RESEARCH ARTICLE

Equivocal associations between small-scale shoreline restoration and subtidal fishes in an urban estuary

Tessa B. Francis[1,2] 🔘, Genoa H. Sullaway[3], Blake E. Feist[4], Andrew O. Shelton[4], Emily Chui[5], Caroline Daley[6], Kinsey E. Frick[7], Nick Tolimieri[4], Gregory D. Williams[8], Jameal F. Samhouri[4]

Restoration of degraded coastal and estuarine habitats owing to human activities is a major global concern. In Puget Sound, Washington, U.S.A., removal of hard armor from beaches and intertidal zones has become a priority for state and local agencies. However, the effectiveness of these shoreline restoration programs for subtidal habitats and fish is unknown. We surveyed six restoration sites in Puget Sound over 2 years to evaluate associations between shoreline restoration and subtidal fish abundance. We measured the abundance of juvenile salmonids and forage fishes along armored, restored, and reference shorelines. Bayesian generalized linear models showed limited support for associations between shoreline restoration and these fishes in the 3–7 years since armor removal. Pacific herring were more abundant at reference shorelines; the shoreline effect for surf smelt varied by survey site. Shoreline restoration was not an important predictor of salmonid abundance; the best models for Chinook and chum salmon included predictors for survey site and eelgrass, respectively. The retention of survey site in several species' top models reveals the influence of the broader landscape context. We also found seasonal variation in abundance for chum salmon and surf smelt. Our results suggest that juvenile forage fish and salmonids in estuaries likely have unique responses to shoreline features, and that the positive effects of armor removal either do not extend into subtidal areas or are not detectable at local scales. To be most effective, coastal restoration programs should consider broader landscape patterns as well as species-specific habitat needs when prioritizing investments.

Key words: coastal restoration, forage fish, habitat, marine infrastructure, nearshore, salmon, shoreline armor, urbanization

Implications for Practice

- Effectiveness monitoring over the short- and long-term is an essential and oft-neglected component of coastal restoration that can inform future restoration efforts.
- Efforts to support recovery and conservation of salmonids and forage fish via small-scale restoration of beaches may not directly affect juvenile fish using subtidal habitats close to shore.
- To be more effective, coastal restoration planning should incorporate landscape-scale features and mechanistic understanding of relationships between habitats and species, and restoration monitoring should occur over longer time scales (>6 years) to evaluate impacts on nearshore habitats and fish communities.

Introduction

Human activities affect coastal ecosystems more than any other ecosystems on the planet (Halpern et al. 2008; Cloern et al. 2016). In the United States, 30–50% of people live in coastal communities (Crossett et al. 2004; Feist & Levin 2016), and urban expansion into undeveloped portions of marine-adjacent watersheds influences biodiversity and ecosystem function (Bulleri et al. 2005). Coastal development can impair the ability of adjacent marine ecosystems to provide services people want and need, including defense of people and property from storms and impacts associated with climate change (Waycott et al. 2009; Arkema et al. 2013; Todd et al. 2019).

Efforts to restore coastal ecosystems and regain lost ecosystem functions and services are widespread in North America, with an increasing focus on "living shoreline" programs (Bilkovic et al. 2016). Coastal and estuarine restoration programs that reduce human impacts on ecosystems do lead to recovery of populations and ecosystems (Lotze et al. 2011; Creighton et al. 2015; Schulz et al. 2020). Yet, a quantitative understanding of how restoration efforts can mitigate the impacts of coastal development on ecosystem structure and function is only recently nascent (Boesch 2006), as are methods to monitor the effectiveness of restoration projects (Gittman et al. 2016; Toft et al. 2021).

Hard shoreline structures, such as bulkheads, seawalls, and breakwaters, collectively referred to here as "armor," are ubiquitous along coastlines, often intended to prevent coastal erosion and flooding. Concerns about coastal protection against sea level rise and coastal flooding associated with climate change are increasing, and the extent of shoreline hardening is projected to continue to expand (Bugnot et al. 2021), despite unintended and major economic consequences (Hummel et al. 2021). By replacing natural shoreline features, including riparian vegetation, armor simplifies the otherwise complex habitat that forms the boundary between marine and terrestrial zones (Lawrence et al. 2021). Artificial marine structures like armor, including those that aim to provide habitat complexity, have strong and well-documented impacts on diversity, benthic and intertidal habitats and communities, and habitat connectivity (Bulleri et al. 2005; Heery et al. 2017; Porter et al. 2018). Through reduction of habitat complexity, armor can affect both nearshore (here, inclusive of supratidal, intertidal, and shallow subtidal zones) and riparian habitat structure and function, with impacts on species and food webs. For example, armor alters sediment dynamics and changes the physical structure and composition of the habitat (Johannessen & MacLennan 2007; Ruggiero 2009; Fresh et al. 2011).

When structures are placed on beaches or in intertidal areas, they reduce the amount of riparian vegetation and diminish the transfer of organic and inorganic debris to the nearshore from terrestrial systems and from offshore areas (Heerhartz et al. 2014; Dethier et al. 2016). Sediments from upland terrestrial and riparian ecosystems can be impounded by armor, leading to changed sediment characteristics and a deficit in supply to beaches (Pilkey & Wright 1988; Fletcher et al. 1997). Reduced fluxes of these materials can directly and indirectly affect the amount of nearshore habitat available, as well as use of beaches and intertidal zones by sessile invertebrates and larger, more mobile species including crabs, fishes, and birds (Chapman 2003; Dugan et al. 2008; Munsch et al. 2017).

