

Flood control structures in tidal creeks associated with reduction in nursery potential for native fishes and creation of hotspots for invasive species

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Abstract: Habitat connectivity is important for maintaining biodiversity and ecosystem processes yet globally is highly restricted by anthropogenic actions. Anthropogenic barriers are common in aquatic ecosystems; however, the effects of small-scale barriers such as floodgates have received relatively little study. Here we assess fish communities in ten tributaries over the spring–summer season of the lower Fraser River (British Columbia, Canada), five with floodgates and five reference sites without barriers, located primarily in agricultural land use areas. While the Fraser River supports the largest salmon runs in Canada, the lower Fraser river–floodplain ecosystem has numerous dikes and floodgates to protect valuable agricultural and urban developments. Floodgate presence was associated with reduced dissolved oxygen concentrations, threefold greater abundance of invasive fish species, and decreased abundances of five native fish species, including two salmon species. These findings provide evidence that floodgates decrease suitable habitat for native fishes, and become hotspots for non-native species. Given climate change, sea-level rise, and aging flood protection infrastructure, there is an opportunity to incorporate biodiversity considerations into further development or restoration of this infrastructure.

Résumé : Si la connectivité des habitats est importante pour le maintien de la biodiversité et des processus écosystémiques, elle est en général fortement limitée par l'activité humaine. Les barrières d'origine humaine sont répandues dans la plupart des écosystèmes aquatiques; toutefois, les effets de petites barrières comme les vannes de décharge ont reçu assez peu d'attention. Nous évaluons les communautés de poissons dans dix affluents du bas Fraser (Colombie-Britannique, Canada) pendant la saison printemps–été, dont cinq présentant de vannes de décharge et cinq sites de référence sans barrière, situés principalement dans des zones agricoles. Si le fleuve Fraser supporte les plus importantes migrations anadromes de saumons au Canada, l'écosystème des plaines alluviales inondables du bas Fraser compte de nombreuses digues et vannes de décharge pour la protection des aménagements agricoles et urbains. La présence de vannes de décharge est associée à des concentrations réduites d'oxygène dissous, une abondance trois fois plus grande d'espèces de poissons envahissantes et une abondance plus faible de cinq espèces de poissons indigènes, dont deux espèces de saumons. Ces constatations indiquent que les vannes de décharge réduisent l'ampleur des habitats convenables pour les poissons indigènes et deviennent des points chauds pour les espèces non indigènes. Dans un contexte de changements climatiques, d'augmentation du niveau de la mer et de vieillissement des infrastructures de protection contre les inondations, il est pertinent d'intégrer des considérations touchant à la biodiversité dans l'aménagement futur ou la remise en état de telles infrastructures. [Traduit par la Rédaction]

Introduction

Estuaries and coastal floodplains are ecologically important yet are some of the most threatened ecosystems on earth (Tockner and Stanford 2002). They provide key ecosystem services such as nursery habitat for fishes of cultural and economic importance (Beck et al. 2001). However, multiple human activities are rapidly changing these systems (Lotze et al. 2006). For example, seagrass meadows, an important nursery habitat for juvenile marine and estuarine fish, have been increasingly in decline since 1990, reaching loss rates of 7% per year globally (Waycott et al. 2009). Conversion for aquaculture and agriculture has resulted in the loss of 25%–50% of coastal tidal wetlands and is expected to continue, resulting in further loss of 20%–45% of existing salt marsh habitat before the end of the century (Kirwan and Magonigal 2013). Coastal developments and ecosystems alike are predicted to be threatened by sea-level rise and increasing flood and coastal storm frequency due to climate change (Church et al. 2013). Developed countries will likely offset flooding risk with engineered infra-

structure such as dikes, which may have ecological consequences, as they reduce connectivity between coastal rivers and their floodplains (Airoidi et al. 2005; Church et al. 2013).

Research on the ecological impacts of barriers in aquatic systems has primarily focused on dams in larger river systems (Januchowski-Hartley et al. 2013). Large dams are known to block the movements of materials and animals, dampen flow regimes, reduce river–floodplain connectivity, extirpate upstream anadromous salmon, and reduce access to different habitats for feeding, spawning, and refugia for fluvial migrants (Arthington et al. 2010; Gustafson et al. 2007; Schlosser and Angermeier 1995). Dams may also facilitate non-native species by providing novel (impounded) habitat (Johnson et al. 2008) or altering flow regimes that native fishes were previously adapted to (Fausch et al. 2001; Propst and Gido 2004). Although these effects of large dams are now recognized, there is arguably less understanding of the ecological effects of smaller-scale structures that also alter aquatic connectivity, such as culverts (Favaro et al. 2014), weirs (Mueller et al. 2011), dikes (Hood 2004), and floodgates (Pollard and Hannan 1994; Boys et al. 2012;

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Wright et al. 2014). These types of small barriers are common in aquatic systems, yet little is known regarding their effects on fish passage, hydrological cycles, or habitat quality.

Small-scale barriers in aquatic ecosystems such as floodgates (also called tide gates) are commonly installed to prevent flooding, yet their effects are largely unknown (Giannico and Souder 2005). Floodgates are installed in low-gradient coastal areas to allow tributaries to drain downstream through dikes while preventing backflows and flooding (Pollard and Hannan 1994). Floodgates consist of culverts with side- or top-mounted hinged gates on the downstream side, which require a hydraulic head difference from the upstream to downstream side to push open the gates and allow the passage of water and organisms; conversely the backpressure from rising water on the downstream side forces them closed (Thomson et al. 1999). Floodgates are a common flood control structure in coastal aquatic ecosystems globally, including North America (Raposa and Roman 2001), Europe (Wright et al. 2014), Australia (Pollard and Hannan 1994), and New Zealand (Doehring et al. 2011). Previous research has found floodgates to be associated with reduced overhanging vegetation (Pollard and Hannan 1994), greater nutrient concentrations, increased abundance of aquatic weeds (Kroon and Ansell 2006), and reduced dissolved oxygen concentrations (Gordon et al. 2015). In estuarine systems, floodgates can be associated with reduced abundance of commercially valuable species (Pollard and Hannan 1994), reduced fish passage (Doehring et al. 2011), including delayed downstream migration of salmonids (Wright et al. 2014), reduced diversity of estuarine fish (Boys et al. 2012), and reduced abundance, biomass, and diversity of juvenile fish (Kroon and Ansell 2006). This body of previous research has focused on floodgates in estuarine areas where they open and close with daily tides. However, the potential effect of floodgates on snowmelt river systems, where prolonged elevated floodwaters may close floodgates for several months at a time, have yet to be extensively studied. In these systems, fish communities may experience greater impacts owing to prolonged floodgate closure blocking passage and changing habitat characteristics, potentially resulting in similar effects to more permanent barriers such as dams.

