

Juvenile Salmon Density on Marsh Surfaces versus within Tidal Channels

W. Gregory Hood¹, Eric Beamer, Rich Henderson

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

¹Corresponding author: ghood@skagitcoop.org

Abstract

The potential use of tidal marsh surfaces by juvenile salmon migrating through Pacific Northwest estuaries has generally been ignored by research ecologists and by biologists, engineers, and planners involved in habitat restoration to support recovery of threatened and endangered salmon populations. In contrast, fish use of marsh plains has been documented for tidal marshes in many other parts of the world. Are the sedge-dominated marshes of the Pacific Northwest an exception to the pattern of fish use that is so common elsewhere? For three consecutive years, fish were sampled bi-monthly in tidal marsh channels and on tidal marsh plains in the meso-tidal marshes of the Skagit Delta to answer this question. Juvenile Chinook and chum salmon, as well as sticklebacks were the most consistently caught and abundant fish in the tidal channels and on the marsh surface, but eight other fish species were also found on the marsh surface. While fish densities were much higher in tidal channels than on marsh surfaces, marsh surface area was much greater than tidal channel area, so sticklebacks and juvenile chum were potentially 50% more numerous on the marsh surface than in tidal channels. However, due to their high channel densities, juvenile Chinook were

nevertheless more abundant in tidal channels than on the marsh surface; those on the marsh surface amounted to 40% of the numbers in tidal channels. The ratio of marsh surface fish density to channel fish density peaks late in the season for all three species of fish, which may be a response to increased prey production and availability over the marsh plain. The substantial use of the marsh surface by juvenile salmon that we observed suggests estuarine habitat restoration for salmon recovery should not neglect the direct value of vegetated marsh plains to juvenile salmon. Tidal marsh habitat for juvenile salmon and other small fish is more than just the tidal channels. Partial habitat restoration that only restores tidal flow to channels and not to adjacent marshes, e.g., using self-regulating tide gates (SRTs), has a direct impact on juvenile salmon habitat use.

Introduction

Many salmon populations in the North Pacific are threatened or endangered, in part because of habitat loss (Ruckelshaus et al. 2002). Juvenile Chinook salmon (*Oncorhynchus tshawytscha*) and, to a lesser degree, chum (*O. keta*) and coho (*O. kisutch*) salmon are dependent on tidal marsh habitat for critical rearing during migration from natal streams to the ocean (Levy and Northcote 1982; MacDonald et al. 1988; Magnusson and Hilborn 2003). Rapid growth in tidal marshes allows juvenile salmon to swim fast enough to escape, as well as outgrow the gape of, many potential predators during early marine residency, thereby improving marine survival (reviewed in Duffy and Beauchamp 2011; Parker 2011). Because these important rearing habitats have been destroyed by agricultural and urban development over the past 150 years (Bortleson et al. 1980; Bottom et al. 2005), there are many efforts

underway to restore estuarine marshes to recover threatened salmon stocks (*cf.* Cereghino et al. 2012; Krueger et al. 2017).

Most ecological research on juvenile Pacific salmon use of estuarine habitats has focused on pelagic habitat or tidal channels, while the possible use of marsh surfaces by juvenile salmon has been generally neglected. Consequently, tidal marsh restoration planning on the Pacific coast of North America implicitly assumes juvenile salmon directly occupy tidal channels, but not the vegetated marsh surface adjacent to the channels, even though the marsh surface may flood by a meter or more during high tides. Juvenile salmon are assumed to only indirectly benefit from vegetated tidal marshes through the production and tidal export of primary and secondary production. This assumption has rarely been tested in the Pacific Northwest. In a study of juvenile chum diel feeding patterns in sedge-dominated tidal marsh (Congleton 1978), feeding was found to be most intense during marsh submergence, when juvenile chum could be captured on the marsh surface by seining in water 0.3 to 1 m deep. The principal prey were Chironomid (Diptera) pupae and adults associated with the vegetation. In another instance, seining compared a marsh channel with its adjacent marsh plain and found chum and Chinook fry on the flooded marsh surface at high tide, but chum and Chinook, respectively, were twice and ten times as abundant in the channel (Beamer and LaRock 1998). In another instance (Simenstad et al. 2002), fish use of vegetated marsh surfaces was assessed through the placement of small-mesh gill nets in transects extending from tidal channel centerlines into the adjacent sedge-dominated (*Carex lyngbyei*) tidal marsh. Juvenile salmon were shown to be common within the channels, as expected, but excluded from the portion of the tidal frame occupied by the sedge canopy, though fish were found swimming above the

~1m-high canopy when it was covered by higher high spring tides. The vegetation was evidently too dense to allow the fish easy access to the marsh surface.

In contrast to sedge-dominated tidal marshes of the northern Pacific coast of North America, there have been many studies in *Spartina*-dominated marshes of the Atlantic and Gulf Coasts of North America that have demonstrated extensive use of vegetated marsh surfaces by small estuarine fish such as mummichog (*Fundulus heteroclitus*), spotfin killifish (*F. luciae*), Gulf killifish (*F. grandis*), striped mullet (*Mugil cephalus*), and at least 16 other less common fish species (e.g., Rozas and Reed 1993; Kneib and Wagner 1994; McIvor and Rozas 1996; Able et al. 2012). Gulf killifish have been shown to benefit directly from marsh surface access; they consumed a greater volume of food when they had access to the marsh surface than when confined to subtidal areas (Rozas and LaSalle 1990). Similarly, mummichogs have been shown to not only feed better on the marsh surface than in tidal channels, but also to grow faster (Weisberg and Lotrich 1982). In a southern California tidal marsh, five fish species (four natives, one exotic) were collected on the marsh surface during year-long sampling (West and Zedler 2000). Gut analysis showed that the marsh surface provided rich foraging during high tides; fish on the marsh surface consumed six times as much food as those in tidal channels and also fed on additional prey types. In Australian salt marshes, up to 21 species of fish were trapped on the marsh surface, though only one to three species were numerically dominant, depending on season and geographic location (Thomas and Connolly 2001). In Chinese marshes eight species of fish, two species of shrimp, and three species of crab were collected at high tide over marshes dominated by either non-native cordgrass (*Spartina alterniflora*) or by native bulrush

(*Scirpus mariqueter*) with no differences in fish usage between areas with native or non-native vegetation (Quan et al. 2011).

In the current study, we tested the hypothesis that juvenile salmon and other common estuarine fish in the Pacific Northwest might occupy the marsh surface when vegetation was absent or very short. Along the North American Pacific Coast, from northern California to Alaska, low-salinity tidal marshes are dominated by tall (up to 1.2 m) and often dense sedges, particularly *Carex lyngbyei*, *Schoenoplectus pungens* (syn. = *Scirpus americanus*), and *Schoenoplectus maritimus* (syn. = *Scirpus maritimus*). Although they are perennial, these species senesce during the winter so that little above-ground vegetation is present from September to April or early May. In more saline tidal marshes, the dominant species are typically very short (0.2 m), such as *Sarcocornia pacifica* and *Distichlis spicata*. Juvenile salmon typically migrate from their natal streams to tidal marshes, from February to June, though this can vary with winter river spates and latitude. Thus, the salmon migratory season overlaps extensively with the period of vegetation senescence in northern Pacific tidal marshes. This suggests juvenile salmon, and other small estuarine fish, could have unobstructed access to tidal marsh surfaces during vegetation senescence. Do fish access northern Pacific marsh surfaces during this time, and if so, to what extent?

Methods

Fish sampling

Fish sampling occurred bimonthly in the North Fork Skagit Delta (Puget Sound, Washington, USA) on spring high tides during the juvenile salmon outmigration season in 2014

(April-July), 2015 (Feb-June), and 2016 (Feb-July). The Skagit River and its delta are the largest in Puget Sound (Washington, USA), and the river contributes about 35% of Puget Sound's freshwater inflow. The delta's tidal marshes are oligohaline, and experience semidiurnal tides with a range of about 4 m. The Skagit basin hosts five Pacific salmon species, as well as related anadromous salmonids such as steelhead (*O. mykiss*) and bull trout (*Salvelinus confluentus*). Given the basin's size (8544 km²), these are among the largest and healthiest salmonid populations in Puget Sound. More details on the natural history of the Skagit tidal marshes can be found elsewhere (Hood 2007, 2012, 2013).