In contrast to the suite of findings linking armor to beach and intertidal ecosystem characteristics, relatively fewer studies have examined the effects of armor on adjacent nearshore subtidal zones. However, a full accounting of armor impacts should extend to subtidal habitats, at minimum to capture shifts in nearshore community composition and species' abundances in subtidal zones at low tide, especially by highly mobile species that may move into the intertidal zone during high tide and retreat to the subtidal zone at low tide. The impacts of armor and

potential benefits of armor removal in subtidal habitats are of particular importance because these areas are critical nurseries for economically, ecologically, and socio-culturally valuable species (Beck et al. 2001). Armor can reduce nursery habitat quantity or quality and homogenize or decrease connectivity between existing nursery habitats, effectively diminishing overall ecosystem function. Armor may affect features influential in determining nursery habitat value, including physical aspects such as sediment composition, bathymetric profile, wave energy, water chemistry (e.g. salinity, oxygen, etc.), prey quality and quantity, and the ability to provide refuge from predation risk (Krueger et al. 2010; Parks et al. 2013). A first step in assessing the impacts of armor on nursery habitat value is to evaluate the abundance, demographics, and movement of juvenile fishes in subtidal areas adjacent to armored and unarmored shorelines, and in relation to restoration experiments, such as armor removal.

While there are reasons to suspect that impacts may not be consistent across beach, intertidal, and subtidal zones (Seitz et al. 2006; Fresh et al. 2011), it is reasonable to expect that the effects of armor extend some distance beyond the narrow intertidal zone before attenuating farther offshore, because of links between riparian, beach, intertidal, and subtidal marine habitats (Ãlvarez-Romero et al. 2011). For example, geomorphic processes, such as sediment supply and transport, extend into subtidal zones (Ruggiero 2009). Because of the complex interplay between eelgrass and sediments (Madsen et al. 2001), we hypothesize that armor will negatively impact critical subtidal eelgrass habitat available as refuge for fishes and/or habitat for their prey. These effects lead to the hypothesis that fish abundance may be reduced at armored sites. Armor may also impact food web dynamics: installation of shoreline armor is associated with decreased terrestrial and epibenthic prey in the diets of salmonids in intertidal habitats (Toft et al. 2007; Duffy et al. 2010), which we hypothesize may also result in reduced fish abundance at armored sites. Increased wave action at armored sites may alter the delivery and retention of aquatic prey, as well as use of these areas by smaller-bodies species. If armor removal results in unimpeded geomorphic processes, positive effects on eelgrass, and an increased supply of prey relative to armored sites, and if foraging and growth opportunities are important determinants of variation in fish abundance, we predict that fish abundance may be elevated at restored and reference shorelines relative to armored shorelines. The impact of armor, and the effectiveness of armor removal, in subtidal areas is an important gap to close in order to answer calls for more strategic investment of resources devoted to coastal restoration (Sutton-Grier et al. 2018).

In Puget Sound, Washington, an urban fjord-like estuary, 29% of the coastline is armored with seawalls, bulkheads, and other artificial structures (Fig. 1; Coastal Geologic Services 2017), and major efforts are underway to reduce this number. In recent years, a suite of investigations has advanced our understanding about the specific impacts of armor on the Puget Sound ecosystem (see Dethier et al. 2016 for a summary). Far less is known about impacts on subtidal ecosystem function and use by nearshore species (Francis 2018; but see Heerhartz & Toft 2015; Munsch et al. 2017), many of which are of cultural,
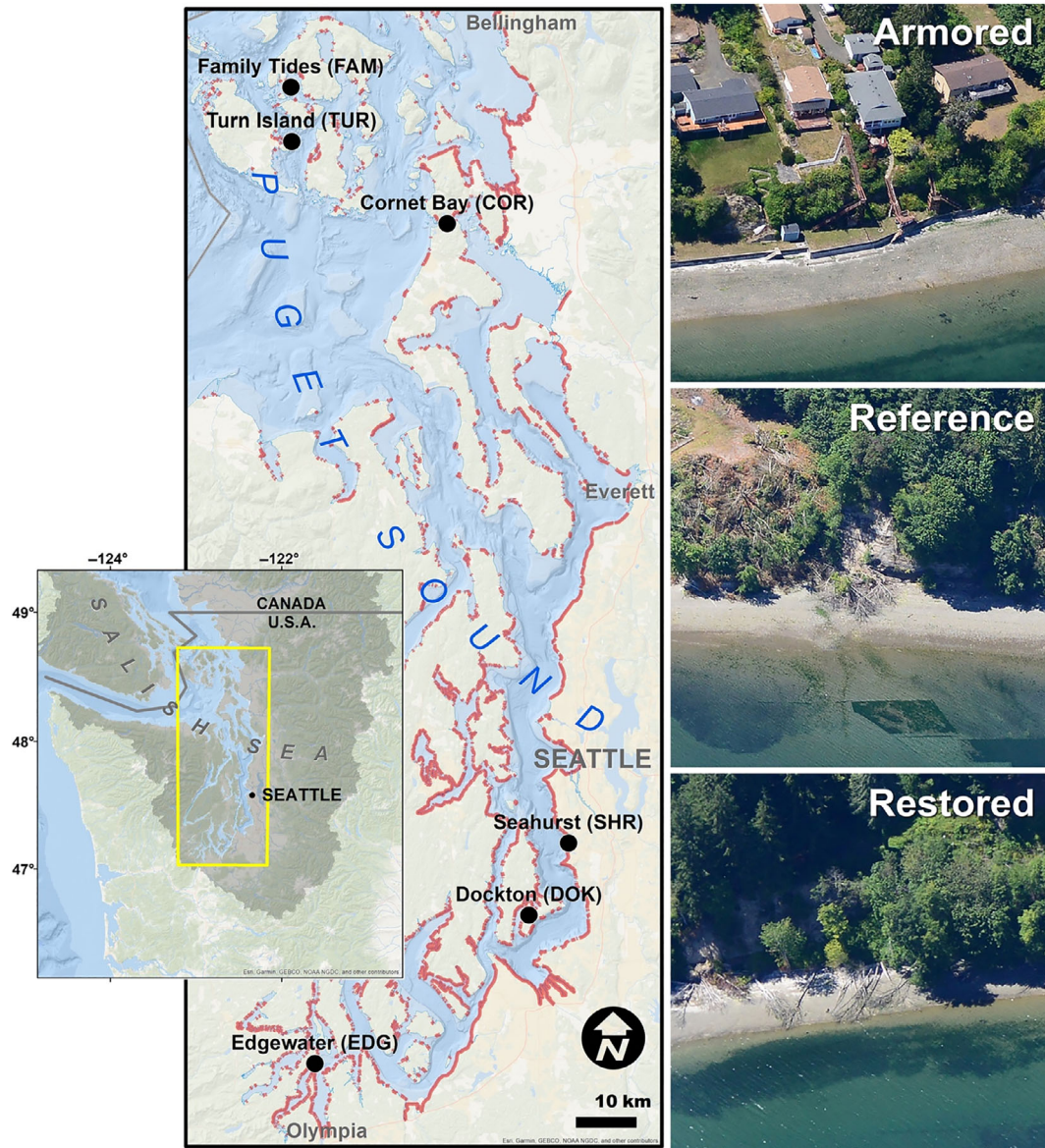
Figure 1. Survey site map with extent of shoreline armoring in Puget Sound (WSPSP 2019) and sample photos of armored (top), reference (middle), and restored (bottom) shorelines from one site, Edgewater (WADOE 2018). The armored photo shows a bulkheaded home. The restored photo shows a portion of the restored shoreline where 241 m of armoring was removed from the base of a bluff.