In this study, we examined the effect of floodgates on fish communities in tidal tributaries of a large river system. The Fraser River (British Columbia, Canada), an enormous (220 000 km²) watershed that supports the largest salmon returns in Canada, is extensively diked in its lower reaches, and floodgates are present on the majority of tidal tributary creeks. In this system, during the yearly spring freshet, river levels rise by several metres for up to several months before receding, likely preventing floodgates from opening (Thomson et al. 1999). We used a comparative approach — we sampled the seasonal dynamics of tidal creeks with and without the presence of floodgates to determine if fish communities upstream of floodgates are different from reference creeks without in-stream barriers. We hypothesized that floodgates would be associated with effects similar to other anthropogenic aquatic barriers and that floodgates would be the key driver of these effects, relative to other differences in environmental variables and land use patterns. We predicted that similar to permanent barriers such as dams, floodgates would be associated with decreases in habitat quality and abundance of anadromous and resident native fish species and increased prevalence of non-native fish species.

Methods

Study system

The lower Fraser River delta in British Columbia is an example of a highly settled coastal floodplain where dikes and their floodgates are a prevalent feature of the landscape. The lower Fraser region contains approximately 1 million people and \$13 billion in infrastructure development, much of it on the floodplain of the

lower Fraser watershed (Fraser Basin Council 2010). The Fraser River is tidal for 115 km upstream of the mouth, and historically the Fraser River delta was an intricate floodplain of tidally influenced freshwater and estuarine creeks (Levings et al. 1995). However, since the early 20th century approximately 70% of the floodplain has become isolated by dikes (Healey and Richardson 1996), and floodgates are a common feature, with an estimated 500 installed to control flows (Thomson et al. 1999). The lower Fraser River is home to 42 fish species, including at least six introduced species (Richardson et al. 2000). The Fraser River contains one of the world's largest populations of Pacific salmon (*Oncorhynchus* spp.), which move through the estuary during their out-migration (Levy and Northcote 1982; Levings et al. 1995). In the lower Fraser, tidal freshwater tributaries provide critical rearing and overwintering habitats for juvenile salmon including Chinook (*O. tshawytscha*), coho (*O. kisutch*), and chum (*O. keta*) (Levings et al. 1995). Previous work has indicated that the use of these nursery habitats is important to the survival of juvenile Chinook salmon migrating seawards from throughout the system (Murray and Rosenau 1989). Floodgates in systems such as this likely remain closed for extended periods of time in the lower Fraser during the spring freshet, low flow periods, and high tide cycles, yet the effects on fish communities are poorly understood (Thomson et al. 1999).

Study sites

We chose 10 tidal creeks as study sites. These sites were selected from a larger pool of potential sites initially identified from the Lower Fraser Valley Streams Strategic Review (Fraser River Action Plan 1999) and Government of British Columbia Ministry of Forests Lands and Natural Resource Operations Lower Mainland Dike Inventory Maps (BC MFLNRO 2011). Sites were chosen from this set based on presence in tidal floodplain areas and similarity in watershed size, gradient, and land use (Table 1). We then conducted preliminary site evaluations to determine accessibility and feasibility of sampling before the final group of sites was selected. Reference sites were geographically close to floodgate sites and in similar tidal, low-gradient areas. Reference sites differed from floodgate sites in that flood protection was in the form of dikes running along the banks of the tributaries' lower reaches subject to backflooding, removing the need for floodgates at the confluence with the main stem. All sites were located in areas that experience mixed semidiurnal daily tidal fluctuations with distances from the ocean ranging from 44 to 57 km. Sites were generally located in agricultural and urban areas and have all been modified in the past through channelizing, diking, and straightening. Floodgate sites were also chosen based on having associated pumping stations, the presence of which is typically related to a threshold in watershed drainage area. We note that pumps only operate when floodgates are closed; therefore, although the local increase in turbulent flow may serve to attract fishes, it occurs when the gates are acting as physical barriers to fish passage.

We studied ten sites located throughout the lower Fraser River floodplain (Fig. 1). Five of our sites were upstream of floodgate barriers and associated pumping stations, and five of the sites were references, with no in-stream flood control structures. The barrier sites included McLean Creek and Fenton Slough that drain directly to the Pitt River, Cranberry Slough that drains directly to the Alouette River, and Yorkson Creek and Nathan Slough that drain directly to the Fraser River. The pump station at Yorkson Creek contained "fish friendly" Archimedes screw pumps, which are thought to impart a lower rate of mortality on out-migrating fish. Cranberry Slough had a single flap gate; however, following our study it was determined to operate solely as a pumping station, with the gate functioning only as an outflow, thereby consistently preventing upstream migration. This diversity of floodgate permeability (ranging from seasonal to near-complete barriers to upstream movement) prevents us from directly analyzing the mechanism by which the floodgates affected fish; however, we

Table 1. Site information, watershed area and proportions of different land uses in the watersheds of our study sites.

Sites	No. of flap gates (year installed)	Distance from ocean (km)	Total area (km ²)	Agriculture (%)	Urban (%)	Other human use (%)	Undeveloped or protected (%)
Reference							
De Boville	—	42.1	8.63	4.17	48.15	1.30	46.39
McKenny	—	46.6	5.42	24.89	51.71	23.06	0.35
Smokwha	—	50.7	4.74	10.87	0.00	0.00	89.13
West	—	52.5	15.29	77.84	0.79	13.33	8.04
Nathan C.	—	55.2	10.54	89.59	0.21	6.87	3.34
Floodgate							
McLean	4 (1984)	42.3	4.06	44.89	0.00	0.00	55.11
Cranberry	* (1984)	44.7	5.27	90.84	0.00	9.10	0.06
Fenton	2 (1984)	45.7	3.33	86.80	8.36	4.84	0.00
Yorkson	2 (1994)	43.3	17.12	34.34	46.34	12.68	6.65
Nathan S.	2 (1950)	57.4	5.20	95.91	0.00	4.09	0.00

Note: Watershed area determination and land use analysis completed using ArcGIS; land use calculations based on MetroVancouver land use dataset created in 2006.

*Following our sampling, it was determined that the structure at Cranberry Slough functions solely as a pumping station.

retain this site in our analysis to focus on the difference in fish communities between sites with and without barriers; therefore, we will refer to all barrier sites as floodgate sites. Reference sites included De Boville Slough and Smokwha Marsh that drain directly to the Pitt River, McKenny Creek that drains directly to the Alouette River, and West Creek and Nathan Creek that drain directly to the Fraser River (Table 1).

Sampling methods

We sampled each of the ten sites once per month from April through August during the summer of 2013. We conducted sampling in 10 consecutive days each month, except April in which Smokwha Marsh was sampled 3 days after completion of the other sites. Sampling generally alternated daily between reference and floodgate sites to reduce the potential effect of within-month variation. Sampling occurred during 11–23 April, 7–16 May, 10–19 June, 9–18 July, and 14–23 August. Water levels at floodgate sites were consistent between different sampling occasions, presumably because of the pump operations and floodgates that buffered tidal and seasonal variation. At reference sites, water levels substantially rose following the start of the spring freshet fluctuating by several metres between lows in April and August and a peak in late May. Water levels at reference sites also fluctuated daily with tides; therefore, we generally conducted sampling at midday when the tide height was low to medium and depths were around 1 m, which maximized accessibility and increased sampling effectiveness. At floodgate sites, water depths were generally around 1 m and were typically controlled by pump operations and therefore are kept consistent.