In blind tidal channels, fish were trapped with fyke nets set at the mouths of the channels. Fyke nets consisted of 0.3-cm mesh knotless nylon with a 0.6 m by 2.7 m diameter cone sewn into the net to collect fish draining out of the channel. All nets were sized to completely span channel cross-sections at high tide. At high tide, the nets were set across the blind channel outlets and fished through the ebb tide (Levy and Northcote 1982). The juvenile Chinook catch was adjusted by a trap recovery efficiency (RE) estimate derived from mark-recapture sampling, i.e., by releasing a known number of marked age 0+ Chinook fry upstream of the trap at high tide. RE is usually related to hydraulic characteristics unique to the site (e.g., change in water surface elevation during trapping, or water surface elevation at the end of trapping). Multiple RE tests (several times per season) at each site were used to develop a regression model to convert the juvenile Chinook catch to a population estimate within the channel upstream of the fyke trap on any sampling day (Rice et al. 2005). While RE estimates were based almost exclusively on juvenile Chinook, we occasionally substituted juvenile chum or even smelt when Chinook were few. To apply RE estimates to the catch of other fish species

requires assuming other fish behave similarly to juvenile Chinook. We believe this is a reasonable approximation for other salmon, sticklebacks, and fish with similar body shapes and behavior, but not for demersal fish such as sculpins and flatfish, or larger pelagic fish. Larger pelagic fish are more likely to emigrate from channels on ebb tides than salmon fry, while demersal fish are more likely to remain in low-tide pools within the channels. Even so, there are documented behavioral differences amongst salmonid species which may challenge this assumption. For example, Chinook and chum fry tend to leave tidal channels late on an ebb tide, while pink leave early (Levy and Northcote 1982). Furthermore, Levy and Northcote (1982) found consistent differences in RE between Chinook fry (average RE of 62%) versus chum and pink fry (average RE of 45% and 49%). Consequently, we compared raw catches as well as RE-adjusted catches to evaluate the influence of RE estimates on the results. In general, differences in fish community composition using adjusted and unadjusted catches were modest, but we feel RE adjustments provide a closer approximation of the real fish population size than unadjusted catches, despite the imperfections of the method.

Marsh surfaces were sampled for fish using a 24.4 m by 1.8 m beach seine with 0.3-cm knotless nylon mesh. The net was set in a round haul fashion, fixing one end of the net on the marsh surface while the other end was deployed by wading, hauling the net in a floating tote, and returning to the other end of the net in a full circle. Average beach seine area was 96 m². Experience in 2014 with round-haul seining on the marsh surface suggested seining efficiency might be affected by vegetation height. Early in the salmon outmigration season, before late April, the vegetation was uniformly absent or only ankle-high. As the season progressed the sedges grew taller, reaching heights of 0.5 m by early June and 1.1 m by July. The taller the

vegetation the more the seine lead-line tended to ride up the vegetation, lifting off the marsh surface and reducing the net's trapping efficiency, particularly low in the canopy. To confirm this impression, notes were made on vegetation height during seining in 2014 and 2015, and its relationship to the catch of the three most abundant fish species was explored using regression analysis. There was no consistent effect of vegetation height on the catch of juvenile Chinook, coho, and sticklebacks (Fig. 1). This negative result may have been due to fish not being abundant low in the canopy, where the seine would be least effective late in the season. Instead, fish may have been concentrated above the canopy or in the upper-most portion of the canopy as previously observed (Simenstad et al. 2000), where the seine would still be effective. Nevertheless, the tendency of the seine to ride up dense, tall vegetation was disconcerting, so when possible, sampling tended to be directed toward areas of less dense vegetation in June and July when vegetation was approaching seasonal maturity.

Tidal channel surface area was measured using GIS analysis of high-resolution, modern, aerial photographs of the tidal marsh. Channel drainage divides on the marsh surface were calculated in GIS as the points equidistant from each tidal channel boundary. Details on this GIS analysis have been previously described (Hood 2007, 2014).

Water temperature and level

Water temperatures were measured with a thermometer to the nearest 0.1C at the beginning and end of each sampling event, whether on the marsh surface or in tidal channels. Water level was measured with a Solinst level-logger from 25 Feb to 16 July 2016 at 15-minute intervals. Levels were corrected for atmospheric pressure by reference to a barologger. The

level-logger's elevation was surveyed with a Leica RTK-GPS with 3 cm vertical resolution. A nearby USGS tidal bench mark was also surveyed for GPS quality control.

Statistical analysis

Replicate fish samples on each date were averaged to produce a mean catch for each date-habitat combination. Statistical analysis of the three most abundant species found over the marsh surface and in tidal channels (juvenile Chinook and chum salmon, as well as sticklebacks) was done using standard parametric methods such as paired sample t-tests (channel vs. marsh surface, paired by sampling date) and ordinary least-squares linear regression (Zar 1984).

All hatchery salmon in the Skagit watershed are marked by clipping their adipose fins, so wild fish can be easily distinguished by their intact fins. Because hatchery fish were so uncommon in our catches, species-scale data analysis for salmonids focused on wild salmon, which were common and abundant. However, analysis at the fish community scale included hatchery salmon as a distinct group from wild salmon. Analysis of fish communities was done using non-parametric multivariate routines in PRIMER (Clarke 1993, Clarke and Warwick 2001; Clarke and Gorley 2006). Fish densities (catches divided by the area sampled) were 4th-root transformed for community analysis to down-weight the influence of the most abundant fish species and thereby allow consideration of less common community members. Such a transformation is nearly routine in multivariate analysis of communities (Clarke 1993, Clarke and Warwick 2001; Clarke and Gorley 2006); it reduced a two-order of magnitude difference between the most and least abundant species to a 3- to 4-fold difference. Bray-Curtis similarity

coefficients for each possible sample pairs were developed from the transformed data and used as inputs for further analysis. Bray-Curtis similarity coefficients reflect differences in relative abundances and composition between sample pairs. The coefficient can be intuitively interpreted as an indication of the percentage difference between two samples (Clarke and Gorely 2006). Non-metric multidimensional scaling (nMDS) was used to visualize differences in overall species composition between channel and marsh surface samples, between years, and between sampling dates. A hierarchical cluster analysis was overlain on the nMDS graphs to facilitate their interpretation. Differences between habitat type (channel vs. marsh surface), year of sampling, and sampling date were tested in a three-way factorial PERMANOVA, a non-parametric analog to multivariate analysis of variance, that relies on permutation tests for statistical significance testing (Anderson et al. 2008). Sampling dates were not identical between years, so they were grouped according to their occurrence in the first or second half of a month, e.g., early April and late April. PERMANOVA was followed with a SIMPER analysis which decomposes average Bray-Curtis similarities into percentage contributions from each species to dissimilarities among factor levels (e.g., channel vs. marsh surface). Finally, PERMDISP analysis was performed to confirm an apparent greater dispersion of similarity values for marsh surface samples compared to channel samples.

For all statistical tests, significance was set at a threshold of $\alpha = 0.05$. Statistical significance for the non-parametric multivariate analyses was determined by reference to 9999 random permutations of the raw data.