ecological, and economic importance in the ecosystem and use nearshore subtidal habitats during early life stages, including Pacific salmonids (Chinook *Oncorhynchus tshawytscha*, coho *O. kisutch*, chum *O. keta*, and pink *O. gorbuscha*) and forage fishes (especially the three most abundant species, Pacific herring *Clupea pallasii*, surf smelt *Hypomesus pretiosus*, and Pacific sand lance *Ammodytes hexapterus*).

Because of the potential effects of armor on subtidal nursery habitat function, here we evaluate whether the abundance and distribution of nearshore fishes are affected by armor, and whether those effects are in turn reversed via restoration. We compare nearshore fish abundance in subtidal zones at six Puget Sound sites, each of which consists of adjacent armored,

restored, and reference unarmored stretches of shoreline. We focus our analysis on four species of fish that are of particular conservation concern in the region: Chinook and chum salmon, Pacific herring, and surf smelt. We also consider the effects of other factors that may influence fish abundance and distribution outside of shoreline structure. Specifically, we consider the influence of sampling site (geographic location), to account for broad spatial patterns of distribution associated with proximity to natal rearing habitats (spawning rivers for salmonids, spawning beaches for forage fishes). We consider the presence of eelgrass as a potential covariate, because of its role in providing refugia. Last, because of seasonal migration patterns—estuary-to-ocean for salmonids, and onshore-offshore ontogenetic shifts

for forage fishes—we consider the role of sampling period on abundance patterns. Because habitat use varies among our four focal species, and therefore they may not have uniform responses to shoreline armor and restoration, we evaluate the influence of these factors separately for each species. We compare the importance of shoreline structure against these other predictor variables to fill a gap common to many restoration efforts, namely the evaluation of the effectiveness of restoration efforts in achieving their aims (Cooke et al. 2018).

Methods

Site Description

The Puget Sound, in Washington State, is a fjord estuary, and the largest estuary by volume in the continental United States (Rice et al. 2015). The Puget Sound is home to 253 species of fish (Pietsch & Orr 2019), including eight species of Pacific salmon (*Onchorynchus* spp.) and three dominant forage fish species: Pacific herring, surf smelt, and Pacific sandlance. The present analyses focus on the relationship between shoreline structure and use of nearshore habitats by two salmon species, Chinook and chum, the juveniles of which commonly occur in Puget Sound nearshore habitats, and two forage fish species, Pacific herring and surf smelt. All of these species are important in the Puget Sound food web and of major interest to state management agencies (Harvey et al. 2010; Puget Sound Partnerships 2021).

We surveyed fish abundance and size at six sites in Puget Sound, monthly between June and September 2018 and April and September 2019 (Table 1; Fig. 1). Each site consisted of three stretches of shoreline having different structure: a restored shoreline, where armor had been removed; an armored shoreline, where armor was in place on the shoreline; and an unarmored reference shoreline, where no armor or physical structure has been in place (Fig. 1). Each shoreline stretch was roughly 30 m in length. All shoreline stretches within a site were in close enough proximity to reduce the potential influence of different tides and material fluxes on fish communities. All shoreline stretches we sampled were residential apart from two, which were a summer camp (Four Winds—armored) and a state park (Turn Island—restored). The time since restoration varied by site, ranging from 3 to 7 years (Table 1). The time since armor was installed on each shoreline is unknown. The nearshore habitat at each site ranged from rocky to sandy/muddy, and the morphometry ranged from steep to relatively flat. To evaluate the potential influence of eelgrass

(*Zostera* spp.) on fish presence, half of our survey sites had eelgrass habitat, and half did not have eelgrass. Eelgrass presence/absence at a survey site was determined based on the Department of Natural Resources Submerged Vegetation Monitoring Program (https://fortress.wa.gov/dnr/adminsa/gisdata/datadownload/SVMP_distribution.zip).

Fish Abundance Surveys

At each site, we surveyed fish abundance using a lampara net, which is a modified purse seine. The net measured 37 m in length on the float (top) line, 32 m in length on the lead (bottom) line, and a maximum of 4.6 m in depth. Mesh size of the net ranged from 48 (on the lateral wings) to 6 mm (in the central bunt). We surveyed at three distances from shore: at a depth of -1 m re. mean lower low water (MLLW), -3 m re. MLLW, and at 50 m offshore from the -3-m isobath. The maximum water depth across all sites was -15.6 m re. MLLW. Except where impossible owing to tides, surveys started at the most offshore station and ended at the shallowest station. Surveys were conducted when tides were as close to $+1.5$ m re. MLLW as possible (not lower), avoiding negative tides. Individual fish collected in lampara nets were enumerated and identified to species, or to the highest resolution possible. All fish were returned to the water after capture.