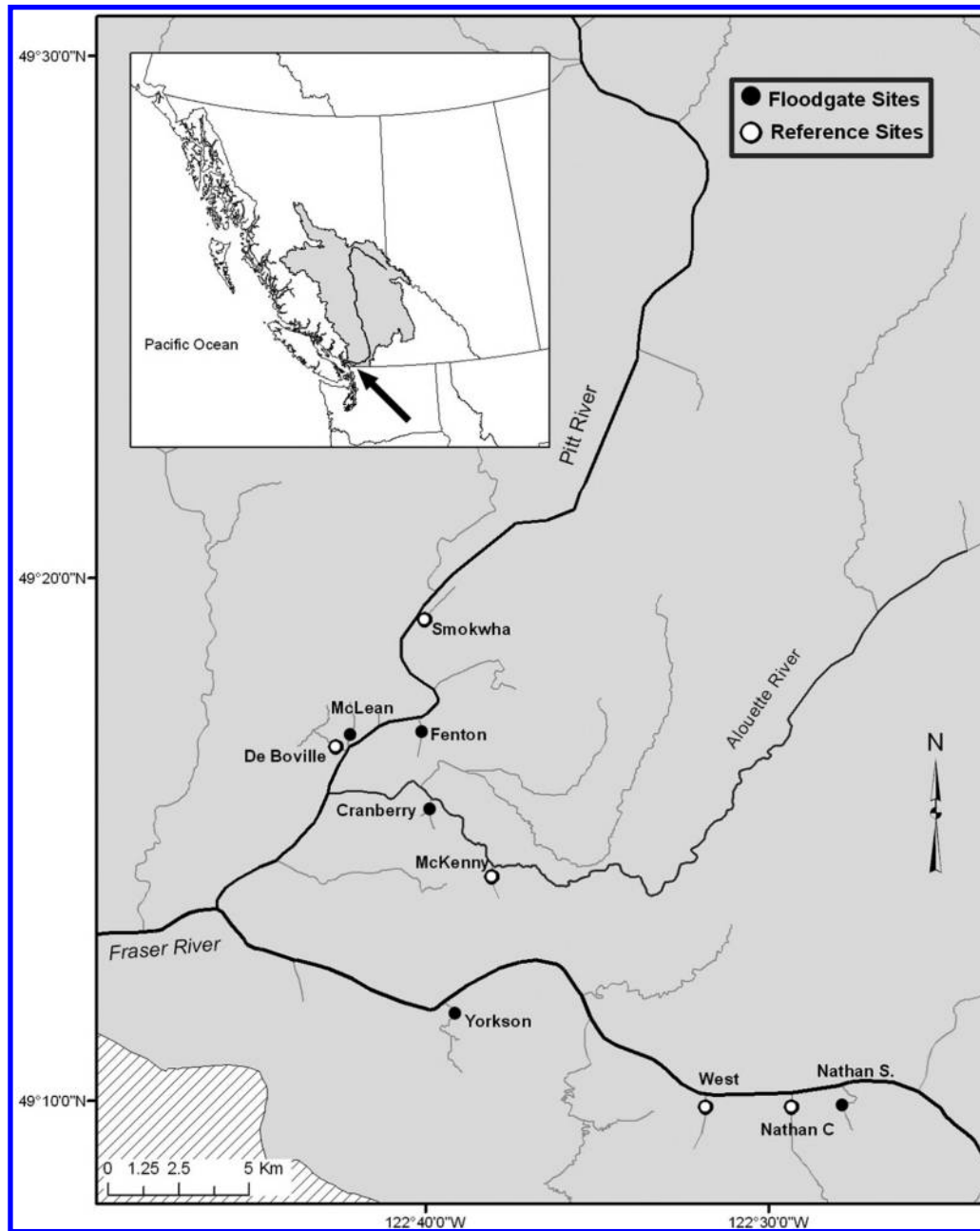
We captured fish on each sampling occasion by seine hauls using a 15.2 m by 2.4 m net with 0.32 cm mesh size. We conducted three seine hauls at each sampling event. Seining started approximately 50 m upstream of the floodgates or confluence at reference sites, and repeated hauls were conducted approximately 50 m upstream of the previous haul. Thus, fish sampling was restricted to the first 150 m upstream of the floodgate or confluence at reference sites. For each haul, two crew members would fully extending the net by having one crew member hold the net while the other walked downstream typically 2 m from the bank before circling towards the bank and pulling the net into a purse, seining an area of approximately 15.4 m by 2 m. Sampling locations had extremely low gradients, and because of the position near the confluence of our sampling sites, there was typically little to no water velocity and the substrate was typically sand or mud. Consecutive seine hauls were typically conducted immediately following completion of identification of fish from previous hauls and were separated by habitat type if habitats were not homogeneous. After identification, fish were temporarily held in aerated buckets to prevent recapture in consecutive hauls. We

also set minnow traps with 0.32 cm mesh size and baited with 20.0 ± 2.0 g cured salmon eggs, approximately 25 m apart, overnight for periods averaging 18 h on each of our sampling occasions. We identified and measured fish caught in traps prior to commencement of seine hauls, and fish were typically held until seining was completed if seine hauls were conducted in the same area as traps. All fish were released following identification. The Simon Fraser University Animal Care Committee approved sampling techniques, and permits were obtained from federal and provincial agencies. To determine if water quality was similar between reference and floodgate sites, water chemistry measurements of salinity, temperature, dissolved oxygen concentration, and conductivity were obtained using a YSI meter (model 556 MPS, YSI Inc.). We took water chemistry measurements just below the water surface within 30 min of noon, upstream (~50 m) of floodgates or the confluence at reference sites.

Watershed land use analysis

To ensure that observed differences were related directly to floodgate presence relative to other anthropogenic stressors, we determined the area of our watersheds and analyzed the proportion of different types of land use to determine if they differed between floodgate and reference sites. We used the watershed tools in ArcGIS using a 25 m resolution digital elevation model, land use spatial layers, and stream and river locations in British Columbia. As our sites are located in extremely low-gradient areas, the software had difficulty determining the correct dimensions for some of our sites. Therefore, we used a dataset outlining streams and rivers in British Columbia created by the Ministry of Environment in 2005, along with Google Earth (version 7.1.2.2041, Google Inc., Mountain View, California, USA) images and our knowledge of the watersheds, to draw polygons outlining our watersheds based on those initially delineated by ArcGIS and then calculated total area. To determine land uses, we obtained a land use dataset created by MetroVancouver in 2006 with 25 m resolution at a 1:20 000 scale that indicated the dominant land use for each parcel. We then grouped watershed use into (i) agriculture, (ii) urban, which represented all forms of residential land use along with commercial and institutional, (iii) other human use, which represented industrial, transportation, recreation, and parks, and (iv) undeveloped or protected areas. Our land use data set did not cover all of the watershed areas for Nathan Creek and Nathan Slough, with data coverage for 44% and 34% of each watershed, respectively. Based on visual inspection of Google Earth images of the remaining portions of each watershed, the land use appeared similar; therefore, we used the available data as a proxy for land use for those two watersheds. Spatial analyses were conducted using ArcGIS version 10.2 (ESRI 2014).

Fig. 1. Map of study area and region. Location of reference and floodgate sites is denoted by white and black circles, respectively, within the lower Fraser River watershed, which is outlined in grey. Inset displays location of Fraser River watershed in western North America.