Results

In 2014, 2015, and 2016, respectively, 19, 13, and 16 species of fish were caught in blind tidal channels, while 8, 7, and 11 species were caught on the flooded marsh surface. All fish caught on the marsh surface were also caught in the tidal channels. Juvenile Chinook and chum salmon (both age 0) were caught on the marsh surface during all three years of sampling. Other fish found on the marsh surface in all three years of sampling included three-spine stickleback (*Gasterosteus aculeatus*), peamouth (*Mylocheilus caurinus*), and prickly sculpin (*Cottus asper*). Fish found on the marsh surface during only one or two years of sampling included Juvenile pink salmon (*O. gorbuscha* -- only expected in even years, because of their 2-year life history cycle), age 0 and age 1 coho (each in different pairs of years), bull trout/Dolly Varden (*Salvelinus* spp.), cutthroat trout (*O. clarkii*), large scale sucker (*Catostomus macrocheilus*), staghorn sculpin (*Leptocottus armatus*), juvenile starry flounder (*Platichthys stellatus*), and the non-native yellow perch (*Perca flavescens*). Fish caught in tidal channels, but not on the marsh surface, included: shiner perch (*Cymatogaster aggregata*), juvenile lamprey (*Lampetra* spp.), longfin smelt (*Spirinchus thaleichthys*), English sole (*Parophrys vetulus*), and the following introduced species: bluegill (*Lepomis macrochirus*), pumpkinseed (*L. gibbosus*), yellow perch (*Perca flavescens*), and American shad (*Alosa sapidissima*).

From mid-April to mid-July 2014, 65 fish were caught on the marsh surface and 4,029 fish were caught in three tidal channels. From late February to early June 2015, 161 fish were caught on the marsh surface, while 4,954 were caught in ten tidal channels. From late February to early July 2016, 130 fish were caught on the marsh surface, while 2,020 fish were caught in ten tidal channels. In all three years, juvenile Chinook salmon were the most abundant fish in the channel catches, in two years amounting to more than half of the catch. Juvenile chum

salmon were generally the second most abundant fish, followed closely by sticklebacks. Shiner perch were abundant in 2015 and less so in 2016. Peamouth were notable in 2014 and 2015, at about 12% of the catch. Adjustments for recovery efficiency had only modest effect on catch estimates (Fig. 2). Marsh surface catches were dominated by juvenile Chinook in 2014, when they were more than a third of the catch. Chinook were only one-fifth to one-sixth of the catch in 2015 and 2016, when they were surpassed by juvenile chum and yearling coho salmon in 2015, and by sticklebacks in 2016, when sticklebacks were half of the marsh surface catch. Sticklebacks were a greater proportion of the total catch over the marsh surface than in tidal channels in 2014 and 2016, and about equally or slightly less proportionally abundant over the marsh surface in 2015. Yearling coho were much more proportionally abundant over the marsh surface than in the channels in 2015, but were uncommon in both habitats in 2014 and 2016. Peamouth were a greater proportion in tidal channels than over the marsh surface in 2014 and 2015, but were equally rare in both places in 2016. Juvenile Chinook, while very abundant over the marsh surface, were proportionally more abundant in tidal channels. Juvenile chum salmon were variable, being more, less, and equally proportionally abundant over the marsh versus in the channels, depending on the year sampled.

Species-scale patterns

Juvenile Chinook and chum salmon, as well as sticklebacks were the most consistently caught and abundant fish in the tidal channels and on the marsh surface. Thus, species-scale comparisons of fish density between these two habitats were limited to these three species. Over all years, the mean RE-adjusted density of juvenile Chinook in tidal channels was 0.32 m^{-2} ,

while on the marsh surface it was 0.0051 m^{-2} , a 63-fold difference. For juvenile chum, tidal channel and marsh surface mean RE-adjusted densities were 0.10 m^{-2} and 0.0054 m^{-2} , respectively, a difference of 19-fold. For sticklebacks, tidal channel and marsh surface mean RE-adjusted densities were 0.11 m^{-2} and 0.0052 m^{-2} , respectively, a difference of 20-fold. Paired sample t-tests of mean densities for each sampling date, with sample date as the blocking factor ($n = 23$ for all three species) to control for seasonal and interannual variation, and habitat type as the comparison factor, showed significant differences for all three species with $p < 0.0002$ for Chinook, $p < 0.01$ for chum, and $p < 0.002$ for sticklebacks.

While fish densities were much higher in tidal channels than on marsh surfaces, marsh surface area was much higher than tidal channel area. For the channels sampled by fyke nets, the mean ratio of marsh drainage basin area to channel surface area was 36, with minimum and maximum values of 14 and 54. To compare the total potential abundance of fish in the two habitats, mean channel and marsh surface fish densities were multiplied by the surface area of each of the 14 channels sampled and by the drainage basin area for each channel. Total potential juvenile Chinook abundance was on average 2.3 (range: 1.4 to 4.1) times higher in tidal channels than on the marsh surface. In contrast, total potential juvenile chum and stickleback abundances were higher on the marsh surface than in tidal channels by, on average, 1.6 (range: 0.8 to 2.4) and 1.5 (range: 0.8 to 2.2) times, respectively.

Fish densities in tidal channels are known to exhibit seasonality, because the seasonal migration of juvenile salmon through the delta typically begins in February, peaks in April or May, and tapers off through July, with variation in this pattern depending on salmon species, latitude, the size of the migrating population, river discharge, and water temperature (Healey

1991; Salo 1991). The last three factors can vary from year to year in the same location. This seasonality in channel density begs the question of whether there is a parallel seasonality of fish density over the marsh surface. A comparison of marsh surface and channel densities, with samples in bimonthly bins, indicates parallel patterns in 2014 for Chinook, but not in 2015 or 2016 (Fig. 3). The mid-season peak in channel fish density for chum in 2015, seems to be associated with a lagged peak in marsh surface fish density. Chum density peaked early for both habitats in 2014. At a coarse scale, stickleback density peaks appear to be roughly parallel for both habitats in 2014 and 2016. Surprisingly, the ratio of mean marsh surface fish density to channel fish density peaks late in the season for all three species of fish (Fig. 4).

Community-scale patterns

nMDS plots showed a clear distinction between channel and marsh surface fish communities across all samples (Fig. 5a). Additionally, there appeared to be significantly greater dispersion among marsh surface samples versus among channel samples; this was confirmed by PERMDISP analysis which found the marsh surface dispersion to be nearly 50% greater than the channel dispersion ($F_{1,44} = 23.2$; $P = 0.0001$). PERMANOVA confirmed the significance of the distinction of channel and marsh surface communities, but also found significant annual and seasonal differences amongst the samples (Table 1). While pairwise comparisons showed differences between each year, the nMDS plot with sampling year labeled showed no apparent annual trend (Fig. 5b). There was also no difference in dispersion from the sample centroids for each year group ($F_{2,43} = 3.05$; $P = 0.11$). The same plot labeled by half-months suggested a seasonal trend from the lower right of the plot (late February through

April) to the upper left (May through early July), for both marsh surface and channel habitats (Fig. 5c). Pairwise comparisons between half-months showed a general pattern of no significant differences within, but significant differences between two groups of half-months: late February through April versus May through early July.

According to SIMPER analysis, juvenile Chinook salmon and sticklebacks contributed most to similarity amongst channel samples (31% and 24%, respectively), with juvenile chum and prickly sculpin being of secondary importance (12% and 11%, respectively), for a total contribution by these four species of 78%; other species contributed less than 5%, each, to make up the remainder. Likewise, juvenile Chinook and sticklebacks contributed most to similarity amongst marsh surface samples (21% and 51%, respectively), with juvenile chum contributing an additional 13%, for a total of 85%; other species contributed less than 6%, each, to make up the remainder. Dissimilarities between both habitats were due mostly to juvenile Chinook, which contributed 21% to the total difference, followed by juvenile chum and sticklebacks, which each contributed 12%, for a total of 46%; shiner perch, prickly sculpin, staghorn sculpin, and peamouth contributed between 5% and 8%, each, while other species contributed less than 5% to make up the remainder.