We summarized the median abundance (and 2.5, 25, 75, and 97.5 percentiles) of each of the four focal species at each study site across all surveys over the two-year study period. We also report the lampara net data in terms of both occurrence (number of sites where a species was observed within a sampling date) and abundance (conditional on presence and standardized by the number of sites where a species was observed during that year and month). Standardized conditional abundance measures the number of fish observed per site in a month/year pair, averaged across all sites where that species was observed at that time.

Model Fitting, Selection, and Diagnostics

We estimated the influence of shoreline structure on nearshore fish abundance by fitting Bayesian generalized linear models (GLMs) with a negative binomial distribution and a log link function (to account for overdispersion and a high abundance of zeros common in ecological count data) to counts of the four focal species, Pacific herring, surf smelt, and Chinook and chum salmon. The basic concept behind a Bayesian approach is that it

Table 1. Nearshore fish survey sites.

Site Name (Abbreviation)	North/Central Puget Sound	Eelgrass/ No Eelgrass	Restoration Year	Maximum Survey Depth, m (re. MLLW)	Lat/Lon
Family Tides (FAM)	North	No eelgrass	2015	-8.5	48.615431, -122.980219
Turn Island (TUR)	North	Eelgrass	2015	-10.8	48.530866, -122.973119
Cornet Bay (COR)	North	Eelgrass	2012	-8.4	48.399871, -122.624612
Seahurst (SHR)	Central	Eelgrass	2014	-15.6	47.479325, -122.362423
Dockton (DOK)	Central	No eelgrass	2013	-6.9	47.372417, -122.452705
Edgewater (EDG)	Central	No eelgrass	2016	-11.1	47.152287, -122.928871

assumes the data are fixed, but the parameters are random; that is, they are assigned a distribution. The question we ask in a Bayesian framework is, given the data, how likely is our prediction/model? The posterior probability distributions describe that likelihood. In contrast, in frequentist approaches, we assume the data are random and the parameters are fixed, and the question becomes, how likely are the data, given our prediction/model? In this case, we are interested in the probability of shoreline effects on fish abundance, not the probability of a given fish abundance, assuming shoreline effects. This framing lends itself to a Bayesian approach (Gelman et al. 2014; Bayesian Statistics and Modeling 2021).

For each species, we estimated the fixed effects of shoreline type (armored, reference, restored), survey site (the six survey sites), and vegetation (presence/absence of eelgrass) on fish abundance (Table 2). Abundance was calculated as a sum of observed fish across all distances sampled for each shoreline type, survey site, and month/year pair. Restoration age (ranging between 3 and 7 years across study sites) was not correlated with abundance either across (adjusted $r^2 = 0.01$, $F_{[1,112]} = 2.2$, $p = 0.14$) or within (adjusted $r^2 = 0.03$, $F_{[4,109]} = 1.9$, $p = 0.12$) species; and therefore, this variable was not included in the modeling exercise.

In addition, because forage fish and Pacific salmonids are known to have seasonal patterns in abundance and distribution, we evaluated the effect of sampling period on the abundance of all target species by first assigning each survey to one of four periods: June 2018, July–September 2018, April–June 2019, and July–September 2019. We then estimated a model using only period as a fixed effect. We model sampling period as a fixed effect because sampling period represents season, and we hypothesize that the nearshore abundance of our focal species varies by season. There are a variety of biological justifications for this, including ontogenetic migration patterns: from estuary to ocean for salmon, and from onshore to offshore for herring and surf smelt, both of which are pelagic species commonly found in offshore deeper waters as older adults. In addition, including sampling period as a fixed effect, versus a random effect, avoids "shrinkage" toward

the mean, that is, pulling estimates for each sampling period toward the across-sampling-period mean, which can mask interesting dynamics in fish abundance associated with season. In models with only a predictor for sampling period, the 89% credible intervals based on Markov chain Monte Carlo (MCMC) draws crossed zero for Chinook salmon and herring, suggesting that there is not a strong seasonal signal in these data (Fig. S1). We therefore included a fixed effect term for sampling period only in models for chum salmon and surf smelt. We recognize that these data and this analytical approach do not allow us to attribute causation to any of the patterns we observed, but instead offer insight into factors that are correlated with variation in fish abundance.

For each of our target species, we assumed that at each survey we observe a count, Y, that follows a negative binomial distribution, as

$$Y_{hse} \sim \text{NegBinomial}(\mu_{hse}, \theta) \tag{1}$$

where subscripts represent the influence of covariates shoreline structure (h), site (s), and the presence of eelgrass (e), μ_{hse} is the mean of the negative binomial, and θ is the overdispersion parameter used to estimate the mean and variance separately. We estimate the mean of the negative binomial as a function of the covariates; for example, in a model including the effects of shoreline, site and eelgrass, the mean is estimated as:

$$\log(\mu_{hse}) = \alpha + \beta_{\text{shoreline}} + \beta_{\text{site}} + \beta_{\text{eelgrass}} \tag{2}$$

with variance

$$\text{Var}(Y_{hse}) = \mu_{hse} + \mu_{hse}^2 / \theta \tag{3}$$

We used a weight-of-evidence approach to compare among the 12 models and identify which covariates had the most influence

Table 2. Candidate models tested for all nearshore fish species, with Bayesian model weights. Models in bold were selected as the best model for the species listed, based on Bayesian model weights. For chum salmon and surf smelt, all models included Period as an additional predictor.