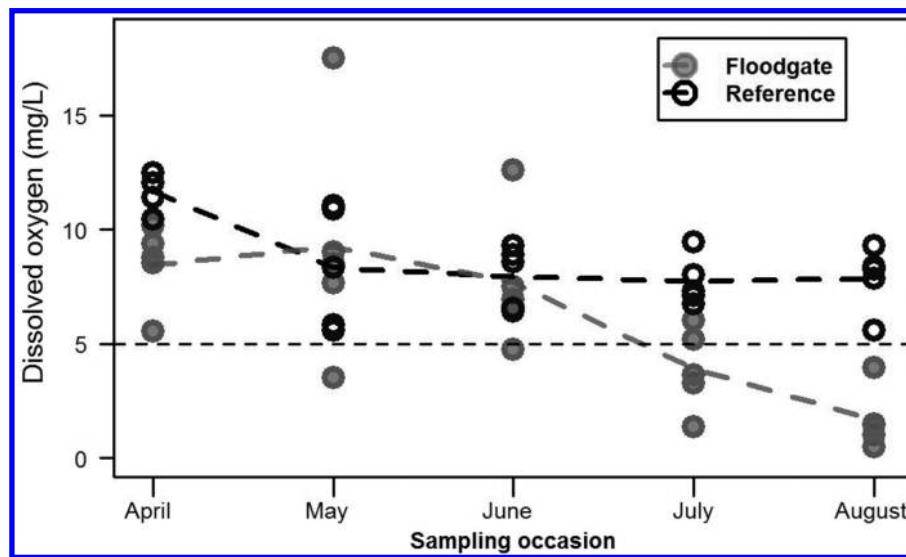
Statistical analysis

We analyzed fish data at the community and species levels. For both sets of analyses, we summed our catch data from our traps and seine hauls for each sampling occasion at each site, as they represented an equal sampling effort for each sampling date. Our aggregated catch data thus represents a metric of the fish community at each site. We used nonmetric multidimensional scaling (NMDS; Prentice 1977) to explore the relationship between floodgate presence and community composition at our sites. NMDS analysis was used to visualize community dissimilarity across sites and across time and to visualize which species were influencing community composition. Species abundances were fourth-root-transformed to satisfy normality for multivariate analysis. Unidentified juvenile minnows were grouped with peamouth chub (*Mylocheilus caurinus*) and northern pikeminnow (*Ptychocheilus oregonensis*) under the category minnow. We also combined fish identified as pumpkinseed

(*Lepomis gibbosus*) and black crappie (*Pomoxis nigromaculatus*) with our unidentified juvenile sunfish under the category sunfish. A Bray–Curtis dissimilarity matrix was generated based on the species composition for each site and sampling occasion. For our NMDS we used two dimensions ($k = 2$), and our stress score was 0.174. We ran a permutational multivariate analysis of variance test (PERMANOVA; Anderson 2001) to test the significance of floodgate presence and date on our community composition. Our model included floodgate presence, date, and an interaction term between floodgate presence and date. These analyses were done in the program R (version 3.1.1; R Core Team 2014), using the vegan package (Oksanen et al. 2013).

We examined the relationship between floodgate presence and abundance for each species with adequate data using generalized additive models (GAMs). GAMs function as an extension of generalized linear models that can incorporate a nonlinear smoothing

Fig. 2. Monthly measurements of dissolved oxygen concentrations taken at each site on each sampling occasion. Each point represents a different site, with broken lines connecting the means for floodgates and reference sites. Grey and black shading indicates reference and floodgate sites, respectively. Measurements were taken just below the surface at noon or within 30 min, just upstream of floodgates or the confluence in reference sites. The horizontal dotted line at 5 mg·L⁻¹ represents the instantaneous minimum dissolved oxygen concentration outlined by the Government of British Columbia's recommended criterion for the protection of aquatic life.



function for an independent variable such as time (Hastie and Tibshirani 1987). We used GAMs to test the effect of floodgate presence on our abundance data for each species while accounting for time with a smoothing function. GAMs allowed us to use multiple measurements through time nested within site, with dates numbered consecutively beginning from the first day of sampling. This smoothing function removes the effect of time allowing us to focus solely on the effect of floodgate presence and accurately compare coefficients among species. For non-salmon species, we ran our GAM with a negative binomial error distribution, as it gave us the best fit based on diagnostics. We normalized our data by dividing our abundances for each sampling occasion by the total standard deviation for each species prior to analysis. This then compares abundances in terms of the number of standard deviations to allow direct comparison among species. We excluded species caught at very low abundances ($n \leq 10$) and frequency, including rainbow trout (*Oncorhynchus mykiss*), redds shiner (*Richardsonius balteatus*), and largescale sucker (*Catostomus macrocheilus*), as sample sizes for these species did not meet conditions of normality. Again, we combined fish identified as pumpkinseed and black crappie with our unidentified juvenile sunfish for analysis. As our salmon data were highly skewed, particularly for Chinook and chum, to satisfy normality we used a $\log_{10}(x + 1)$ transformation prior to analysis, divided by the standard deviation to allow comparison, then ran our GAM using a quasi-Poisson error distribution. As Chinook and chum salmon were only captured in the first two and three sampling periods, respectively, we only used those data for our GAMs. GAMs were run using the mgcv package in R (Wood 2001; R Core Team 2014). We used an alpha level of 0.05 to determine statistically significant results.