The prominence of juvenile Chinook, chum, and sticklebacks in the SIMPER results likely reflects their greater abundance relative to the other species. To test this, the SIMPER analysis was repeated on presence/absence data instead of 4th-root transformed data. The results were similar for within habitat similarities, with the same few species being important. However, between habitat dissimilarities were more evenly dispersed among a larger number of species. Juvenile Chinook and chum were unexceptional in their contributions of 7%, each, to total

dissimilarity, but sticklebacks trailed most other species, contributing only 2% to total dissimilarity. These results suggest the high frequency of occurrence of juvenile Chinook, chum, and sticklebacks compared to other species accounted for their relative importance in contributing to within habitat similarities and to their diminished importance in discriminating between habitats. The SIMPER analyses based on both transformations indicate that relative abundance and frequency of occurrence were both factors in distinguishing fish communities.

Juvenile Chinook, chum, and stickleback were similarly prominent in SIMPER analyses of similarities and dissimilarities within and between years and half-months, but other fish species occasionally were also prominent during particular half-months. Pink salmon were important in interannual patterns, for example, as expected from their two-year life-cycle, but they were still less important than the much more abundant juvenile Chinook, chum, and sticklebacks. Wild yearling coho salmon were very important in late May samples, as much as or more than juvenile Chinook, chum, and sticklebacks. However, given the large number of pairwise comparisons for 10 half-month categories, further details are omitted.

Discussion

The assumption that juvenile salmon occupy only tidal channels and not marsh surfaces has affected tidal marsh habitat restoration in the Pacific Northwest. For example, in some situations self-regulating tide gates (SRTs) have been proposed in lieu of full site restoration. SRTs allow tidal inundation of remnant channels up to a pre-set elevation, so that adjacent lands, e.g., agricultural fields that historically were marsh, are not inundated. This type of limited restoration aims to allow fish access to remnant channel habitat, which is presumed to

be most important to fish, while minimally impacting property owners by restoring little if any of their property to marsh, since marsh is presumed to have little direct benefit to salmon. While there are many objections to such limited tidal restoration (Giannico and Souder 2005; Greene et al. 2012), the results of the current study suggest an additional objection by showing that fish access to naturally inundated tidal marsh surfaces is common, extensive, and likely important. Scientists, engineers, and planners involved in tidal marsh habitat restoration should no longer ignore the potential for juvenile salmon to directly access and benefit from flooded tidal marsh surfaces.

The results presented here, along with previous work, allow us to develop a conceptual model of how juvenile salmon and other small estuarine fish may be using tidal marsh surfaces. While juvenile salmon may be excluded from the dense sedge canopy, they can swim above the canopy when the tide is high enough (Simenstad et al. 2000). As vegetation grows taller, fish swim higher in the water column, remaining above the sedge canopy as long as the tide covers the canopy. Thus, while our nets rode up the dense vegetation when it was tall, the nets were still capable of catching fish swimming above the canopy. Meanwhile, they were not missing any fish within the canopy, because fish are excluded from dense vegetation. Consequently, there was no relationship between vegetation height and fish density over the marsh surface.

The difference between a marsh with tall vegetation and one with short vegetation is likely the amount of time that fish can spend on the marsh surface during high tide. Tall vegetation only allows brief use of the marsh surface, until the tide drops below the top of the vegetation canopy, and it only allows access on the higher high diurnal tides. Short vegetation allows fish more time on the marsh surface. It also allows access to the marsh surface during a

greater range of high tides, e.g., during the lower high diurnal tides. For example, data from a water level logger installed near the fish sampling sites indicates that from February to mid-April in 2015 and 2016, when sedges were only a few cm high, sedge habitat was flooded by ≥ 20 cm above the marsh surface for 36% of the time (averaged over the sedge elevation range, *cf.* Hood 2013). The 20-cm depth was assumed to be a minimum tolerable water depth for juvenile salmon movement (*cf.* Hood 2012). From mid-April to early June, when the sedge canopy was about 50 cm high, sedge habitat was flooded by ≥ 50 cm for 22% of the time, i.e., marsh surface accessibility was reduced by a third. From early June to mid-July, when the sedge canopy was 1 m high, sedge habitat was flooded by ≥ 1 m for 11% of the time, for an additional halving in marsh surface accessibility.

Sedge canopy height in the Skagit Delta can be strongly affected by grazing by migratory snow geese. Wrangel Island snow geese (*Chen caerulescens*) breed in the arctic and overwinter in the Skagit Delta, where they graze extensively on sedges. Since 1990, the overwintering Skagit population has increased from 30,000 to a current population size of 80,000-100,000 due to arctic warming creating favorable breeding conditions (Demarchi 2006). Extensive snow goose grazing on intertidal sedges stunts the height of the vegetation canopy for 2-4 weeks, thereby lengthening the period of increased marsh surface accessibility for juvenile salmon during their estuarine residency. Thus, there is an interesting interaction between migratory geese and migratory fish mediated by intertidal sedges. However, it is unclear if goose grazing is a net benefit, since the grazing may impact secondary production of invertebrate prey on which juvenile salmon feed.

While the sedges, *C. lyngbyei* and *S. pungens*, are the dominant marsh plants at lower elevations in the Skagit Delta, cattail (*Typha angustifolia*) is dominant at higher elevations, and sweetgale (*Myrica gale*), a shrub, is dominant an additional 15 cm higher than the cattail zone (Hood 2013). These higher vegetation zones are only briefly flooded by the higher high tides, typically to depths of less than 30 cm. Thus, while fish might use the marsh surface in these vegetation zones, it would be for brief moments on higher high tides, or during significant river floods. For example, the 2015 and 2016 water level data indicate that, from late February to mid-April, cattail and sweetgale habitats would be inundated by ≥ 20 cm 13% and 10% of the time, respectively, compared to 36% for sedges. This is an example of different vegetation zones in the tidal delta providing different habitat functions for juvenile salmon (*cf.* Hood 2012 for tidal shrub habitat use by juvenile salmon).

In contrast, many tidal marsh restoration projects occur on sites that have subsided as a result of historical diking, draining, and agricultural use. Monitoring of two such sites in the Skagit Delta found high abundances of juvenile salmon and other fish, not only in the restored tidal channels, as expected, but also on the low-elevation marsh surfaces (Beamer et al. 2015, 2017). The high fish abundance on the subsided marsh surface was attributed to a combination of high primary productivity, thermal heterogeneity, and prolonged flooding caused by subsidence and constrained drainage. While the hydroperiod of these two subsided restoration sites was not comparable to reference marshes, the low-elevation marsh surface nevertheless provided habitat for juvenile salmon with opportunity for prolonged occupancy.

More than any other species, sticklebacks were a greater proportion of the marsh surface catch than of the channel catch. This is perhaps because at least some sticklebacks

spend a large proportion of their life cycle on the marsh surface, regardless of tide level. Qualitative observations of marsh surface tidepools, formed by large logs with rootwads stranded on the marsh, show that sticklebacks were abundant in the tidepools from March to July during all stages of their life history: as non-breeding adults, adults with breeding colors, gravid adults, and juveniles. This extensive occupation of marsh surface tidepools suggests a portion of the Skagit population may be nearly continuously resident on marsh surfaces. One reason sticklebacks may be disproportionately found on the marsh surface compared to juvenile salmon is that they have a higher thermal tolerance. Stickleback have a lethal thermal maximum of 28.8 C (Jordan and Garside 1972), while juvenile Chinook, coho, and chum salmon have maxima of 25.1, 25.0, and 23.7 C, respectively (Brett 1952). While these temperature extremes were not encountered during our sampling period, they might be encountered later in the summer, particularly in marsh plain tide pools, and thus influence the propensity for a species to loiter on the marsh surface.

The higher proportion of fish above the marsh surface relative to the channel from late May to July may be due to greater prey production and availability in late spring and early summer. It is not due to high fish density in the channels causing some fish to be competitively displaced from the channel to the marsh, because Chinook densities were highest earlier in the season, in February and March, while chum densities were highest from late March through April. Water temperature could also not account for differences in fish distribution, because temperature differences between the two habitats were negligible during the time periods sampled (paired-sample t-test, channel vs. marsh surface, paired by sample date: $t = 0.923$, $df = 17$, $p = 0.369$).