Model	Predictors	Chinook	Chum	Herring	Smelt
		Bayesian Stacked Weights			
Model 1	Period	0	0	0	0.04
Model 2	Site	**0.51**	0.19	0	0
Model 3	Eelgrass	0.23	**0.23**	0	0
Model 4	Shoreline Structure	0	0.11	0.14	0.06
Model 5	Eelgrass + Shoreline Structure	0	0.07	0	0
Model 6	Site + Eelgrass	0	0	0	0
Model 7	Site + Shoreline Structure	0.05	0	0	0
Model 8	Site + Eelgrass + Shoreline Structure	0	0.19	**0.55**	0
Model 9	Eelgrass + Shoreline Structure + Eelgrass × Shoreline Structure	0	0	0	0.01
Model 10	Site + Shoreline Structure + Site × Shoreline Structure	0.22	0	0.18	0.01
Model 11	Site + Eelgrass + Shoreline Structure + Eelgrass × Shoreline Structure	0	0	0.14	0
Model 12	Site + Eelgrass + Shoreline Structure + Site × Shoreline Structure	0	0.04	0	**0.75**
Model 13	Site + Eelgrass + Shoreline Structure + Eelgrass × Shoreline Structure + Site × Shoreline Structure	0	0	0	0

on fish abundance. To determine the amount of support for each model, we used Bayesian model weights and specifically the stacking of predictive distributions (Yao et al. 2018). The advantage of Bayesian stacked weights is that they allow results to be presented in terms of the weight of evidence for including predictor variables, evaluating over all the candidate models,
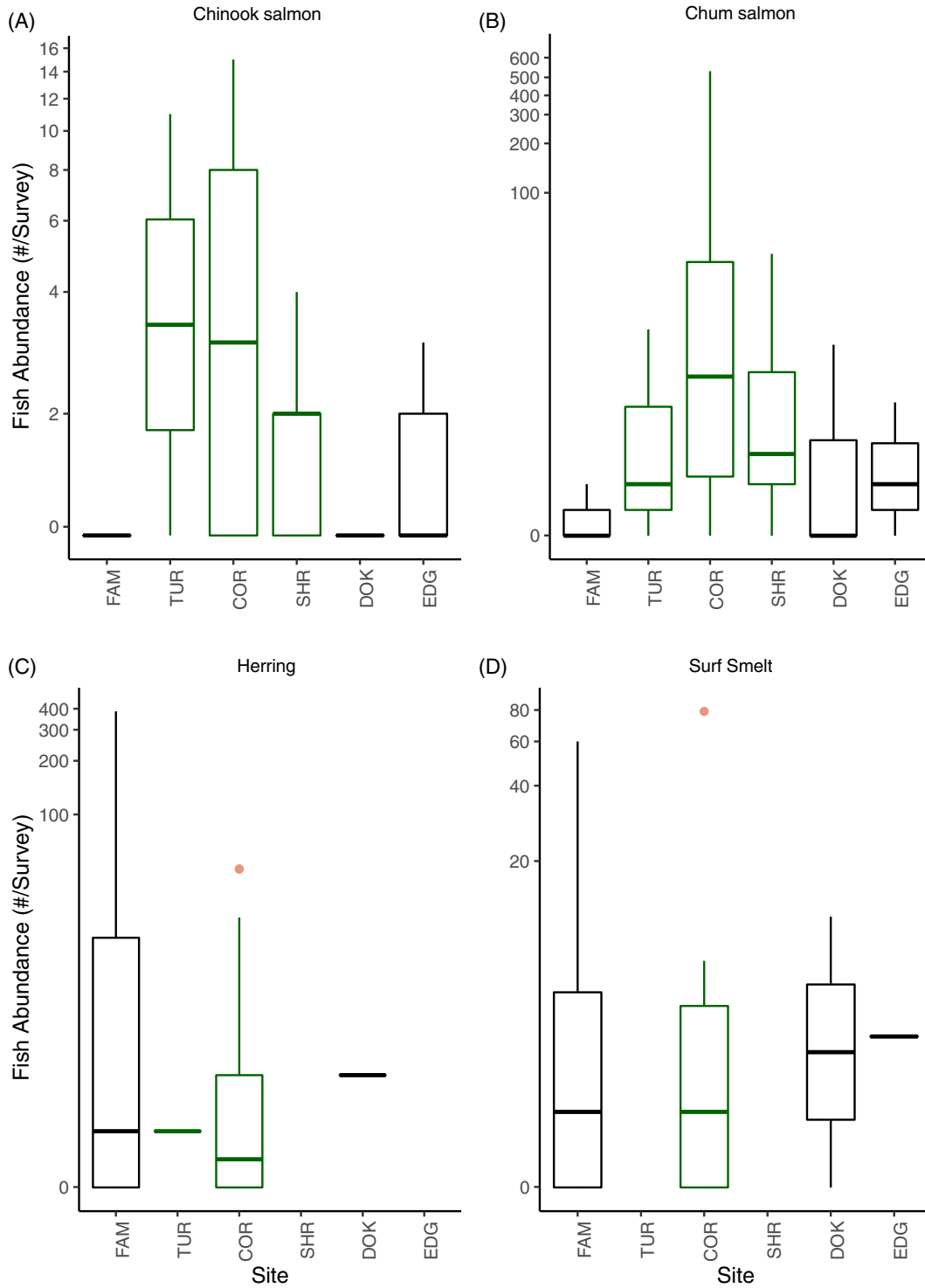

Figure 2. Observed abundance of nearshore (A) Chinook salmon, (B) chum salmon, (C) Pacific herring, and (D) surf smelt at six Puget Sound shorelines, where each point represents catch per lampara survey. To facilitate interpretation and appropriately scale the outliers, *y*-axis values are plotted on a natural log scale, but we transform the labels to integers. Solid symbols represent observations. Boxes incorporate the 25th–75th percentiles of abundance with lines for the 50th percentile. Upper and lower whiskers extend to 97.5 and 2.5 percentiles, respectively. Green boxes and points indicate sites with eelgrass.

which is analogous in many cases to information criteria approaches to model ranking. Stacked weights involves first calculating the predictive ability of each model based on leave-one-out (LOO) cross-validation (Vehtari et al. 2017), which provides an expected predictive probability density for each model. The LOO method returns a point estimate and a standard error of the estimate. The Bayesian weight approach maximizes the sum of expected probability densities for all competing models and standardizes the sum of weights to one so that the model weight, or degree of support for each model, is expressed as fraction of one. We opted to consider the model with the most weight as the best model for each species. For each best model, where 89% Bayesian credible intervals of the marginal posterior distributions for individual coefficients did not overlap zero, covariates were considered to have significant explanatory power.

