2008–2010 (our study years) was needed to provide at least 2 years of survey data for each subsection of the delta (subsections were not surveyed every year, and different subsections were not always surveyed in the same years). These data were obtained recently; they were not used in delineating our sampling polygons.

Analyses.— We framed five null hypotheses concerning abundance and body size of Chinook Salmon, Pacific Herring, Surf Smelt, and Shiner Perch in relation to eelgrass and water column properties:

H_1: Abundance of each species does not differ between eelgrass and unvegetated habitat. This test used data from paired eelgrass and unvegetated habitat from 2009–2010 and zones 2–4.

H_2: Abundance of each species in eelgrass does not differ among zones 1–4. This test used data from all sampling years (2008–2010).

H_3: Abundance of each species is not related to water column depth, water temperature, or salinity.

H_4: Body size (length) of each species does not differ between eelgrass and unvegetated habitat.

H_5: Body size (length) of each species in eelgrass does not differ among the four zones.

We tested hypotheses 1–3 with general linear models appropriate for count data (Zuur et al. 2009; Zuur and Ieno 2016). Because the target species exhibited schooling behavior and schools were patchily distributed, the raw count data (number of fish caught in each set of the net) included many 0 values and many counts > 1, which created overdispersion and zero inflation. We used negative binomial models because they improved fit without loss of interpretability (see Supplement 2 available separately online).

Categorical variables included in the initial models were vegetation (eelgrass or unvegetated, H_1 only), zone, year, and month. Depth was included in all initial models. Because temperature and salinity were not measured in 2008 they were included in initial models for H_1 but not H_2. Effects of depth, temperature, and salinity (H_3) were assessed by referring to results of H_1 and H_2 models. Temperature and salinity were normalized before analysis (see below). Low sample sizes and model convergence problems precluded testing all possible interactions among independent variables. We included two-way interactions involving vegetation and another categorical variable in initial models for H_1: vegetation × year, vegetation × month, and vegetation × zone. We included zone × year and zone × month interactions in initial models for H_2. Due to small sample sizes we combined months into three 2-month-long periods: April–May, June–July, and August–September.

Temperature and salinity varied seasonally. The factor month accounted for this seasonal variation, but it did not account for short-term variation in temperature and salinity as would occur over a tidal cycle. To assess effects of this short-term variation, we normalized temperature and salinity by computing the mean for a trip (i.e., the two consecutive days during which all sites were sampled) and then subtracting the trip mean from each site-specific measurement made that trip.

Final models were arrived at through backwards selection by dropping terms that were not significant and assessing fit with the Akaike information criterion (AIC) (Zuur et al. 2009). Models were validated for meeting assumptions of homogeneity and independence by examining plots of residuals against fitted values and each explanatory variable (Zuur et al. 2009). Negative binomial models were fit with the glm.nb routine in the MASS package (Venables and Ripley 2002) in R version 3.3.1 (R Core Team 2016). Least-squares means computations and pairwise comparisons a posteriori of main effects means, interaction contrasts, and simple main effects means were performed with the phia package (de Rosario-Martinez 2015) in R. *P*-values were adjusted for multiple comparisons by the Holm method. Least-squares means were used because they accounted for effects of other model terms and unequal sample sizes.

We tested H_4 and H_5 with nonparametric tests based on ranks (Kruskal–Wallis tests) (Pohlert 2014; R Core

Team 2016) because fish length data were not normally distributed due to the presence of multiple age-classes. We additionally tested H_5 for the dominant (i.e., most abundant) age-group of each target species. Membership in the dominant age-group was determined by examining scatter plots of length versus capture date. We used linear models fit by ordinary least squares (lm routine in the stats package in R) (R Core Team 2016) to test whether mean length adjusted to mean capture date differed among zones. Initial models included zone and year as categorical variables, capture date as a covariate, and all possible interactions. Final model selection and pairwise comparisons a posteriori were conducted as described above for count models. Too few fish of the dominant age-group were captured in unvegetated habitat to allow similar tests of H_4 for any target species.

We compared species richness between eelgrass and unvegetated habitat with species accumulation curves (Clarke and Gorley 2015), which accounted for the difference in sampling effort between habitat types. Curves were computed by the undirected graph evaluation (UGE) method, which gives smoothed, mean curves over all permutations of sample order.

RESULTS

Habitat

The mean area of individual eelgrass meadows sampled for fish abundance (i.e., within polygons; Figure 1) was least in zone 2 (five meadows) and greatest in zone 3 (a single meadow) (Table S1-2). Mean cover of eelgrass within meadows was also least in zone 2 (89%) and greatest in zone 3 (95%), and the variation in cover was greatest in zone 2 and least in zone 3 (Table S1-2). Eelgrass was present at GPS coordinates for the sites for 87% of the netting events in eelgrass meadows and 11% of the events in unvegetated habitat. Eelgrass in habitat designated as unvegetated was sparse when present.

Total cover of eelgrass within sampled polygons was 22% of the total eelgrass cover on the entire Skagit Delta (Figure 1; Table S1-2). Whole-delta cover estimates were derived from estimates made in five subsections (Washington Department of Natural Resources Nearshore Habitat Program 2017). Coefficient of variation (100·SD/mean) in eelgrass cover among years (at least two survey years in each subsection during 2006–2011) averaged 12% over subsections (range, 2–23% among subsections), suggesting that eelgrass cover was relatively stable during our study.

Water column properties are summarized in Table S1-3. Depth averaged 2.5 m and ranged from 0.6 to 5.9 m during netting. Temperature ranged from 9.1°C to 15.8°C, salinity from 3.1‰ to 29.6‰, and water clarity (Secchi disk depth) from 0.3 to 4.0 m. Mean temperature increased from 10.6°C in April–May to 13.1°C in August–September. Mean salinity and clarity were lowest in June–July (16.7‰ and 1.8 m) and highest in August–September (26.2‰ and 2.4 m). Zone 1 water was the coolest, saltiest, and most turbid among zones. Temperature increased from north to south (warmest in zone 4) whereas salinity and clarity were relatively similar among zones 2–4.