Much of this discussion has focused on the three fish species dominant during the period that we sampled (late February to early July). A broader focus on the fish community also provides some insights into marsh surface use. For example, the greater dispersion in Bray-Curtis similarities among marsh surface samples compared to channel samples suggests that marsh surface fish composition may be a random sample of channel fish communities. If a marsh surface sample is a random sample of tidal channel community composition, then overwhelmingly abundant species in tidal channels will be frequently found in marsh surface samples, while fish that are much less common in tidal channels will be rare or absent on marsh surfaces. The marsh surface samples will consistently have representation by species common in the tidal channels, but have highly variable representation by species uncommon in channels. Sampling effect could be due to random movement of fish from channels to marsh surfaces (a natural sampling effect), or to sampling low-density populations of fish over the marsh surface with finite seining (a research sampling effect), likely both. Seasonal and annual variation in the abundances of individual species due to their natural history, e.g., migratory timing of yearling coho, peamouth, and shiner perch, can change sampling probabilities in the tidal channel and over the marsh surface. Of course, the biology of each species may play a role in habitat preferences, but that could not be ascertained with our sampling design.

Summary

A preliminary conceptual model of how juvenile salmon use seasonally vegetated marsh plains in the Pacific Northwest can now be developed from the work presented in this paper, as well as antecedent work (Congleton 1978, Simenstad et al. 2000). Marsh surfaces in the Pacific

Northwest are occupied by significant numbers of juvenile salmon and other small estuarine fish during higher high spring tides that inundate the marshes. Access to the marsh surface is likely maximal early in the juvenile salmon migratory season, when vegetation is very short. As the vegetation grows in height over the season, the dense vegetation canopy increasingly impedes fish movement and reduces their opportunity for access to the marsh plain to only the times when the highest tides overtop the canopy. In marshes where waterfowl grazing on sedges is significant, fish access to the marsh plain can be prolonged by several weeks to a month. While fish movement is impeded by a dense vegetation canopy, the attractiveness of the marsh plain to fish may be greatest during full canopy development, because fish densities over the marsh surface peak later in the season and salmonid feeding is most intense during vegetation submergence. The likely cause of greater fish density and feeding intensity is increasing invertebrate prey production (e.g., aphids and Chironomid flies) in tandem with increasing primary production as spring transitions to summer.

The direct value of marsh plain habitat to juvenile salmon and other small estuarine fish appears to have been underestimated or overlooked by many researchers and restoration planners and ecologists. The results presented here should spur reevaluation of marsh plain habitats for Pacific Northwest fish, particularly when self-regulating tide gates (SRTs) are proposed for salmon recovery in lieu of full tidal habitat restoration. SRTs may be useful when there is no better alternative, but their benefits relative to full habitat restoration should not be overestimated.

Acknowledgements

Thanks to the fish sampling crew: Bruce Brown, Jason Boome, Josh Demma, Ric Haase, and Len Rodriguez. Marsh surface sampling, data analysis, and writing was funded by the U.S. Environmental Protection Agency (grant no. PA-00J322-01). Tidal channel sampling was funded by the Washington Department of Ecology's Intensively Monitored Watersheds Program (IAA # C1700092), through funding provided by the U.S. Department of Commerce under CFDA # 11.438-Award Number NA16NMF4380329.

References

- Able, K. W., D. N. Vivian, G. Petruzzelli, and S. M. Hagan. 2012. Connectivity among salt marsh subhabitats: Residency and movements of the mummichog (*Fundulus heteroclitus*). *Estuaries and Coasts* **35**:743–753.
- Beamer, E., R. Henderson, C. Ruff, K. Wolf. 2017. Juvenile Chinook salmon utilization of habitat associated with the Fisher Slough Restoration Project, 2009-2015. Skagit River System Cooperative, La Conner, WA. Available at <http://skagitcoop.org>.
- Beamer, E., R. Henderson, and B. Brown. 2015. Juvenile Chinook salmon utilization of habitat associated with the Wiley Slough Restoration Project, 2012-2013. Skagit River System Cooperative, La Conner, WA. Available at <http://skagitcoop.org/wp-content/uploads/Wiley-Slough-2012-2013-Final.pdf>. Accessed 10 Oct 2017.
- Beamer, E.M. and R.G. LaRock. 1998. Fish Use and Water Quality Associated with a Levee Crossing the Tidally Influenced Portion of Browns Slough, Skagit River Estuary, Washington. Report to Skagit County Diking District No. 22, prepared by Skagit System Cooperative. Available at http://skagitcoop.org/wp-content/uploads/EB1476_Beamer_and_LaRock_1998.pdf. Accessed 10 Oct 2017.
- Bortleson, G. C., M. Chrzastowski, and A. K. Helgerson. 1980. Historical changes of shoreline and wetland at eleven major deltas in the Puget Sound region, Washington. U.S. Geological Survey, U. S. Dept. of Justice, U.S. Bureau of Indian Affairs, Reston, Va.
- Bottom, D.L., C.A. Simenstad, J. Burke, A.M. Baptista, D.A. Jay, K.K. Jones, E. Casillas, M.H. Schiewe. 2005. Salmon at river's end: the role of the estuary in the decline and recovery

- of Columbia River salmon. U.S. Dept. Commerce, NOAA Tech. Memo. NMFS-NWFSC-68, 246 p.
- Brett, JR. 1952. Temperature tolerance in young Pacific salmon, genus *Oncorhynchus*. J. Fish. Res. Bd. Can. 9: 265-323.
- Cereghino, P., J. Toft, C. Simenstad, E. Iverson, S. Campbell, C. Behrens, J. Burke. 2012. Strategies for Nearshore Protection and Restoration in Puget Sound. Tech. Report No. 2012-01. Prepared in Support of the Puget Sound Nearshore Ecosystem Restoration Project, for the U.S. Army Corps of Engineers, Seattle District Seattle, Washington and Washington Department of Fish and Wildlife Olympia, Washington.
- Clarke KR (1993) Non-parametric multivariate analysis of changes in community structure. *Aust J Ecol* 18: 117–143.
- Clarke KR, Gorley RN (2006) Primer v6: user manual/tutorial. PRIMER-E, Plymouth.
- Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Plymouth.
- Congleton, J. L. 1978. Feeding patterns of juvenile chum in the Skagit River salt marsh. Pages 141-150 in S.J. Lipovsky and C.A. Simenstad (eds.), Gutshop '78: Fish Food Habits Studies Proceedings of the Second Pacific Northwest Technical Workshop. Washington Sea Grant, University of Washington, Seattle.
- Demarchi, M. W. (2006). Are lesser snow geese, *Chen caerulescens caerulescens*, exceeding the carrying capacity of the Fraser River Delta's brackish marshes? Canadian Field-Naturalist **120**: 213-224.

- Duffy, E. J. and D. A. Beauchamp. 2011. Rapid growth in the early marine period improves the marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, Washington. *Canadian Journal of Fisheries and Aquatic Sciences* **68**:232-240.
- Giannico, Guillermo Roberto, and Jon A. Souder. 2005. *Tide gates in the Pacific Northwest: operation, types, and environmental effects*. Vol. 5. No. 1. Oregon Sea Grant, Oregon State University.
- Greene, C., J. Hall, E. Beamer, R. Henderson, B. Brown. 2012. Biological and physical effects of “fish-friendly” tide gates. Final Report for the Washington State Recreation and Conservation Office. http://skagitcoop.org/wp-content/uploads/EB2673_Greene-et-al_2012.pdf (accessed ****).
- Healey, M. C. 1991. Life history of Chinook salmon. Pp. 313-393 in *Pacific Salmon Life Histories*, C. Groot and L. Margolis, eds. University of British Columbia Press, Vancouver, Canada.
- Hood WG. 2014. Differences in tidal channel network geometry between reference marshes and marshes restored by historical dike breaching. *Ecological Engineering* **71**:563-573.
- Hood WG. 2013. Applying and testing a predictive vegetation model to management of the invasive cattail, *Typha angustifolia*, in an oligohaline tidal marsh reveals priority effects caused by non-stationarity. *Wetlands Ecology and Management* **21**:229-242.
- Hood WG. 2012. Beaver in tidal marshes: Dam effects on low-tide channel pools and fish use of estuarine habitat. *Wetlands* **32**:401–410.
- Hood WG. 2007. Scaling tidal channel geometry with marsh island area: a tool for habitat restoration, linked to channel formation process. *Water Resources Research*. **43**, W03409, doi:10.1029/2006WR005083.