We estimated Bayesian parameters using Stan (Carpenter et al. 2017) in R (R Core Team 2020), and the R package *rstanarm* (Goodrich et al. 2020), with default priors on each parameter (location of 0 and scale of 2.5) to aid in model convergence. Each model was run for four MCMC chains and 5,000 iterations, with a warmup of 3,000 iterations that was discarded. Leave-one-out and Bayesian model weight calculation procedures were conducted using the *loo* package in R (Vehtari et al. 2020).

We conducted several diagnostic procedures to evaluate model specification and fit to the data (Vehtari et al. 2017; Gabry et al. 2019). Traceplots showed convergence among MCMC chains and there were limited or no posterior dependencies among predictor variables based on MCMC draws. Pareto-smoothed importance sampling leave-one-out (PSIS-LOO) cross-validation showed that posterior distributions were not overly sensitive to individual observations. In addition, posterior distributions of overdispersion parameters, included in the Bayesian GLMs to account for extra variance in count data, were appropriately small and normally distributed. Simulated datasets from the posterior predictive distribution were used to estimate the number of zeros in the data, which were quite high (many lampara net catches = 0), and simulations matched observations well. Last, kernel density estimates for 1,000 simulated datasets drawn from the posterior predictive distributions were good fits to density estimates of observed counts. Additional diagnostic details are described in Supplement S1, R code for diagnostic procedures can be found in Supplement S2 (and at https://zenodo.org/record/5484907), and the original lampara net survey data are in Supplement S3.

Results

Across the 12 monthly surveys, we found strong spatial variation across survey sites in the abundance of our four target species (Chinook, chum salmon, Pacific herring, and surf smelt; Fig. 2). Occurrence and abundance of the four target species were not only patchy in space, but also in time, with some seasonal patterns (Fig. 3). For example, juvenile Chinook and chum salmon were mostly observed in the spring and early summer months, as expected based on seasonal migration patterns (Duffy et al. 2005). Chum salmon, herring, and smelt were occasionally observed in large schools, while Chinook salmon were not (Fig. 3A), and both salmon species were more commonly observed than the two forage species (Fig. 3B).

Factors Associated With Nearshore Fish Abundance

The most important factors influencing abundance of each species, based on Bayesian model weights, varied across the four
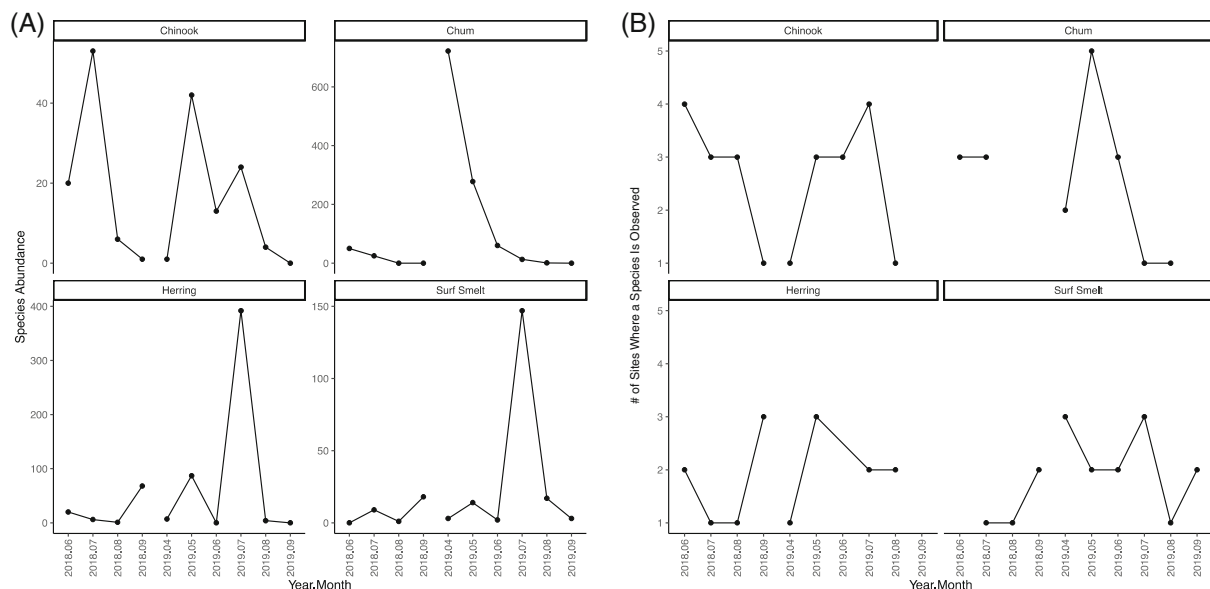

Figure 3. Time series of observed nearshore fish (A) abundance and (B) occurrence from lampara net surveys. Species abundance in panel A is the sum of individuals observed across all sites and distances from shore within a month/year pair, standardized by the number of sites where a species was observed during that year and month.

species (Tables 2 and S1). Variation in the abundance of forage fish species was associated with whether a shoreline was armored, restored, or reference, but the same was not true for salmonids.