Results

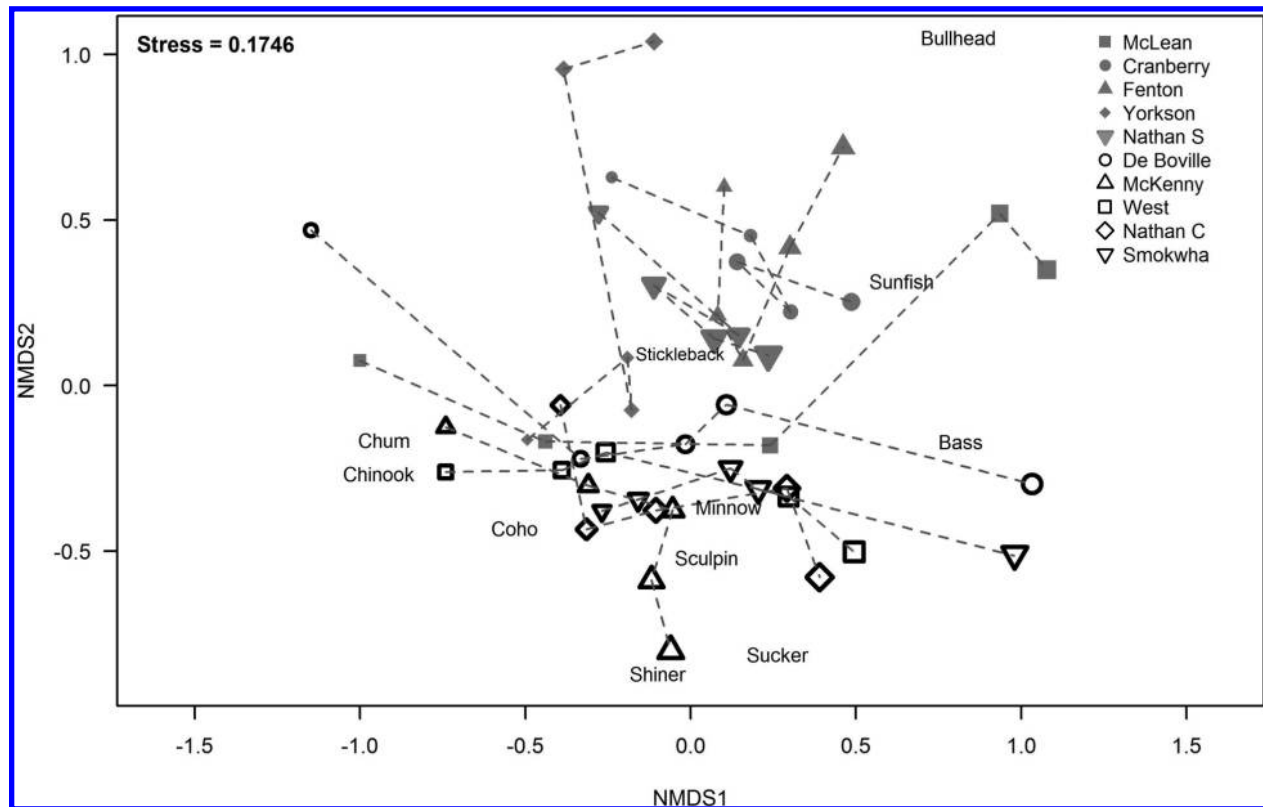
Reference and floodgate sites were similar in watershed area and dominant land uses (Table 1). Study watersheds were typically small; floodgate watersheds averaged 7.00 km², ranging from Fenton Slough at 3.33 km² to Yorkson Creek at 17.12 km², whereas reference watersheds averaged 8.92 km² and ranged from Smokwha Marsh at 4.74 km² to West Creek at 15.29 km². Land use was predominantly agriculture and urban in four of five reference

sites and four of five floodgate sites. The exceptions were the floodgate site McLean Creek, which runs through an agricultural area in its lower reaches, but the majority (55%) of the watershed is a protected forested area, and the reference site Smokwha Marsh, which is mostly situated in what is now a protected area but was historically used for agriculture and as such is channelized, diked, and does not experience a natural hydrological cycle (Table 1). As these sites are highly modified by human activity, they are arguably similar to our other sites. Floodgate and reference sites were also similarly distributed through the region (Fig. 1).

Variation in measured water quality parameters was associated both with sampling date and floodgate presence. Temperatures increased throughout the summer at all sites, with no trends related to floodgate presence. Salinity and conductivity were measured at nearly negligible concentrations at both floodgate and reference sites throughout the study period; therefore, these parameters will not be further discussed (Table A1). More notably, floodgates were associated with decreased dissolved oxygen levels (Fig. 2). Dissolved oxygen concentrations were initially similar among all sites; however, by later sampling periods, concentrations decreased in floodgate sites compared with reference sites. During our August sampling period, dissolved oxygen concentrations at all floodgate sites fell to levels below BC Ministry of Environment's safe minimum standards (5 mg·L⁻¹) for the protection of aquatic life (GBCME 1997) (Fig. 2). A concurrent study by our research group found that floodgates were associated with significant lower levels of dissolved oxygen that extended at least 100 m upstream of the floodgates (Gordon et al. 2015).

We captured a total of 30 759 fish of 21 different species throughout our sampling. We captured 674 juvenile salmon of five different species, 29 351 fish from 10 different non-salmon native species (hereinafter referred to as "other native species"), and 734 fish of six different non-native species (Table A2). The majority of juvenile salmon species captured were chum, Chinook, and coho, respectively, while a few pink (*Oncorhynchus gorbuscha*) and sockeye (*Oncorhynchus nerka*) were also captured at one site. Native threespine stickleback (*Gasterosteus aculeatus*) dominated catches, with 27 791 individuals captured. Other native species captured in abundance included the northern pikeminnow, prickly sculpin

Fig. 3. Nonmetric multidimensional scaling (NMDS) plot using data for all fish species captured throughout our sampling. Unidentified juvenile minnows are grouped with peamouth chub and northern pikeminnow under the category minnow. Unidentified juvenile sunfish are grouped with pumpkinseed and black crappie under the category sunfish. Each point represents one sampling occasion for one site; grey and black shading indicates reference and floodgate sites, respectively; and size of points scales from beginning to end of sampling period going from smallest to largest. Position of points is relative to Bray–Curtis dissimilarity matrix generated from our catch data; the position of species names represent the weighted mean scores of species for ordination configuration. The stress score indicates the degree to which the ordination explains the dissimilarity matrix in two dimensions.



(*Cottus asper*), and peamouth chub. Non-native species captured included pumpkinseed, largemouth bass (*Micropterus salmoides*), common carp (*Cyprinus carpio*), brown bullhead (*Ameiurus nebulosus*), black crappie, and weather loach (*Misgurnus anguillicaudatus*).

Community-level analyses indicated fish community composition to be significantly different between floodgate and reference sites. Fish communities differed significantly based on floodgate presence ($F = 12.46, P = 0.001$), date ($F = 11.58, P = 0.001$), and an interaction between floodgate presence and date ($F = 2.09, P = 0.015$; Fig. 3). Visualization of fish communities with NMDS indicated that the community composition was primarily dominated by stickleback at all sites. However, through the summer we saw reference sites shift from communities with salmon to communities with higher abundance of minnow (Cyprinidae) and prickly sculpin, while floodgate sites showed higher abundances of sunfish (Centrarchidae) and brown bullhead.