Fish Overview

During 3 years of netting (560 events; Table S1-1) we captured 26 species of fish and nearly 9,000 individuals (Table A.1 in the Appendix). Surf Smelt, Pacific Herring, Shiner Perch, Chinook Salmon, and Threespine Stickleback *Gasterosteus aculeatus* occurred in more than 10% of the sampling events (Table A.1). Pacific Sand Lance *Ammodytes hexapterus* and Pink Salmon *O. gorbuscha* were present in relatively large numbers but occurred in less than 4% of the samples (Table A.1). Of the Chinook Salmon we caught, 22% were marked hatchery fish and the other 78% were unmarked, naturally produced fish. Hatchery and naturally produced Chinook Salmon were pooled in analyses unless otherwise noted.

Catch of Chinook Salmon peaked in June (Figure S1-1 in Supplement 1). Catches of Pacific Herring and Shiner Perch peaked in August, while catch of Surf Smelt was greatest in spring (Figure S1-1). Chinook Salmon comprised subyearlings and yearlings in May but were primarily subyearlings thereafter (Figure S1-2). Multiple age-classes were also present for herring, smelt, and Shiner Perch (Figure S1-2). Pacific Herring and Shiner Perch subyearlings first became abundant in July, whereas Surf Smelt subyearlings were also present in May and June. Older individuals of all three forage fish species were mostly yearlings (Anderson and Bryan 1970; Therriault et al. 2002; Stick and Lindquist 2009) and were present throughout April–September (Figure S1-2). Based on cumulative frequency distributions of number of fish per set of the net (Figure S1-3), Chinook Salmon schooled least, and smelt and Shiner Perch the most. We never caught more than seven Chinook Salmon in a set, whereas there were many sets with more than 20 Surf Smelt or Shiner Perch.

All 26 of the species we encountered were caught in eelgrass, but only 13 of them were caught in unvegetated habitat (Table A.1). Our effort was greater in eelgrass (411 events) than in unvegetated habitat (149 events); nevertheless, the number of species at which species accumulation curves approached their asymptote suggested that species richness in eelgrass was about twice that in unvegetated habitat (Figure S1-4). Diversity in eelgrass habitat was similar among the four zones with 20–21 species captured in each zone (Table A.1).

TABLE 1. *P*-values of factors included in, and deviance explained by, final models relating fish abundance to vegetation (eelgrass versus unvegetated), or fish abundance in eelgrass to zone; $^{**}P < 0.01$, $^{*}P < 0.05$, NS = not significant. Blank cells indicate that the factor was not included in the final model.

		Species			
Test	Factors	Chinook Salmon	Pacific Herring	Surf Smelt	Shiner Perch[a,b]
Vegetation	Vegetation	**	NS	NS	**
	Zone	NS		NS	
	Month	*	**		
	Year		NS		**
	Depth	**	*	**	**
	Vegetation × Zone	**		**	
	Vegetation × Month	**			
	Vegetation × Year		*		
	Deviance explained (%)	23	31	21	54
Zone	Zone		**	NS	NS
	Month	**	**	NS	**
	Year			NS	**
	Depth	**	**	**	**
	Zone × Month			*	*
	Zone × Year			**	
	Deviance explained (%)	23	31	24	58

[a] The factor month had two levels, April–June and July–September.

[b] Vegetation test data are for July–September only because zero catch in April–June in unvegetated habitat prevented the model from running.

Hypothesis Tests

H_1: *Abundance of each species does not differ between eelgrass and unvegetated habitat, 2009–2010, zones 2–4.—* The final model for Chinook Salmon included significant interactions between vegetation and month and between vegetation and zone (Table 1), indicating that the effect of vegetation on salmon abundance was not consistent among months or zones. There were relatively more salmon in eelgrass compared with unvegetated habitat in June–July than in April–May with an intermediate response in August–September (Figure 2; Table S1-4). Chinook Salmon were significantly more abundant in eelgrass than in unvegetated habitat in June–July but not in April–May or August–September (Figure 2; Table S1-4). There were relatively more salmon in eelgrass compared with unvegetated habitat in zones 3 and 4 than in zone 2; however, salmon abundance did not differ significantly between eelgrass and unvegetated habitat within any single zone (Figure 2; Table S1-4). Chinook Salmon were moderately abundant in eelgrass but absent from unvegetated habitat in zone 3 during June–July and in zone 4 during June–September (Figure 3). Results of H_1 tests for naturally produced Chinook Salmon only (i.e., hatchery fish excluded) were similar to those with hatchery fish included; the final model included the same factors, salmon abundance was significantly higher in eelgrass than in unvegetated habitat in June–July, and salmon abundance was relatively higher in eelgrass compared with unvegetated habitat in zone 3 than in zone 2 (not significant) and in zone 4 than in zone 2 ($P = 0.07$).

The final model for Pacific Herring included month and a significant interaction between vegetation and year (Table 1); however, herring were significantly more abundant in eelgrass than in unvegetated habitat in both 2009 and 2010 (Figure 2; Table S1-4). The vegetation × year interaction indicated that the difference in herring abundance between eelgrass and unvegetated habitat was greater in 2010 than in 2009 (Figure 2; Table S1-4). Pacific Herring abundance increased significantly from April–May to June–July and from June–July to August–September (Table S1-4).

The final model for Surf Smelt included a significant interaction between vegetation and zone (Table 1). There were relatively more smelt in eelgrass compared with unvegetated habitat in zone 3 than in zones 2 or 4 (Figure 2; Table S1-4), and smelt were significantly more abundant in eelgrass than in unvegetated habitat in zone 3 but not in zones 2 or 4 (Figure 2; Table S1-4).

During April–June we caught a total of 236 Shiner Perch in eelgrass and no perch in unvegetated habitat (data pooled over 2009–2010 and zones 2–4). April–June data were excluded from the H_1 analysis because zero catch in unvegetated habitat prevented the model from