For herring, the greatest model weight (55%) was associated with a model containing predictors for site, shoreline structure, and eelgrass (Fig. 4). Instead of detecting a positive effect of restored shorelines on herring abundance, we found
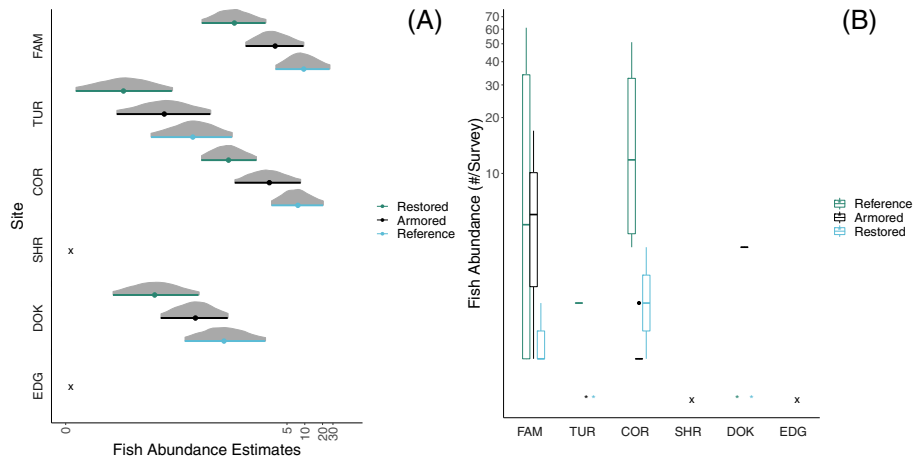

Figure 4. (A) Estimated effects of survey site and shoreline type on the abundance of herring in nearshore habitats. We plot the natural log posterior distribution of model estimates for fish abundance and transform the *y*-axis labels to integers to facilitate interpretation. Points are posterior estimate means, lines and gray density distributions represent an 89% high density interval (HDI) posterior distribution for model fits. "X" indicates a site where we did not observe any fish. (B) Observed herring abundance at each survey site and shoreline structure. Box and whisker plots show the median (inner horizontal line), 75th and 25th percentiles (upper and lower box hinges, respectively), and 1.5 times the inter-quartile range (whiskers) of the data.
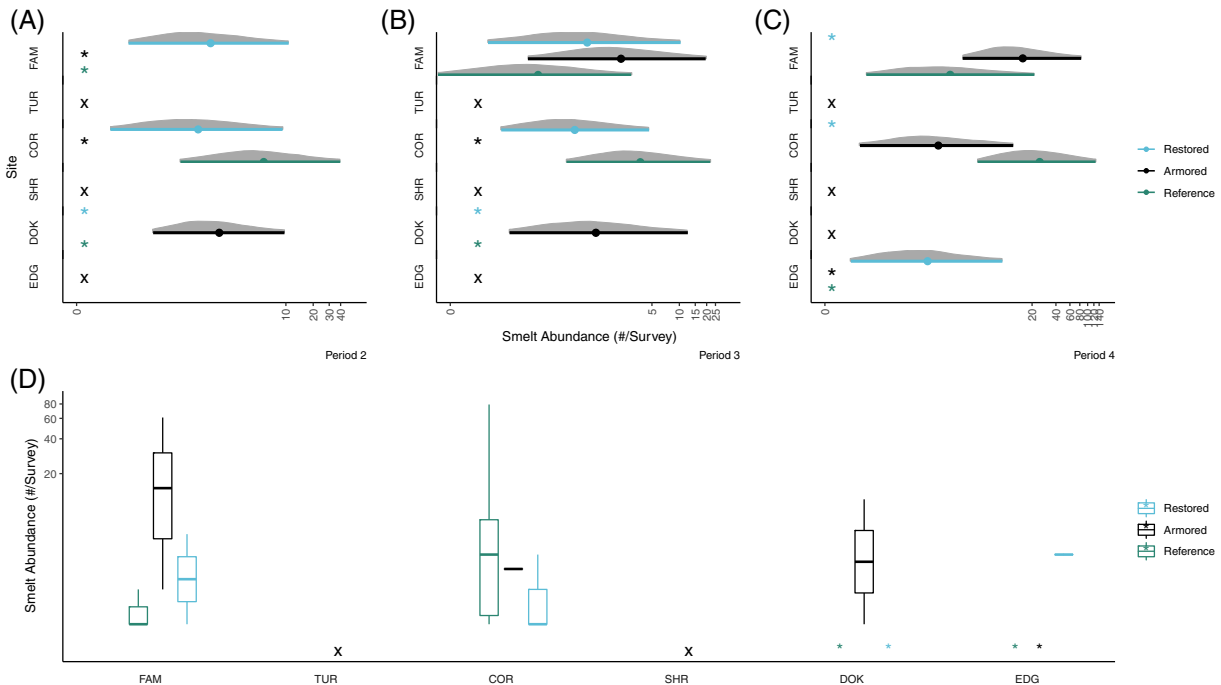

Figure 5. (A–C) Estimated effects of survey site and shoreline type on the abundance of surf smelt in nearshore habitats across sampling periods. We plot the natural log posterior distribution of model estimates for fish abundance and transform the *y*-axis labels to integers to facilitate interpretation. Points are posterior estimate means, lines and gray density distributions represent an 89% high density interval (HDI) posterior distribution for model fits. No smelt were observed in sampling period 1 (not shown). (D) Observed surf smelt abundance at each survey site and shoreline structure, for all periods combined. Box and whisker plots show the median (inner horizontal line), 75th and 25th percentiles (upper and lower box hinges, respectively), and 1.5 times the interquartile range (whiskers) of the data. "*" indicates a shoreline-type where we observed fewer than five fish, "X" indicates a site where we did not observe any fish.

that herring were least abundant along restored shorelines. Posterior mean estimates showed that reference sites had >4× greater abundance of herring than armored shorelines, and >14× more than restored sites. There was also geographic variation in herring abundance, with herring abundance at Family Tides 1.2× greater than the next most abundant site, Cornet Bay, and 20–78× greater than the other sites where herring were observed (Dockton and Turn Island). No herring were observed at either Edgewater or Seahurst. While the best

model for herring abundance included the effect of eelgrass, 89% credible intervals for the coefficient associated with eelgrass absence crossed zero.