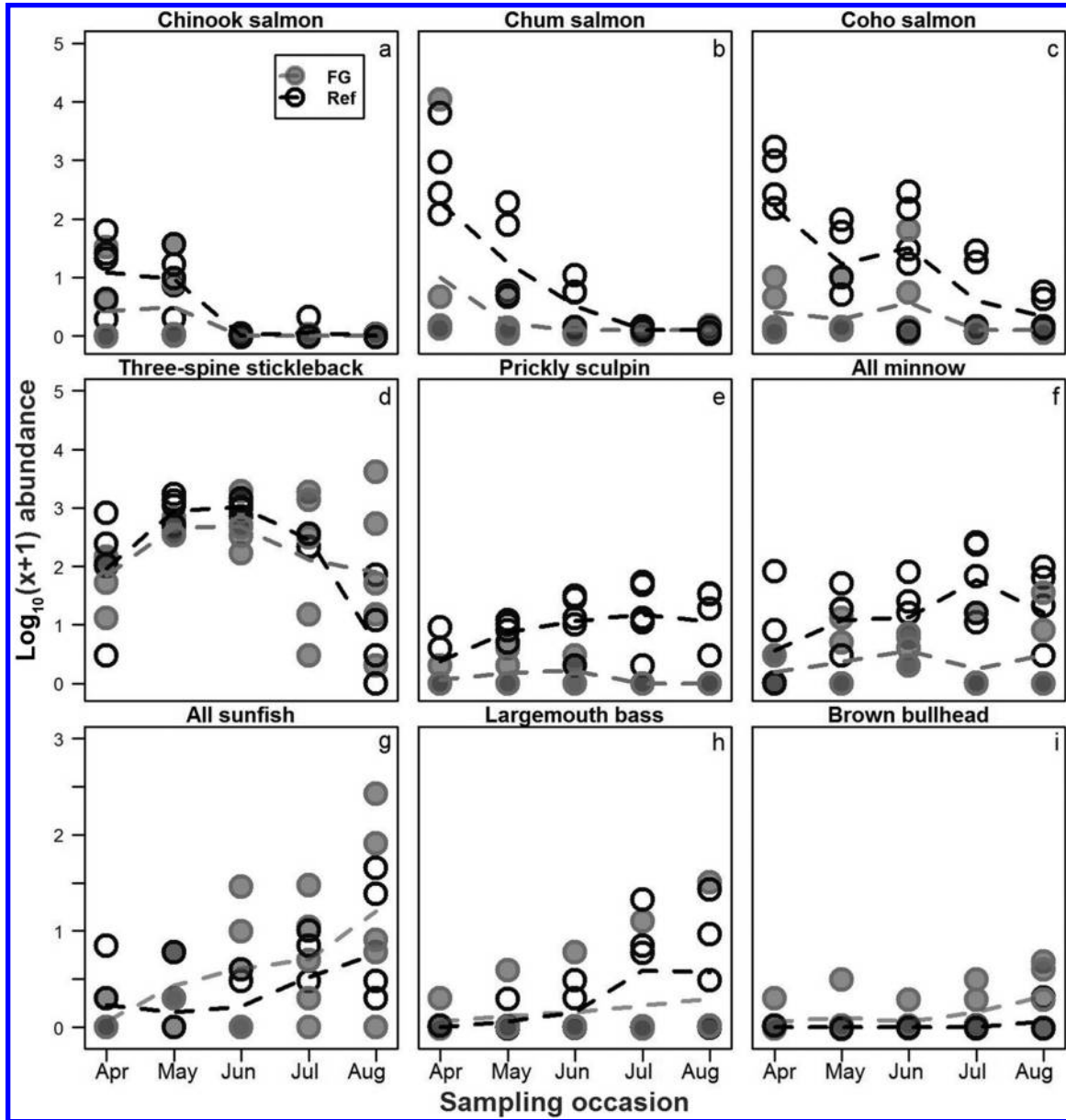
Juvenile salmon abundances were consistently lower at sites where floodgates were present relative to reference sites. Juvenile salmon were captured at all five reference sites but at only two floodgate sites. Total juvenile salmon abundance was 2.5 times greater in reference sites relative to floodgate sites. Total abundance was also on average consistently greater for each sampling period and for each juvenile salmon species (Fig. 4). Total abundance was 11.7 times greater for coho, 1.5 times greater for chum, and 2.2 times greater for Chinook salmon in reference sites relative to floodgate sites. There was also a strong seasonal trend in abundance as would be expected for out-migrating fish, with the majority of individuals captured in April and May (Fig. 4). These differences in total abundance in floodgate sites relative to refer-

ence sites were statistically significant for coho (GAM: $\beta = -1.700, SE = 0.381, t = -4.466, P = 0.0001$) and chum ($\beta = -1.319, SE = 0.492, t = -2.683, P = 0.013$) but not for Chinook salmon ($\beta = -0.808, SE = 0.444, t = -1.819, P = 0.087$; Fig. 5).

Floodgates were also associated with the decreased abundance of the majority of other native species. Threespine stickleback, which comprised 95.6% of our catch of other native fish species, were similar in abundance between floodgate and reference sites throughout the summer (Fig. 4). Prickly sculpin and native minnow (Cyprinidae) species were 37.2 and 11.7 times more abundant, respectively, at reference sites relative to floodgate sites throughout our sampling periods (Fig. 4). Using GAMs, we found these differences to be statistically significant for prickly sculpin (GAM: $\beta = -3.607, SE = 0.796, t = -2.62, P = 0.0001$), northern pikeminnow (GAM: $\beta = -2.094, SE = 0.592, t = -3.540, P = 0.001$) and peamouth chub (GAM: $\beta = -1.350, SE = 0.395, t = -3.423, P = 0.0015$; Fig. 5).

Floodgates were positively associated with the majority of non-native fish species. In total, non-native species were 3.1 times more abundant at floodgate sites relative to reference sites. Sunfish were 4.3 times more abundant at floodgate sites (Fig. 4), which was statistically significant (GAM: $\beta = 1.477, SE = 0.577, t = 2.560, P = 0.0137$; Fig. 5). We found a similar statistically significant positive effect of floodgate presence on brown bullhead (GAM: $\beta = 2.733, SE = 0.969, t = 2.819, P = 0.007$; Fig. 5) and common carp abundance (GAM: $\beta = 2.037, SE = 0.843, t = 2.417, P = 0.020$; Fig. 5). Largemouth bass were the only non-native species that were not statistically higher in floodgate sites (GAM: $\beta = -0.276, SE = 0.537, t = -0.515, P = 0.61$; Fig. 5) of those with suitable numbers for statistical analysis.

Fig. 4. Abundances of specific fishes through time in floodgate (FG) and reference (Ref) sites. Abundance data after $\log_{10}(x + 1)$ transformation of (a) juvenile Chinook salmon, (b) juvenile chum salmon, (c) juvenile coho salmon, (d) threespine stickleback, (e) prickly sculpin, and (f) all minnow species (northern pikeminnow, peamouth chub, redbside shiner, and unidentified juvenile minnows combined), (g) all sunfish (pumpkinseed, black crappie, and unidentified juvenile sunfish combined), (h) largemouth bass, and (i) brown bullhead. Points represent the sum of three seine hauls and six minnow traps for an individual site for each sampling occasion, with black open circles representing reference sites and grey circles representing floodgate sites. Broken lines connect means across sites for floodgate and reference sites on each sampling occasion.



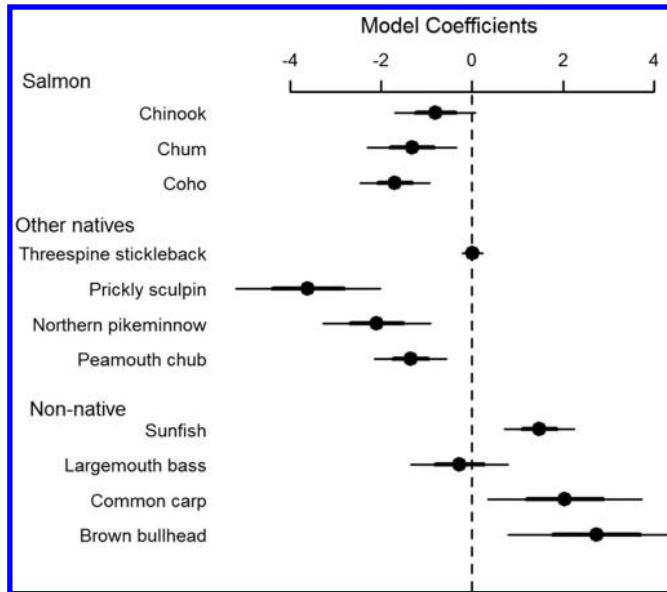
Discussion

Our results demonstrate that floodgates are associated with significant differences in fish communities in the tidal creeks we studied. We found floodgate presence to be associated with decreased abundance of salmon and other native fish species, greater abundance of non-native fishes, and depressed dissolved oxygen concentrations. Given that all of our sites were similar and are in areas impacted by human land uses, our results provide evidence that floodgate presence is a driver of fish community change. Furthermore, the differences in fish communities we found are supported by previous findings from Australia, which found reductions in eight commercially valuable species when comparing sites with floodgates to ungated reference channels (Kroon and

Ansell 2006). While large dams are known to profoundly impact freshwater aquatic systems, our results demonstrate that small-scale barriers have similar affects, impairing native fish while facilitating non-native fishes. As floodgates are ubiquitous in many coastal aquatic systems, such as the lower Fraser River, the collective impact of these small structures may be an important yet relatively unconsidered driver of undesirable change.