- Jordan, C. M. and E. T. Garside (1972). "Upper lethal temperatures of threespine stickleback, *Gasterosteus aculeatus* (L.), in relation to thermal and osmotic acclimation, ambient salinity, and size." *Canadian Journal of Zoology* 50(11): 1405-1411.
- Kneib, R. T. and S. L. Wagner. 1994. Nekton use of vegetated marsh habitats at different stages of tidal inundation. *Marine Ecology Progress Series* **106**:227-238.
- Krueger, KL, DL Bottom, WG Hood, GE Johnson, KK Jones, RM Thom. 2017. An expert panel process to evaluate habitat restoration actions in the Columbia River estuary. *Journal of Environmental Management* 188:337-350.
- Levy, D., and T. Northcote. 1982. Juvenile salmon residency in a marsh area of the Fraser River Estuary. *Can. J. Fish. Aquat. Sci.* 39:270-276.
- MacDonald, J. S., C. D. Levings, C. D. McAllister, U. H. M. Fagerlund, J. R. McBride. 1988. A field experiment to test the importance of estuaries for chinook salmon (*Oncorhynchus tshawytscha*) survival: Short-term results. *Canadian Journal of Fisheries and Aquatic Sciences* 45:1366–1377.
- Magnusson, A., Hilborn, R., 2003. Estuarine influence on survival rates of Coho (*Oncorhynchus kisutch*) and Chinook salmon (*Oncorhynchus tshawytscha*) released from hatcheries on the U.S. Pacific Coast. *Estuaries* 26, 1094–1103.
- McIvor, C.C. and L.P. Rozas. 1996. Direct nekton use of intertidal saltmarsh habitat and linkage with adjacent habitats: a review from the southeastern United States. Pages 311-334 *in* *Estuarine Shores: Evolution, Environments, and Human Alterations*. Edited by K.F. Nordstrom and C.T. Roman. John Wiley & Sons, Ltd., Chichester, England.

- Parker, R.R. 2011. Size Selective Predation Among Juvenile Salmonid Fishes in a British Columbia Inlet. *J. Fisheries Research Board Canada* 28: 1503-1510.
- Quan, W., L. Shi, Y. Chen. 2011. Comparison of Nekton Use for Cordgrass *Spartina alterniflora* and Bulrush *Scirpus mariqueter* Marshes in the Yangtze River Estuary, China. *Estuaries and Coasts* 34: 405-416.
- Rice, CA, WG Hood, LM Tear, CA Simenstad, LL Johnson, GD Williams, P Roni, BE Feist. 2005. Monitoring rehabilitation in temperate North American estuaries. Pp. 165-204 IN: P. Roni (ed), *Monitoring River Restoration*. American Fisheries Society, Bethesda, Maryland.
- Rozas, L. P., D. J. Reed. 1993. Nekton use of marsh-surface habitats in Louisiana (USA) deltaic salt marshes undergoing submergence. *Marine Ecology Progress Series* 96:147-157.
- Rozas, L. P., M. W. LaSalle. 1990. A comparison of the diets of gulf killifish, *Fundulus grandis* Baird and Girard, entering and leaving a Mississippi brackish marsh. *Estuaries* 13:332–336.
- Ruckelshaus, M. H., P. Levin, J. B. Johnson, and P. M. Kareiva. 2002. The Pacific salmon wars: What science brings to the challenge of recovering species. *Annual Review of Ecology and Systematics* 33:665-706.
- Salo, E.O. 1991. Life history of chum salmon. Pp. 233-309 in *Pacific Salmon Life Histories*, C. Groot and L. Margolis, eds. University of British Columbia Press, Vancouver, Canada.
- Simenstad, CA, WG Hood, RM Thom, DA Levy, DL Bottom. 2000. Landscape structure and scale constraints on restoring estuarine wetlands for pacific coast juvenile fishes. Pp. 597-632 IN: MP Weinstein & DA Kreeger (eds), *Concepts and Controversies in Tidal Marsh Ecology*. Kluwer Academic Publ., Dordrecht.

- Thomas, B. E. and R. M. Connolly. 2001. Fish use of subtropical saltmarshes in Queensland, Australia: relationships with vegetation, water depth and distance onto the marsh. *Marine Ecology Progress Series* **209**:275-288.
- Weisberg, S.B. and V.A. Lotrich. 1982. The importance of an infrequently flooded intertidal marsh surface as an energy source for the mummichog *Fundulus heteroclitus*: An experimental approach. *Marine Biology* 66: 307-310.
- West, J. M. and J. B. Zedler. 2000. Marsh-creek connectivity: Fish use of a tidal salt marsh in Southern California. *Estuaries* 23: 699-710.
- Zar, J. H. (1984), *Biostatistical Analysis*, Prentice-Hall, Upper Saddle River, N. J.

Table 1. PERMANOVA table of results

Source	df	SS	MS	Pseudo-F	P(perm)	Unique permutations
habitat	1	18159	18159	19.819	0.0001	9956
year	2	7896.4	3948.2	4.3089	0.0001	9935
month	9	21071	2341.3	2.5552	0.0002	9865
haxye	2	5567.1	2783.6	3.0379	0.0019	9930
haxmo	9	15173	1685.9	1.8399	0.0064	9887
yexmo**	11	8859	805.36	0.8790	0.7081	9870
Res	11	10079	916.28			
Total	45	92926				

** Term has one or more empty cells

Figure Legends

Figure 1. Marsh surface fish density relative to vegetation height.

Figure 2. Relative abundance of the most common fish caught over the marsh surface and in tidal channels. Tidal channel fish catches were adjusted by net trapping efficiency. Adjusted and unadjusted catches are both shown for comparison.

Figure 3. Comparison of fish densities within tidal channels versus on the marsh surface. Note that the y-axis is one to two orders of magnitude greater for channel density compared to marsh surface density.

Figure 4. Seasonality in the ratio of marsh surface to channel fish density for all three years of sampling (2014-12016). Note the discontinuity in the y-axis scale.

Figure 5. nMDS plots of Bray-Curtis similarities of 4th-root transformed fish density samples: (a) distributions of samples by habitat; (b) distributions of samples by year; (c) distributions of samples by sample dates—the month prefixes, l and e, represent “late” and “early”, indicating the first and second halves of a month. Overlying polygons, derived from cluster analysis, enclose samples with > 50% similarity to each other. The largest polygon encloses the channel habitat samples.