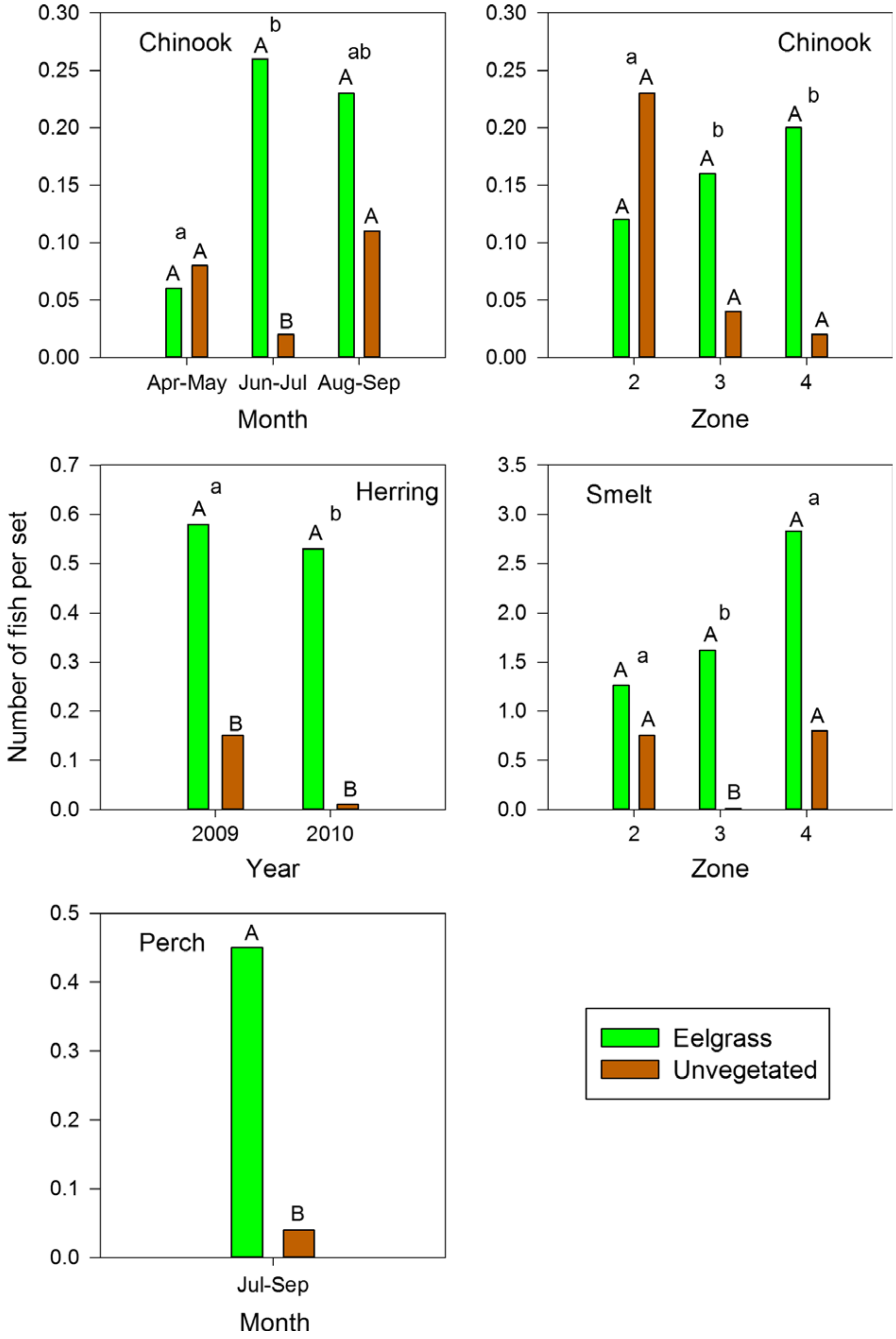

FIGURE 2. Least-squares means for each level of each significant vegetation factor in final models relating fish abundance to vegetation (Table 1). Text headings in each panel indicate species. The uppercase letters over each bar in a bar pair (eelgrass versus unvegetated) indicate significant differences between means (letters differ) or not (letters do not differ). The lowercase letters over each bar pair show interaction contrasts: letters differ if the difference between within-pair means (eelgrass versus unvegetated) differs significantly between bar pairs; otherwise letters do not differ. Pairwise comparison results are also given in Table S1-4, along with bar height values. For Shiner Perch, data are for July–September only because zero catch in April–June in unvegetated habitat prevented the model from running.

running. During July–September we caught 243 perch in eelgrass and 66 in unvegetated habitat. The final model for July–September included vegetation and year. Shiner Perch were more abundant in eelgrass than in unvegetated habitat (Figure 2) and were also more abundant in 2010 than in 2009 (Table S1-4).

H_2: *Abundance of each species in eelgrass does not differ among the four zones, 2008–2010.*— The final model

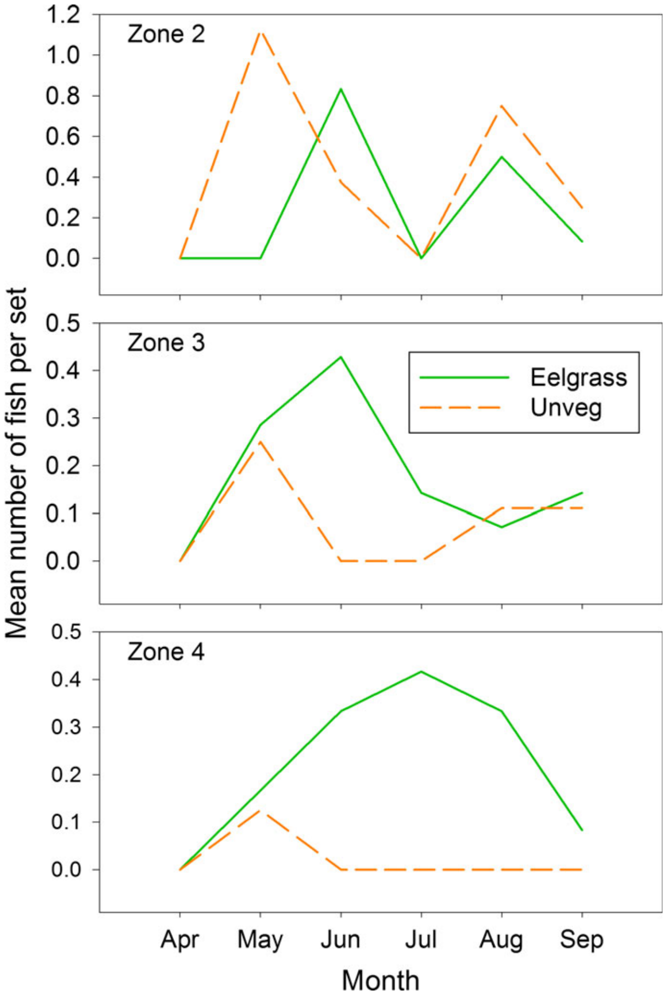

FIGURE 3. Abundance of Chinook Salmon by zone, month, and habitat for data pooled over the years 2009–2010; Unveg = unvegetated.

for Chinook Salmon did not include zone (Table 1), indicating that abundance of salmon in eelgrass did not differ among zones. Month was included in the final model; salmon were less abundant in April–May than in June–July or August–September (Table S1-5).