Although floodgates were not associated with differences in temperature or conductivity, they were strongly associated with decreased dissolved oxygen concentrations, a key attribute of habitat quality commonly affected by anthropogenic stressors. Dissolved oxygen concentrations were lower in floodgate sites than in reference sites, particularly in August when they fell below the

Fig. 5. Points representing model coefficients for the effect of floodgate presence on abundance of each fish species. More positive values indicate larger positive impacts of floodgates on fish abundance, more negative values indicate more negative impacts of floodgates on fish abundance. Data were normalized by division by the standard deviation for each species prior to analysis; the model coefficients thus indicate the impact of floodgate relative to observed variation of that species. Data coefficients are derived from generalized additive models for the effect of floodgates on abundance data with a smoothing function for the effect of date. Error distributions used for salmon and non-salmon species data were quasi-Poisson and negative binomial, respectively, out of necessity to satisfy normality. The thick and thin lines represent 1 and 2 standard errors for these estimates, respectively.



local British Columbia Provincial Criteria for the Protection of Aquatic Life of $5 \text{ mg}\cdot\text{L}^{-1}$, while reference sites remained near saturation levels. Similarly, Santucci et al. (2005) studied a river fragmented by low-head dams and found that in impounded reaches dissolved oxygen concentrations regularly fell below local protection criteria, while in free-flowing reaches they remained at safe levels. Concurrently, we also investigated the spatial extent of floodgate-related hypoxia in our study system and found that oxygen concentrations at dawn and dusk, in surface and bottom waters, were below safe minimum levels and that this extended at least 100 m upstream of floodgates, yet conditions remained safe downstream of floodgates (Gordon et al. 2015). Thus, floodgates may result in upstream “dead zones”, creating areas that are no longer suitable habitat for oxygen-sensitive fishes (Gordon et al. 2015) and potentially leading to hypoxic fish kills (Breitburg 2002). While it is unclear how far upstream these effects occur, they potentially represent a chemical barrier (Whitmore et al. 1960), potentially altering fish passage to upstream areas that may not be affected. While there is widespread appreciation for large-scale hypoxia in coastal oceans, there is less appreciation for the potential cumulative impacts of small-scale hypoxia (Pressey and Middleton 1982; Gordon et al. 2015). Floodgate-related hypoxia is an important implication of tidal restriction for managers to consider in developed coastal floodplains.

Similar to the effects of other aquatic barriers, floodgates were found to be associated with decreased abundance of juvenile salmon. Large barriers are known to extirpate salmon (Sheer and Steel 2006), and our results demonstrate that small-scale barriers, which are much more abundant, also can exclude salmon. Floodgates could negatively affect salmon by preventing adults from

reaching spawning grounds, preventing or delaying the redistribution of juveniles (Wright et al. 2014) or by reducing water quality, thereby making areas uninhabitable. Floodgates are closed during much of spring freshet, as high mainstem water levels prevent upstream flows from opening gates, potentially preventing the passage of juveniles. In late summer and fall, low flows may not sufficiently open gates, particularly heavy top-mounted cast iron gates or those improperly designed, preventing the upstream passage of adults. Tributary habitats like the ones we studied are also known to be important for winter growth and survival of juvenile coho, which have been shown to be impacted by diking (Beechie et al. 1994) and other small barriers such as culverts (Davis and Davis 2011). Chum salmon typically spend less time in fresh water before migrating towards the ocean; therefore, reduced abundance of juveniles is likely related to differences in spawner abundance or distribution. We documented juvenile Chinook salmon presence in two of our floodgate sites, and as Chinook do not spawn in our study areas, their presence suggests successful upstream passage of juveniles through floodgates at these sites. Conversely, the absence of juvenile Chinook salmon at three of our floodgate sites may indicate that floodgates impede Chinook salmon access to some gated tidal creeks. Given that there are approximately 500 floodgates in the lower Fraser area (Thomson et al. 1999), these structures may have large cumulative effects. Considering floodgates are highly concentrated specifically in the lower Fraser, they may have contributed to diminishing the nursery capacity for juvenile Fraser salmon.

Floodgate presence appeared to have no effect on threespine stickleback abundance; however, floodgates were associated with reduced abundance of three other common native fish species in our system. Stickleback exist in freshwater resident and anadromous forms in our system; therefore, decreases in abundance of anadromous forms may be compensated by increases in the resident population, which are known to be adaptable to a broad range of habitats (Nosil and Reimchen 2005). Conversely, floodgate presence was associated with dramatic decreases in prickly sculpin, which are typically present in coastal streams of the Pacific Northwest but are limited by small barriers, including culverts (Favaro et al. 2014) and fish ladders that are passable by salmon and trout (LeMoine and Bodensteiner 2014). Prickly sculpin adults spawn in rivers and streams, and larvae drift downstream to a lake, estuary, or other lentic habitat to rear before moving back up as 1+-year-old fish (Krejsa 1967); floodgates may prevent this upstream migration.

Floodgate presence was also associated with decreased abundance of northern pikeminnow and peamouth chub, the primary native minnow (cyprinid) species we studied. While there is little information regarding the effects of barriers on northern pikeminnow and peamouth chub, Winston et al. (1991) described the upstream extirpation of four minnow species related to construction of a mainstem dam, and Porto et al. (1999) found reduced abundances of seven species of stream fishes upstream of low-head dams relative to reference sites. Our results further demonstrate that small-scale barriers can also influence native stream fish communities. How floodgates affect the species we studied may be related to reproductive strategy, for example, Platania and Altenbach (1998) found that interactions between dam-related flow modifications and downstream transport of eggs and larvae led to declines in seven minnow species they studied. Northern pikeminnow spawn in mainstem and tributary habitats in the Columbia River system, and juveniles are known to rear in shallow low-velocity areas (Gadomski et al. 2001). In our system, floodgates may prevent local migrations and interfere with access to different habitats across life stages, resulting in effects similar to other types of barriers such as dams.