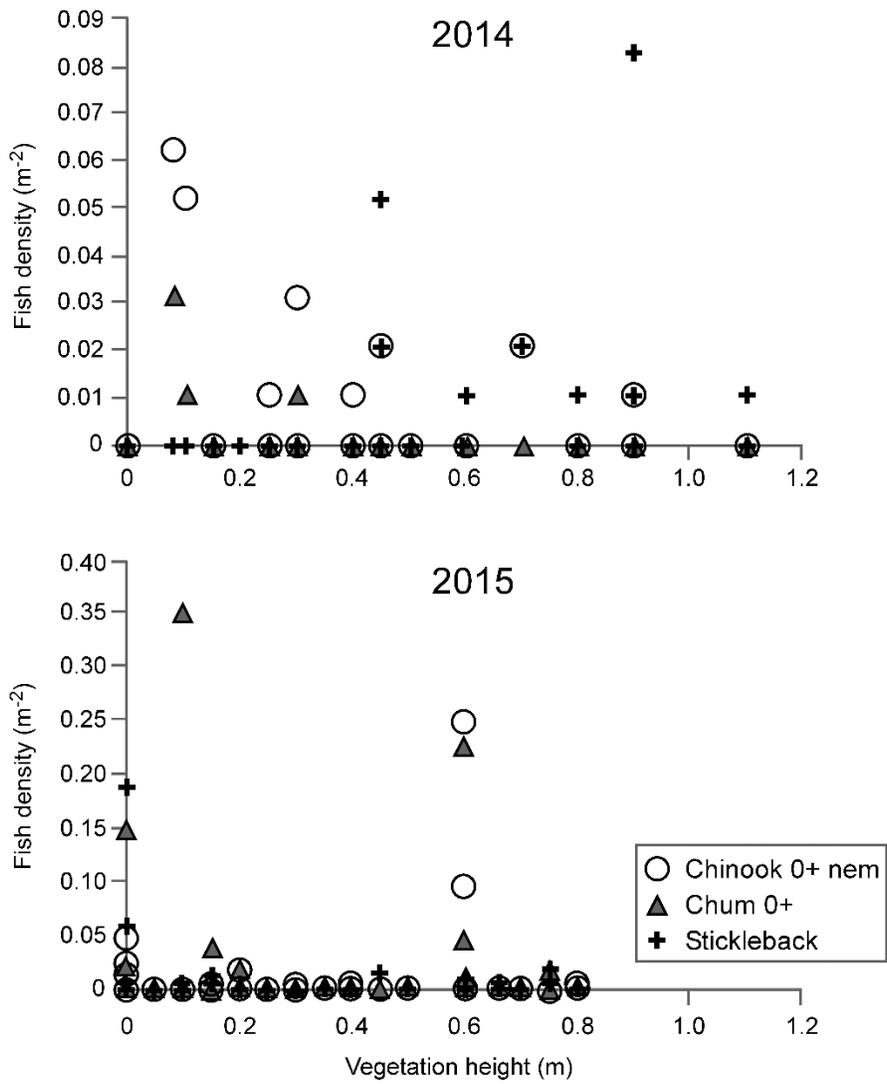


Figure 1. Marsh surface fish density relative to vegetation height.

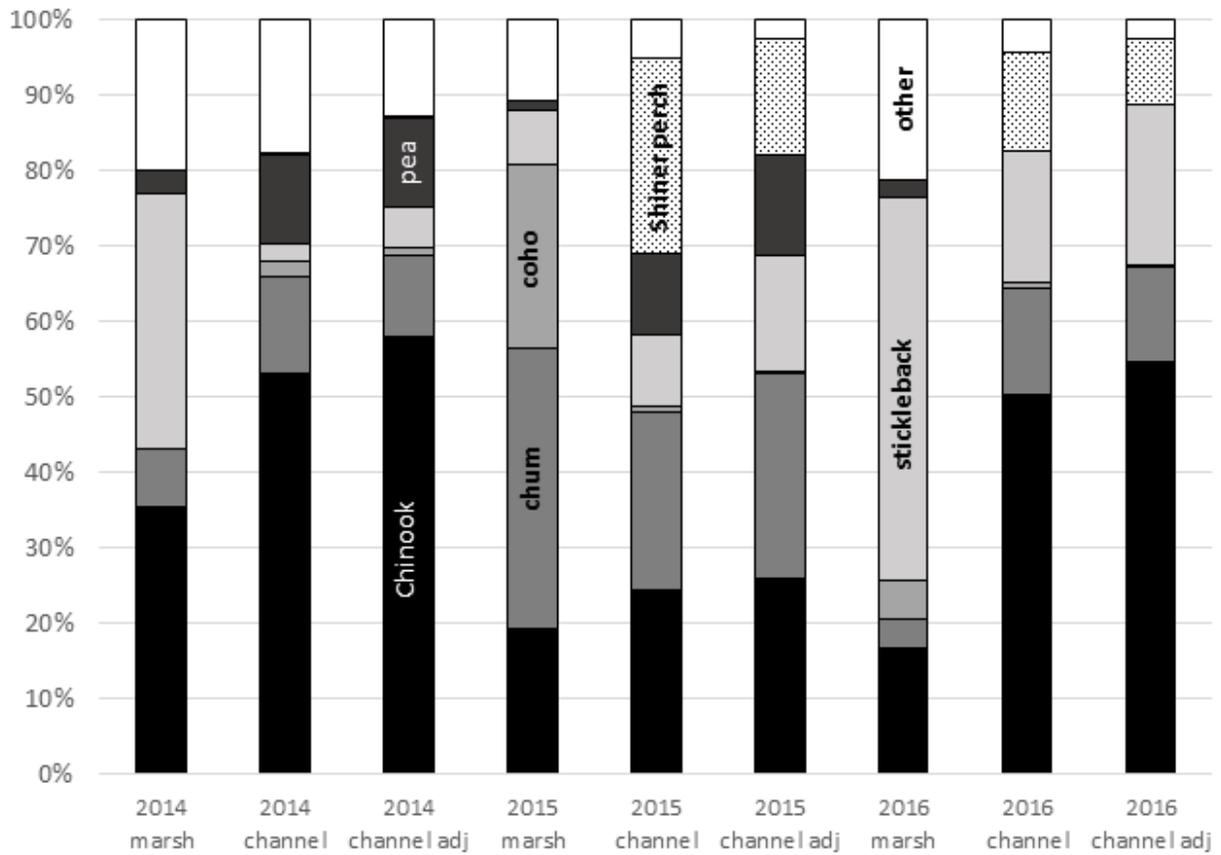


Figure 2. Relative abundance of the most common fish caught over the marsh surface and in tidal channels. Tidal channel fish catches were adjusted by net trapping efficiency. Adjusted and unadjusted catches are both shown for comparison.