The final Pacific Herring model included zone and month (Table 1). Herring abundance in zone 1 was at least four times that in zones 2, 3, or 4 (Table S1-5). Herring were significantly less abundant in zone 2 than in zone 4 (Table S1-5). Herring abundance increased from April–May to June–July and from June–July to August–September (Table S1-5), in agreement with the H_1 model for herring (Figure 2; Table S1-4).

The final model for Surf Smelt included significant interactions between zone and year and between zone and month (Table 1). The effect of zone on smelt abundance differed significantly between 2009 and 2010 and was intermediate in 2008 (Table S1-5). Surf Smelt were more abundant in zone 1 than in zones 2 or 4 in 2009, whereas smelt abundance did not differ among zones in 2008 or 2010 (Table S1-5). The effect of zone on Surf Smelt abundance differed significantly between April–May and August–September and was intermediate in June–July (Table S1-5). Smelt were less abundant in zone 2 than in zone 4 in April–May but did not differ among zones in June–July or August–September (Table S1-5).

To be consistent with the H_1 analysis, we combined Shiner Perch counts into two 3-month-long groups, April–June and July–September. The final perch model included year and a significant interaction between zone and month (Table 1). Shiner Perch abundance was lower in zone 3 than in zones 1 or 4 in July–September but did not differ among zones in April–June (Table S1-5). Perch were more abundant in 2010 than in 2008 or 2009 (Table S1-5).

H_3: *Abundance of each species is not related to water column depth, water temperature, or salinity.*— The effect of depth was assessed by referring to the depth term in H_1 and H_2 final models. Depth was significant in all H_1 and H_2 final models (Table 1). Furthermore, estimated depth coefficients were always <1 (Tables S1-4, S1-5), indicating that fish abundance was always inversely related to depth. The depth coefficients quantify the fractional decrease in fish abundance associated with each 1-m increase in depth; for example, for a depth coefficient = 0.1, abundance would decrease from 100 to 10 fish with a 1-m increase in depth and from 10 to 1 fish with an additional 1-m increase in depth. Depth coefficients ranged from 0.02 to 0.55 among models (Tables S1-4, S1-5) and were considerably lower for Shiner Perch (0.02–0.09) than for the other three species (0.32–0.55). We found no evidence that the relationship between abundance and depth differed between eelgrass and unvegetated habitat. Although model convergence problems prevented including a vegetation × depth interaction term in the initial H_1 models (i.e., the full models upon which backwards selection was performed), vegetation × depth was never significant when it was added back into the final H_1 models ($P > 0.5$).

Temperature, normalized to remove seasonal trends (see Methods section), was not included in any of the final H_1 models (and was not tested by H_2 models because temperature and salinity were not measured in 2008). Temperature was moderately correlated with depth ($r = -0.23$). Stronger correlations between salinity (also normalized) and depth ($r = 0.41$) and salinity and temperature ($r = -0.44$) precluded separating the effect of salinity on fish abundance from effects of depth or temperature.

H_4: *Body size (length) of each species does not differ between eelgrass and unvegetated habitat, 2009–2010, zones 2–4.*— Median length of Chinook Salmon did not differ between eelgrass and unvegetated habitat (Figure 4). Pacific Herring were longer in eelgrass than in unvegetated habitat because eelgrass harbored a higher percentage of

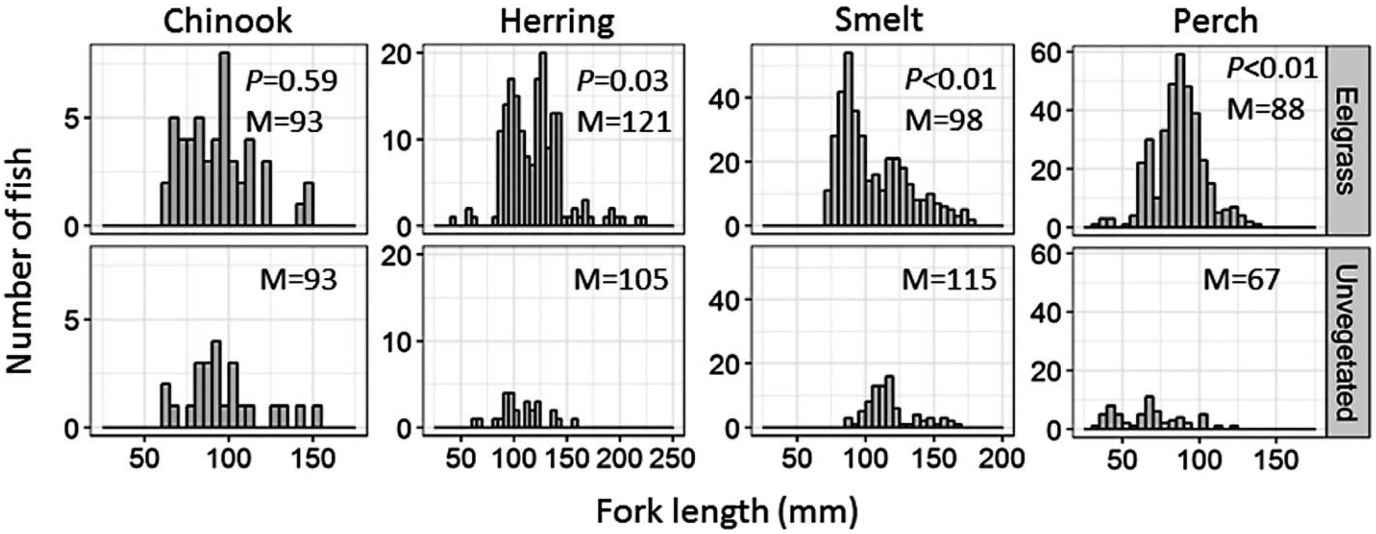

FIGURE 4. Length frequencies by species and habitat for data pooled across months, zones 2–4, and the years 2009–2010; M = median length. Within a species, *P* = *P*-value of a test for difference in median fish length between habitats.

herring longer than 120 mm (Figure 4). In contrast, Surf Smelt were shorter in eelgrass than in unvegetated habitat because of a higher percentage of smelt shorter than 100 mm in eelgrass (Figure 4). The difference in length of smelt between eelgrass and unvegetated habitat was primarily driven by large catches of smelt shorter than 100 mm in eelgrass in 2010 in zone 4. Shiner Perch were longer in eelgrass than in unvegetated habitat (Figure 4).