We found floodgate sites to be a hotspot for non-native fish species, including pumpkinseed, brown bullhead, and common carp, all of which are considered to be invasive. Interestingly,

although these species have very different life history traits, they were all similarly in greater abundance at floodgate sites, possibly benefitting from decreased competition with native species. Our results are consistent with a recently growing body of literature associating invasive species' abundance with river impoundments (Johnson et al 2008; Clavero et al. 2015). When river levels are high, floodgates remain closed, creating small impoundments that can remain stagnant for days or weeks until pumps are activated or river levels fall. Chu et al. (2015) found increased numbers of low-head dams to be associated with increased non-native abundances, and our data demonstrate similar patterns. Pumpkinseed, the most common invader in our study sites, are found in high abundances downstream of dams, indicating they may gain an advantage in highly altered flow regimes (Clavero et al. 2015). Common carp, which are part of the minnow family, appear to be positively associated with floodgate presence despite the negative association with native minnow species. Further research into the mechanisms by which small barriers differentially affect fish species would help to illuminate why invasive species appear to be benefitting. While these invasive species were introduced to the lower Fraser River long ago (Dextrase and Mandrak 2006), floodgates may support source populations of these invasive species, facilitating their spread into nearby areas, enabled by dispersal through the periodic barriers that floodgates represent.

While our results demonstrate that floodgates are associated with altered fish communities, we acknowledge that other differences among our sites may have contributed to these effects and that the spatial extents of these effects are unclear. Floodgate presence is likely nonrandom and associated with local history, topography, land use, and the comparative cost of choosing to build dikes along the lowest reaches. Furthermore, our reference sites were similar in size and gradient to the floodgate sites, the main difference being they were typically isolated from their floodplain by parallel dikes. Another challenge is that floodgate sites unavoidably differ in the number and construction of flap gates, as well as the height at which they are installed, inevitably leading to differences in the timing, duration, and magnitude of flap gate opening versus closure. Although we observed dramatic differences in fish communities in the areas directly upstream of the floodgates we studied, the spatial extent of these effects remains unclear; ongoing research will examine fish communities further upstream and downstream of floodgates to provide further understanding of the cumulative effects of these barriers. Overall, while differences between individual sites may result in some variability, we saw a similar pattern across the floodgate sites we studied, indicating our results generally represent the effect of floodgates on lower Fraser tributaries.

Although our study design prevented isolation of the precise mechanisms by which floodgates are affecting fish communities, probable mechanisms include changes in hydrologic connectivity and habitat quality. Floodgates may directly prevent passage, reducing access to habitats important for survival, growth, or reproduction for both native and non-native species. In snowmelt-driven systems such as the Fraser River, high mainstem levels during spring freshet may prevent gates from opening for long periods (Thomson et al. 1999). Floodgates have been shown to delay migration of salmonids (Wright et al. 2014), and floodgate opening during low tide cycles depends on upstream hydraulic head differential, which may create high velocity barriers for less mobile species such as sculpin. Floodgates may also impact fish communities indirectly by altering habitat through impounding water (Johnston et al. 2005), leading to oxygen depletion (Gordon et al. 2015). Hypoxia alters habitat quality for fishes and can drive fish kills (Richardson 1981). Reduced oxygen concentrations have also been shown to result in avoidance behaviour in juvenile salmon and other fish species (Whitmore et al. 1960) and therefore may act as a chemical barrier to fish passage. Respiration rates necessary to deplete oxygen concentrations are likely influenced

by high nutrient concentrations from agricultural runoff, as fertilizer and manure applications in our study areas typically exceed soil needs (Hall and Schreier 1996). Non-native species may benefit from reduced competition because of reduced abundance of native species in floodgate sites or from highly disturbed hydrology and habitat alteration (Moyle and Light 1996). Although, we did not determine the mechanisms by which floodgates impacted the fish species we studied, it seems likely they affect different species in different ways related to individual species traits (Poff 1997).

Our results demonstrate that the effects of small-scale flood control barriers such as floodgates, combined with their ubiquity in coastal river systems around the world, may be an important yet relatively unconsidered contributor to cumulative habitat alteration for native fishes. Our data indicate that flood control trades off against local abundance of salmon and is associated with shifts in freshwater fish community structure in favour of non-native species. Flood risk is predicted to increase as a result of climate change and sea-level rise (Arnell and Gosling 2016), which will undoubtedly lead to an increase in the use of flood protection structures in coastal aquatic systems worldwide. Sea-level rise will also impact the function of existing structures, requiring their modification or replacement to continue to protect against flooding (Walsh and Miskewitz 2013). This need to invest in infrastructure represents an opportunity to design future flood control structures that are friendlier to native fish. As restoring connectivity between otherwise quality habitats is the most cost-effective means for watershed restoration (Roni et al. 2002), floodgates may represent an efficient opportunity to restore coastal habitats for anadromous and resident species. Just as dam operations are modified to mimic natural flow regimes (Olden and Naiman 2010), resulting in relative increases in native fishes and decreases in non-natives (Propst and Gido 2004), a similar approach could guide the management and re-engineering of small-scale barriers in coastal systems.

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Appendix A

Table A1. Mean water chemistry measurements with standard deviations for each site type from each sampling month.

Month	Type	Temperature (°C)	Dissolved oxygen (mg·L ⁻¹)	Salinity (ppt)	Conductivity (mS·cm ⁻¹)
April	Reference	10.3 (±2.0)	11.69 (±0.79)	0.042 (±0.026)	0.084 (±0.053)
	Floodgate	9.8 (±1.0)	8.48 (±1.76)	0.064 (±0.026)	0.135 (±0.056)
May	Reference	14.4 (±0.6)	8.34 (±2.63)	0.046 (±0.029)	0.100 (±0.061)
	Floodgate	16.7 (±3.3)	9.25 (±5.10)	0.092 (±0.047)	0.194 (±0.098)
June	Reference	15.2 (±0.9)	7.95 (±1.36)	0.054 (±0.033)	0.113 (±0.066)
	Floodgate	17.0 (±0.9)	7.70 (±2.94)	0.122 (±0.053)	0.263 (±0.115)
July	Reference	17.6 (±2.1)	7.73 (±1.08)	0.056 (±0.038)	0.123 (±0.081)
	Floodgate	18.7 (±1.8)	3.91 (±1.82)	0.122 (±0.051)	0.257 (±0.109)
August	Reference	18.2 (±4.4)	7.88 (±1.38)	0.062 (±0.033)	0.133 (±0.067)
	Floodgate	18.8 (±2.1)	1.68 (±1.33)	0.120 (±0.060)	0.251 (±0.124)

Note: Measurements were taken just upstream of the floodgates or at equivalent locations at reference sites, just below water surface at noon (1200 h) plus or minus 30 min on each sampling occasion.

Table A2. Total number of each species of fish captured by type of site.

Species	Floodgate	Reference
Brown bullhead	15	1
Black crappie	1	2
Bull trout	0	1
Common carp	32	4
Chinook salmon	77	172
Chum salmon	102	152
Coho salmon	13	152
Cutthroat trout	1	1
Juvenile sunfish	391	26
Pacific lamprey	0	3
Largemouth bass	52	70
Largescale sucker	0	117
Unidentified minnow	4	95
Peamouth chub	33	207
Northern pikeminnow	55	608
Pink salmon	0	2
Prickly sculpin	9	335
Pumpkinseed	61	77
Rainbow trout	0	47
Redside shiner	0	44
Sockeye salmon	0	4
Threespine stickleback	14 500	13 291
Weather loach	2	0

Note: This represents the sum of three seine hauls and six minnow traps over five sampling occasions at five floodgate and five reference sites.