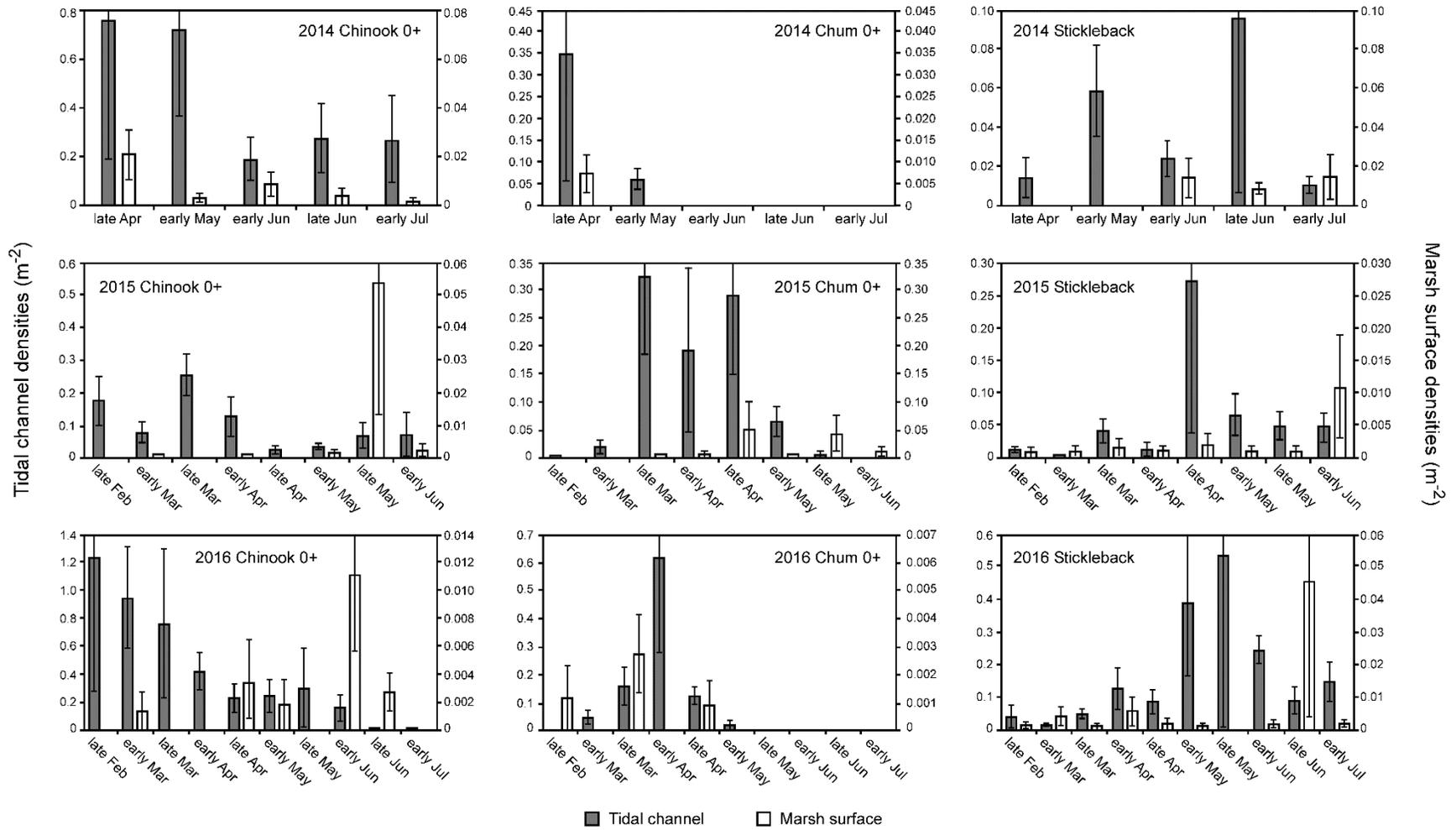


Figure 3. Comparison of fish densities within tidal channels versus on the marsh surface. Note that the y-axis is one to two orders of magnitude greater for channel density compared to marsh surface density.

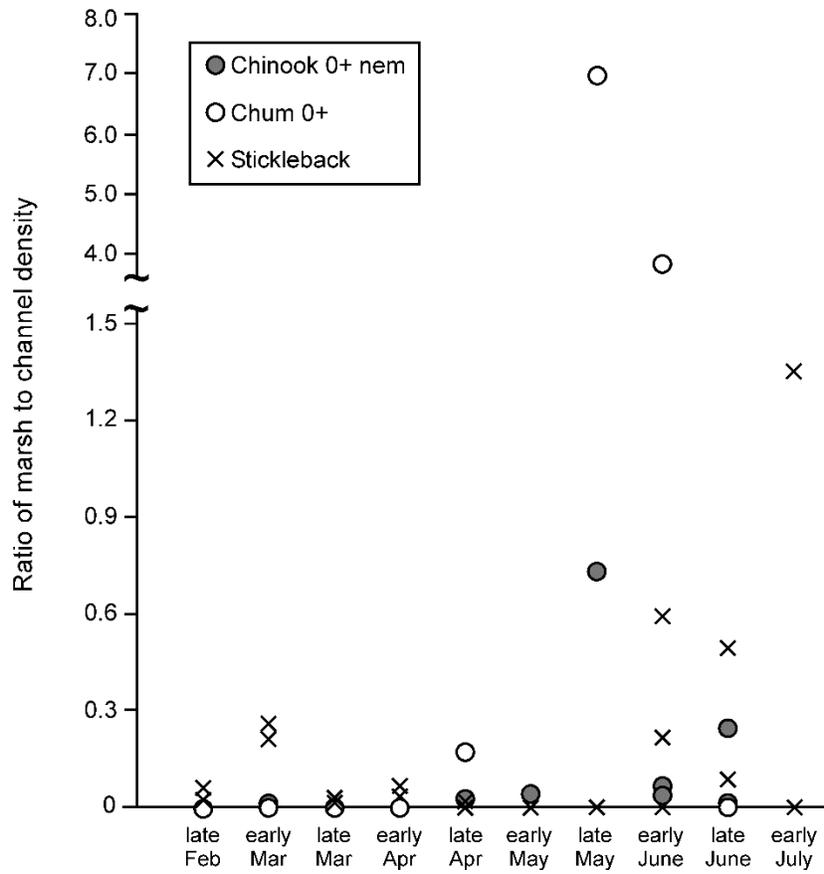


Figure 4. Seasonality in the ratio of marsh surface to channel fish density for all three years of sampling (2014-12016). Note the discontinuity in the y-axis scale.

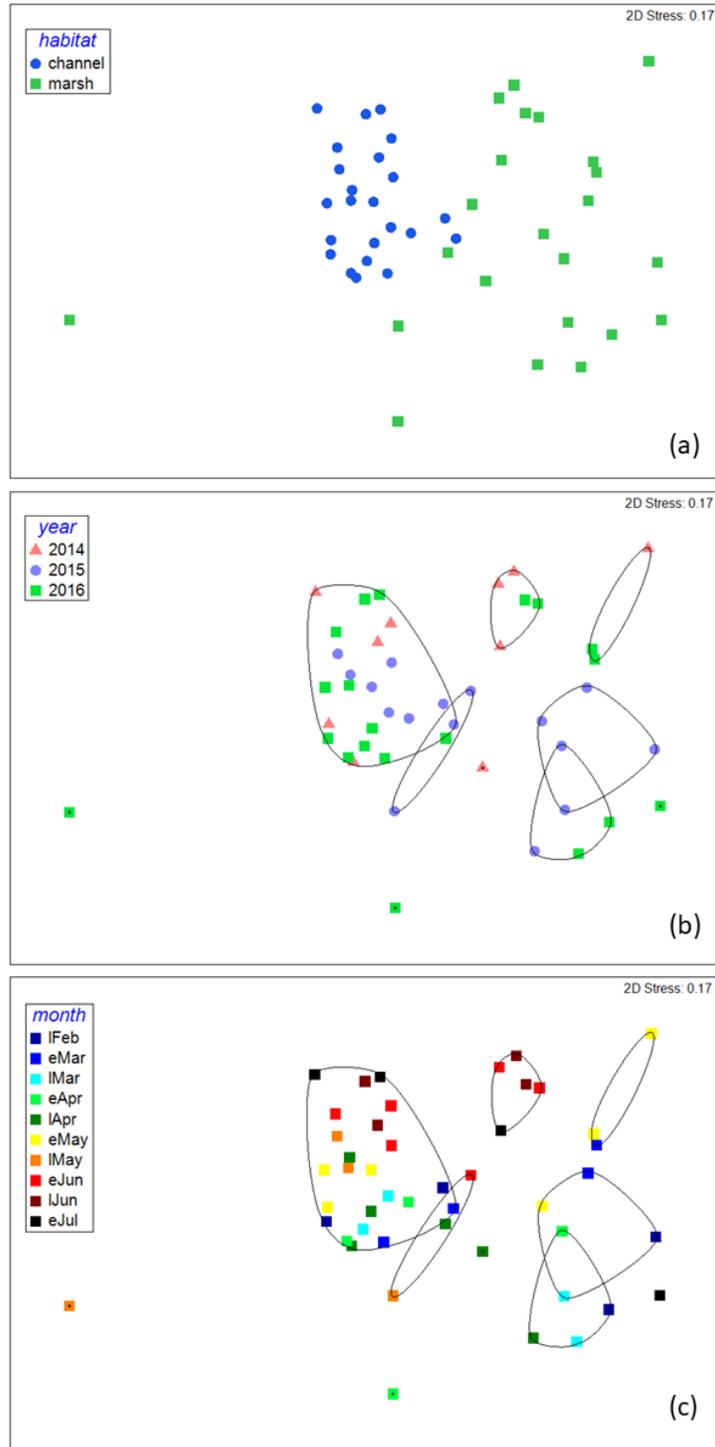


Figure 5. nMDS plots of Bray-Curtis similarities of 4th-root transformed fish density samples: (a) distributions of samples by habitat; (b) distributions of samples by year; (c) distributions of samples by sample dates—the month prefixes, I and e, represent “late” and “early”, indicating the first and second halves of a month. Overlying polygons, derived from cluster analysis, enclose samples with > 50% similarity to each other. The largest polygon encloses the channel habitat samples.