H_5: *Body size (length) of each species in eelgrass does not differ among the four zones, 2008–2010.*— Median length of Chinook Salmon did not differ among zones (Figure 5); however, mean of length of subyearling Chinook Salmon adjusted for capture date did differ among zones (see below). Pacific Herring were shorter in zone 1 than in the other three zones because of a higher percentage of herring shorter than 75 mm (Figure 5). In contrast, Surf Smelt were longest in zone 1, intermediate in zones 2 and 3, and shortest in zone 4 (Figure 5). Shiner Perch were shortest in zone 1, longest in zone 2, and of intermediate length in zones 3 and 4 (Figure 5).

Subyearling Chinook Salmon could be differentiated from yearlings starting in June (Figure S1-2). Length of subyearling salmon in eelgrass was significantly related to zone, year, and capture date (Figure 6; Table S1-6). Mean length adjusted to mean capture date was greatest in zone 3 and least in zone 1 (Figure 6). Chinook Salmon length in zone 2 was more similar to that in zone 1 than in zones 3 or 4, and length in zone 4 was more similar to that in zone 3 than in zones 1 or 2 (Figure 6). The significant effect of zone (Table S1-6) on length indicates a significant difference in length among at least two zones even though pairwise comparisons did not show significant differences (Figure 6).

Length of early spawned subyearling Surf Smelt (the dominant age-group of smelt; Figure S1-2) in eelgrass was significantly related to zone, year, capture date, and the interaction between zone and capture date (Figure 6; Table S1-6). Mean length of smelt adjusted to mean capture date was significantly less in zone 4 than in the other three zones (Figure 6). Length of subyearling Pacific Herring (Figure S1-2) in eelgrass was inconsistently related to zone, year, and capture date (significant three-way interaction; Table S1-6). Length of yearling Shiner Perch (the dominant age-group of perch; Figure S1-2) was significantly related to year and capture date but not zone (Table S1-6). Shiner Perch length was nonlinearly related to capture date (Table S1-6), primarily because length did not increase with capture date for days of the year > 200. Too few fish of the dominant age-group of any species were captured in unvegetated habitat to allow tests for differences in length at capture date between eelgrass and unvegetated habitat.

DISCUSSION

The degree to which eelgrass on river deltas provides critical habitat for estuarine fishes, especially out-migrating juvenile salmon, is an important scientific and management issue that bears on efforts to conserve and restore both eelgrass and fish. We report on spatiotemporal variation in abundance and body size of juvenile Chinook Salmon and three forage fish species in relation to eelgrass on a large river delta in Puget Sound. We also consider how diking and river channelization potentially influenced eelgrass use by these fish. Fish–eelgrass associations were unique for each species and are discussed as follows.

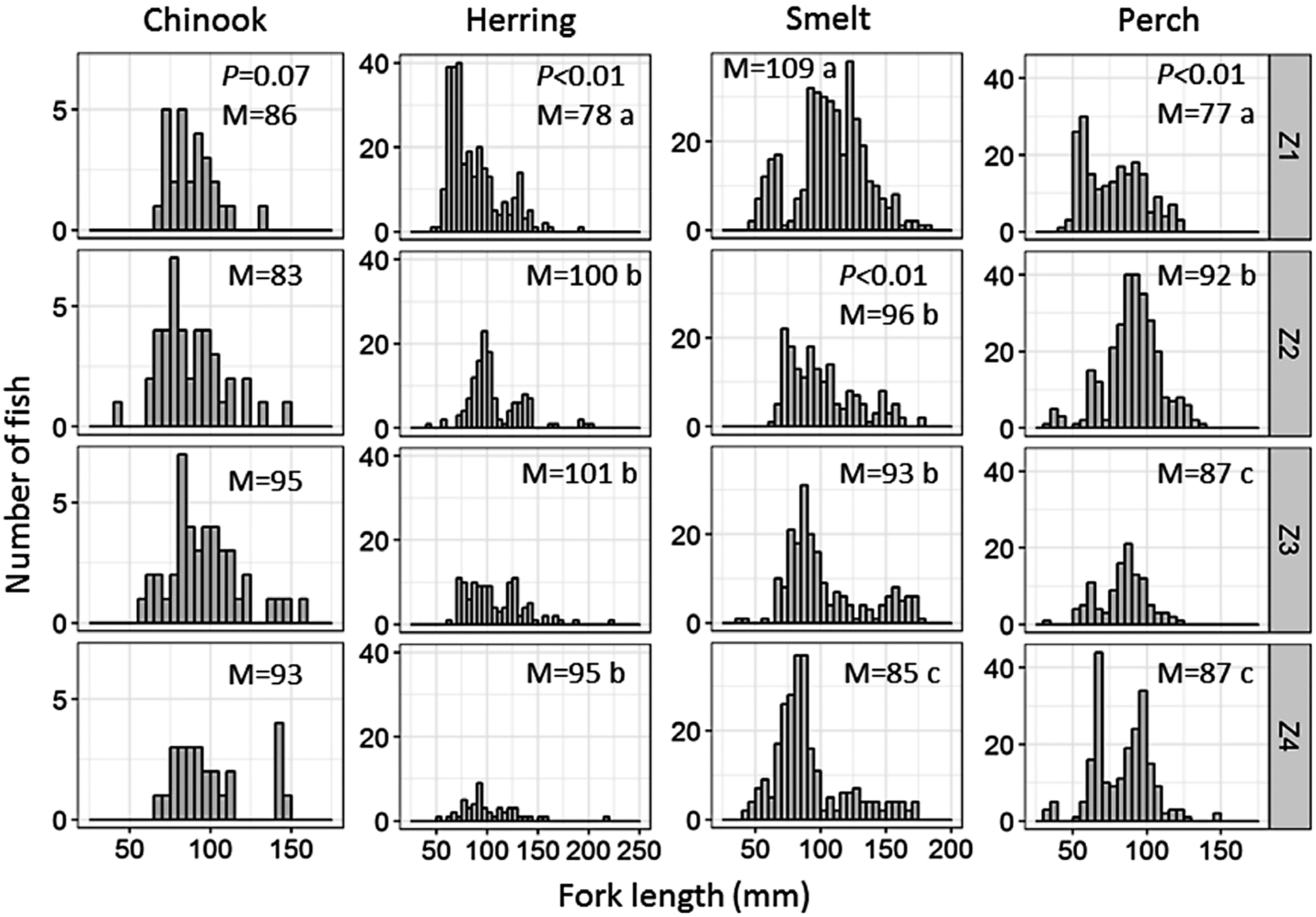

FIGURE 5. Length frequencies by species and zone for data from eelgrass habitat pooled across months and the years 2008–2010; M = median length. Within a species, P = P-value of a test for differences in median length among zones, and letters to the right of medians indicate results of paired comparisons between zones; medians without a letter in common differ ($P < 0.05$).

Chinook Salmon

Use of eelgrass by Chinook Salmon varied with date and with location on the delta. From June on, when almost all of our catch were subyearlings, eelgrass in zones 3 and 4 stood out as important habitat. During June–July, Chinook Salmon in these zones were moderately abundant in eelgrass but absent from unvegetated habitat. From June on, body size of salmon in eelgrass tended to be greater in these zones than in zones 1 or 2. However, in May, when we caught a mix of subyearlings and yearlings, salmon were not more abundant in eelgrass than in unvegetated habitat in zone 3 or 4, and salmon were never more abundant in eelgrass than in unvegetated habitat in zone 2 (unvegetated habitat was not sampled in zone 1). We caught almost no Chinook Salmon in April.

Differences in eelgrass morphology and water column conditions may have contributed to differences in Chinook Salmon use of eelgrass between zone 2 and zones 3 or 4. Individual eelgrass meadows were smaller, and cover of eelgrass within meadows was slightly lower, in zone 2 than in zones 3 or 4. These differences likely stemmed from closer proximity of zone 2 eelgrass to a channelized major distributary outlet (the Skagit River North Fork) that focused river discharge and routed river-born sand offshore to the eelgrass meadows, increasing their fragmentation (Grossman et al. 2011; Hood et al. 2016). Note, however, that we always sampled within eelgrass meadows, not in the channels between meadows, so differences in eelgrass use were not due to sampling more channel area and less meadow area in zone 2 than in zones 3 or 4. Temperature differences may have contributed to body size differences among zones. Temperature increased from north (zone 1) to south (zone 4) and may have been more optimal for salmon growth in zones 3 and 4 than in zone 1 or 2 (Beauchamp 2009).

Migration pathways may also have contributed to differences in Chinook Salmon use of eelgrass among zones. Because the North Fork carries more flow than the South

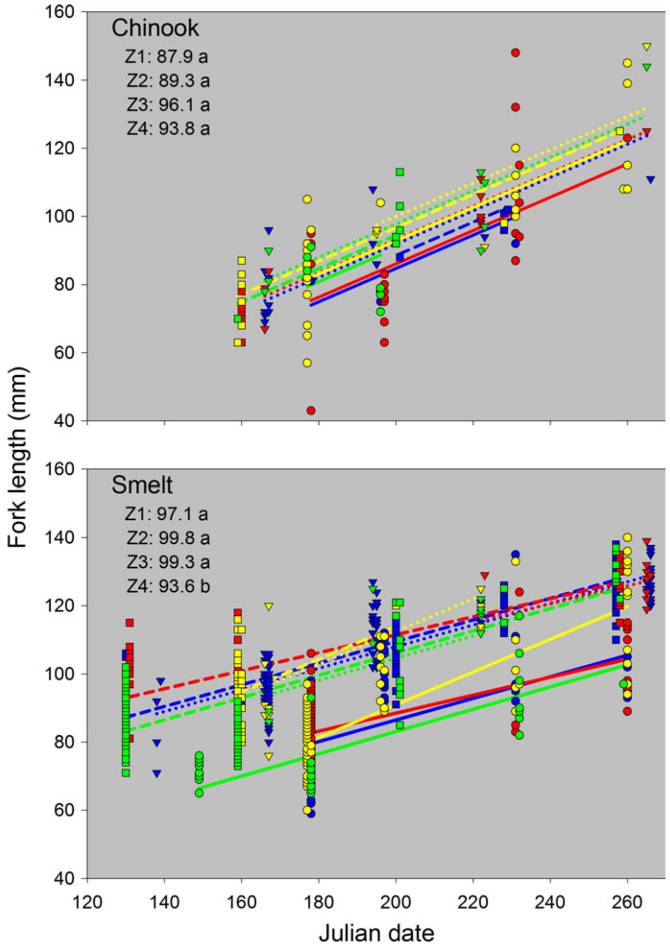

FIGURE 6. Length versus capture date by zone and year for the dominant age-group (Figure S1-2) of Chinook Salmon (subyearlings, top panel) and Surf Smelt (early spawned subyearlings, bottom panel) caught in eelgrass. Color indicates zone: blue = 1, red = 2, yellow = 3, green = 4. Point shape and line type indicate year: circle and solid line = 2008, triangle and dotted line = 2009, square and dashed line = 2010. Lines are regression lines from final models relating length to zone, year, and capture date (Table S1-6); lines are plotted only for the range of dates when fish were caught (and there is no line for Chinook Salmon in zone 2 in 2010 because they were caught on only one date). Text under "Chinook" and "Smelt" indicates for each zone, mean length (mm) adjusted to mean capture date and pairwise comparison results; means without a letter in common differ significantly ($P < 0.05$). Day of the year: 120 = April 30, 140 = May 20, 160 = June 9, 180 = June 29, 200 = July 19, 220 = August 8, 240 = August 28, 260 = September 17.

Fork except at particularly high flows (Curran et al. 2016), more salmon may have exited the river via the North Fork than the South Fork, and therefore new arrivals may have been more abundant off the North Fork (in zone 2) than farther south (in zones 3 and 4). We would expect new arrivals through most of our sampling period because out-migration of Skagit River Chinook Salmon extends at least through August (Zimmerman et al. 2015). As hypotheses for future testing we propose that (1) Chinook Salmon were large in zones 3 and 4 because they had been residing and growing there for an extended time, whereas salmon were smaller in zone 2 because they were new arrivals, and (2) Chinook Salmon were more abundant in eelgrass than in unvegetated habitat in zones 3 and 4 because eelgrass provided suitable rearing habitat, whereas salmon were equally abundant in eelgrass and unvegetated habitat in zone 2 because they were passing through rather than rearing. Residence time of naturally produced subyearling Chinook Salmon in natal tidal delta and estuarine habitats can range from 1 to 12 weeks (Bottom et al. 2005; Lind-Null and Larsen 2010). Further, most tagged hatchery subyearlings recaptured in northern Puget Sound (Whidbey Basin including Skagit Bay) originated from local hatcheries, and mean time from hatchery release to recapture was 3 weeks by nearshore beach seining (Duffy et al. 2005) and 8 weeks by offshore townetting (Rice et al. 2011). Thus, extended residence and growth of Skagit River Chinook Salmon subyearlings in eelgrass in zones 3 and 4 is plausible. High habitat suitability for subyearling Chinook Salmon from June on agrees with a study by Hodgson et al. (2016) showing that subyearling abundance during July–August was higher in delta eelgrass than in other delta and nearshore habitats in southern Puget Sound (the Nisqually Reach). Diets of Chinook Salmon caught in the near shore during June–September at body sizes similar to the salmon we caught included relatively large proportions of potentially eelgrass-associated invertebrates (e.g., gammarid amphipods, polychaetes), suggesting the possibility of foraging opportunities for Chinook Salmon in eelgrass (Brennan et al. 2004; Duffy et al. 2010). Kennedy et al. (2018) found a link between diet composition of small Chinook Salmon and abundance of epibenthic invertebrate prey in eelgrass in May.

Forage Fishes

Abundances of Pacific Herring and Shiner Perch were consistently and substantially higher in eelgrass than in unvegetated habitat (≥3 times higher for herring and ≥10 times higher for perch; Figure 2; Table S1-4). This is not surprising for Shiner Perch (see Introduction), but it is more so for Pacific Herring, which typically feed on pelagic zooplankton (Miller et al. 1980) and do not generally associate with eelgrass. Both Pacific Herring and Atlantic Herring *Clupea harengus* are pelagic fishes that rely on schooling for predator avoidance (Nøttestad and Axelsen 1999; Axelsen et al. 2001; Beauchamp and Duffy 2011), making it seem unlikely that herring in this study were seeking cover in eelgrass, and perhaps more likely that they were foraging. We examined one individual caught in eelgrass (May 10, 2010; 186 mm long) and found its stomach to be full of amphipods of the genus *Eogammarus*, which can be associated with eelgrass or other submerged vegetation (Pomeroy and Levings 1980). Surf Smelt were considerably more abundant in eelgrass than in unvegetated habitat in zone 3 but not in zone 2 or 4 (Figure 2).

Abundance and/or size of all three forage fish species in eelgrass differed between zone 1, north of the jetty, and zones 2–4 south of the jetty. Pacific Herring were ≥3 times more abundant in zone 1 than in zone 2, 3, or 4 and were also smaller in zone 1 than in the other zones. Recently settled subyearlings (<75 mm long) were mostly restricted to zone 1, accounting for the smaller size and contributing to the higher abundance of herring in eelgrass in that area. Surf Smelt were larger in zone 1 than in the other zones, but the zone 1 population included small subyearlings. Shiner Perch were smaller in zone 1 than in the other zones because of a higher percentage of subyearlings.

Several physical characteristics differed between the area north of the jetty (zone 1) and areas to the south (zones 2–4) including salinity (higher to the north), temperature and water clarity (lower to the north), and sediment grain size (mud to the north, sand farther south). The jetty was at least partly responsible because it forced North Fork river discharge to the west and blocked it from going north, making water north of the jetty more saline and cooler (i.e., more marine) than in the south, and the jetty also disrupted tidal currents, creating an eddy and fine sediment deposition zone north of it (Grossman et al. 2011). These physical differences may have contributed to the differences in forage fish abundance and size, although the mechanism is not clear. Perhaps salinity and temperature preferences played a role. Or perhaps settlement of subyearlings or concentration of zooplankton prey was greater north of the jetty than south of it due to entrainment.

Size of Surf Smelt in zone 4 was distinct in some respects. Large catches of subyearlings in eelgrass in 2010 in zone 4 resulted in shorter median length of smelt in eelgrass than in unvegetated habitat (Figure 4). Plots of length versus capture date suggested that subyearling smelt comprised an early spawned and a late-spawned component (Figure S1-2), and the length of the early spawned component was consistently shorter in zone 4 than in the other zones (Figure 6; Table S1-6) for unknown reasons.

Response to River Channelization, Diking, and the Jetty

As discussed previously, the jetty caused conditions to differ on either side of it, thereby potentially influencing the abundance and size of forage fishes in eelgrass. Chinook Salmon abundance in eelgrass did not differ between zone 1 and the other zones. Size of subyearling Chinook Salmon in eelgrass from June on tended to be smaller in zone 1 than in the other zones, particularly in zones 3 and 4.

Eelgrass in zone 2, offshore from the outlet of the channelized North Fork, was likely more fragmented than in the past due to burial and abrasion from focused discharge velocities and increased delivery of sand. In contrast, eelgrass in zones 3 and 4 to the south comprised larger meadows that were likely less impacted by sediment disturbance. We found some evidence of differential fish response between eelgrass off the North Fork and eelgrass farther south, but it was relatively subtle. Mainly, Chinook Salmon were more abundant in eelgrass than in unvegetated habitat in zones 3 and 4 but were equally abundant in the two habitat types in zone 2, and in eelgrass they tended to be larger in zones 3 and 4 than in zone 2. Surf Smelt did not show a consistently different response between zone 2 and the zones to the south, and Pacific Herring and Shiner Perch showed no response difference. A possible reason for the lack of stronger fish responses may be that cover of eelgrass within eelgrass meadows was relatively similar between the North Fork (89%) and zones to the south (94–95%). Perhaps the main effect of sediment disturbance following diking and river channelization was to reduce eelgrass extent (i.e., more meadow fragmentation, less total meadow area) rather than to degrade the eelgrass that remained.

Sampling Gear Pros and Cons

An advantage of the lampara net was that it did little harm to eelgrass. When the depth was shallow enough for the lead line to contact the bottom, it slid over eelgrass rather than uprooting it. Other types of gear have also been used to sample fish in eelgrass and other nearshore habitats of similar depth. Modified tow nets (Dumbauld et al. 2015) and fyke nets (Hosack et al. 2006) have been used with success. Beach seines are often used (Murphy et al. 2000; Johnson et al. 2010), but they require sampling at low tide when pelagic species may have moved offshore and are difficult to use in low-gradient habitats like delta tidal flats.

Lampara nets were originally designed for use in open water to catch forage fish near the surface (Hayes et al. 1996); however, we found that catch was inversely related to depth. The inverse relation likely owed partly to fishing a smaller fraction of the total water column as depth increased. The relation was steeper for Shiner Perch than for the other species, probably because Shiner Perch maintained positions closer to the bottom. But the inverse relationship may also indicate that fish were more able to avoid or escape from the net as depth increased. Nevertheless, our assessment of eelgrass use was not confounded because we were able to account for the effect of depth on fish abundance in our analyses.

Management Implications

Key management questions are whether conservation and restoration of eelgrass on river deltas would benefit the target species, and if so under what conditions and in what settings would these actions be of most benefit. To demonstrate benefit with certainty it would be necessary to show that eelgrass habitat was a bottleneck that limited population productivity, or in other words, that carrying capacity of eelgrass was limiting populations such that conservation would prevent further declines and restoration would result in increases. This is a difficult task beyond the scope of our study; however, we did demonstrate greater use of eelgrass compared with unvegetated habitat, which implies habitat preference and a benefit to occupying that habitat (Fretwell and Lucas 1970). If populations are currently below carrying capacity, maintaining that habitat at current levels or increasing it via restoration would accommodate any future population increases. It should be noted that eelgrass is by far the most abundant structured habitat on the outer Skagit Delta. The alternative to eelgrass is unvegetated tidal flats.

Our results for Chinook Salmon suggest there is value in conserving intact eelgrass habitats like those on the Skagit Delta in zones 3 and 4. They also support the contention that reducing river channelization and diking could benefit eelgrass and Chinook Salmon. Such actions may increase eelgrass extent by reducing discharge velocities and dispersing flow and sediments more widely (Goehring et al. 2015; Christiaen et al. 2016), which could also enhance salmon rearing habitat. A final point concerns the value of eelgrass on river deltas compared with other settings. Our study did not address this, but Hodgson et al. (2016) found that eelgrass fringing a nearshore beach did not retain high abundances of Chinook Salmon in July and August whereas delta eelgrass did, suggesting particular value to delta eelgrass.

Pacific Herring and Shiner Perch were consistently and strongly associated with eelgrass suggesting they would benefit from any conservation or restoration of eelgrass on river deltas. Still, high abundance and broad body size distributions for forage fishes in zone 1 eelgrass, especially Pacific Herring, suggest that restoring similar eelgrass habitat would be particularly beneficial. Surf Smelt were less consistently associated with eelgrass than the herring or perch, but smelt were never less abundant in eelgrass than in unvegetated habitat suggesting a potential benefit to Surf Smelt from eelgrass restoration as well.

ACKNOWLEDGMENTS

We thank two anonymous reviewers for excellent comments that greatly improved this manuscript. We thank Bart Christiaen for help with obtaining and understanding eelgrass survey data. We thank Karl Stenberg and Lisa Wetzel for field assistance. We thank Reginald Reisenbichler, Theresa Liedtke, and Collin Smith for help developing fish sampling methods suitable for eelgrass and tidal flats. We thank Eric Beamer and Rich Henderson for guidance, discussion, and orientation to the study area at study initiation. This work was funded by the U.S. Geological Survey Coastal Habitats in Puget Sound program. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. All data files are publicly available from the USGS ScienceBase database (https://doi.org/10.5066/P9YMXJAF). There is no conflict of interest declared in this article.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.

Appendix: Catch of All Species in Eelgrass and Unvegetated Habitat

TABLE A.1. Percent of net sets each species occurred in, and number of individuals of each species captured for all sampling events combined (n = 560 sets; 411 in eelgrass and 149 in unvegetated habitat).

		Number of fish		
Common name	Occurrence (%)	Total	Eelgrass	Unvegetated
Surf Smelt *Hypomesus pretiosus*	26.1	1,573	1,490	83
Pacific Herring *Clupea pallasii*	20.2	923	8,96	27
Shiner Perch *Cymatogaster aggregata*	17.5	1,166	1,100	66
Chinook Salmon *Oncorhynchus tshawytscha*	14.6	159	134	25
Threespine Stickleback *Gasterosteus aculeatus*	10.9	434	299	135
Snake Prickleback *Lumpenus sagitta*	7.0	378	358	20
Saddleback Gunnel *Pholis ornata*	5.5	65	65	0
Bay Pipefish *Syngnathus leptorhynchus*	5.0	51	51	0
Pacific Sand Lance *Ammodytes hexapterus*	3.6	3,148	2,731	417
Tubesnout *Aulorhynchus flavidus*	3.6	65	65	0
Starry Flounder *Platichthys stellatus*	2.5	23	9	14
Coho Salmon *Oncorhynchus kisutch*	2.3	22	20	2
Chum Salmon *Oncorhynchus keta*	2.1	21	12	9
Pile Perch *Rhacochilus vacca*	2.1	21	21	0
Pink Salmon *Oncorhynchus gorbuscha*	1.8	619	56	563
Unknown gunnel	1.8	29	28	1
Pacific Cod *Gadus macrocephalus*	1.6	12	12	0
Crescent Gunnel *Pholis laeta*	1.4	19	8	11
River Lamprey *Lampetra ayresii*	1.3	8	8	0
American Shad *Alosa sapidissima*	1.1	7	5	2
English Sole *Parophrys vetulus*	0.9	5	5	0
Unknown sculpin	0.5	6	6	0
Unknown flatfish	0.4	2	2	0
Northern Anchovy *Engraulis mordax*	0.2	2	2	0
Cutthroat Trout *Oncorhynchus clarkii*	0.2	1	1	0
Unknown perch	0.2	1	1	0
Penpoint Gunnel *Apodichthys flavidus*	0.2	1	1	0
Snailfish, family Liparidae	0.2	1	1	0
Pacific Sandfish *Trichodon trichodon*	0.2	1	1	0
Staghorn Sculpin *Leptocottus armatus*	0.2	1	1	0
Unknown	0.2	1	1	0