The majority of model weight for smelt (75%) was associated with a model containing the same predictors as for herring, but with additional terms for period and the interaction between site and shoreline structure; that is, smelt abundance varied across sites, shoreline structures, and sampling periods, and the effect of shoreline structure on smelt abundance varied by site
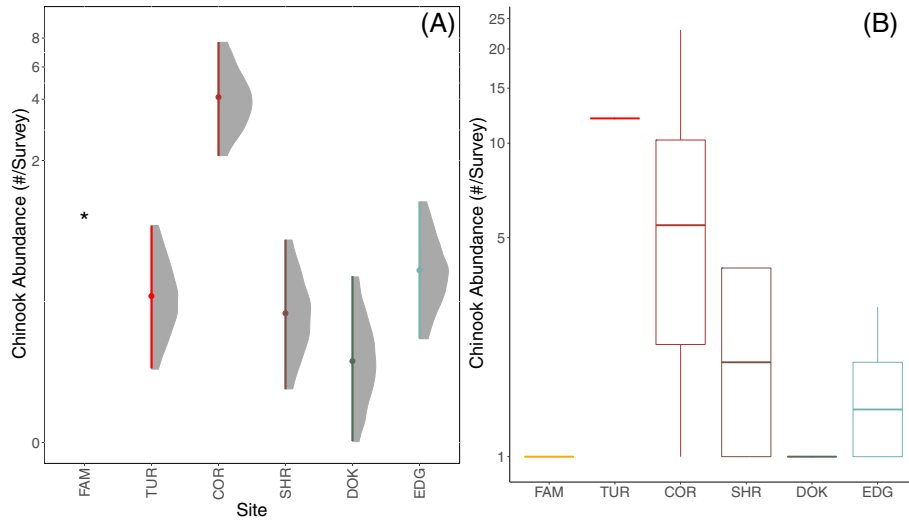

Figure 6. (A) Estimated effects of survey site on the abundance of Chinook salmon. We plot the natural log posterior distribution of model estimates for fish abundance and transform the *y*-axis labels to integers to facilitate interpretation. Points are posterior estimate means, lines and gray density distributions represent an 89% high density interval (HDI) posterior distribution for model fits. "*" indicates a site where we observed fewer than five fish. (B) Observed abundance of Chinook salmon at survey sites. Box and whisker plots show the median (inner horizontal line), 75th and 25th percentiles (upper and lower box hinges, respectively), and 1.5 times the interquartile range (whiskers) of the data.
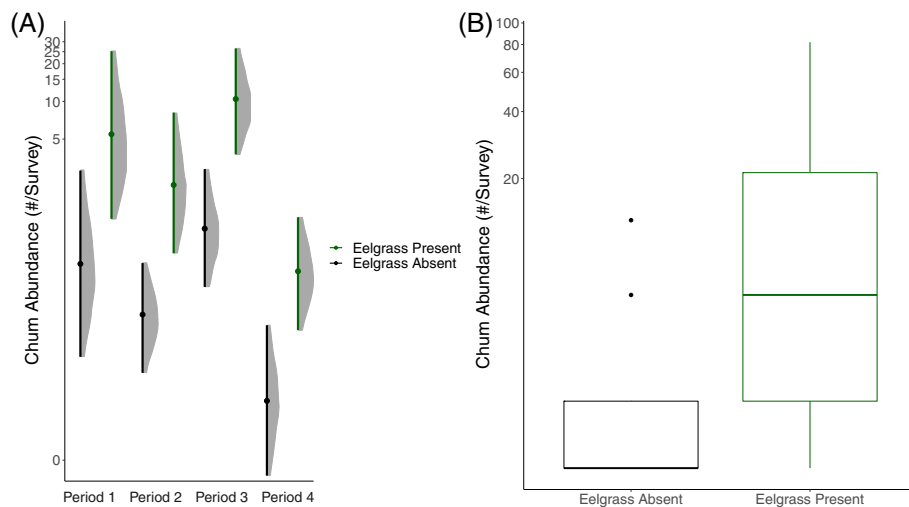

Figure 7. (A) Estimated effects of eelgrass presence and sampling period on the abundance of chum salmon in nearshore habitats. We plot the natural log posterior distribution of model estimates for fish abundance and transform the *y*-axis labels to integers to facilitate interpretation (note: scales on the *y*-axes are different). Points are posterior estimate means, lines and gray density distributions represent an 89% high density interval (HDI) posterior distribution for model fits. (B) Observed abundance of chum salmon at sites with and without eelgrass. Box and whisker plots show the median (inner horizontal line), 75th and 25th percentiles (upper and lower box hinges, respectively), and 1.5 times the interquartile range (whiskers) of the data. "*" indicates a site where we observed fewer than five fish.

(Fig. 5). The 89% credible intervals for many coefficients in the smelt model crossed zero, making it challenging to identify associations between smelt abundance and the predictors (Table S1). Site differences were largely associated with absence of smelt from two sites, Turn Island and Seahurst. At some sites, smelt were not found at all shoreline types: smelt were only observed at the armored shoreline at Dockton, and at the restored shoreline at Edgewater. At sites with more frequent smelt observations, the shoreline structure effects were different across sites. For example, the highest abundance of smelt observed at Family Tides was along the armored shoreline, but along the reference unarmored shoreline at Cornet Bay. As with the herring model, the smelt model included a negative effect of eelgrass absence; however, the credible intervals associated with that coefficient crossed zero, and smelt were only observed at one site with eelgrass, Cornet Bay. The period effect was largely associated with a greater abundance of smelt in period 4 (note the different *x*-axis scale in Fig. 5), and the absence of smelt in period 1.

Chinook salmon abundance was most influenced by survey site; the top model for Chinook salmon (51% of the model weight) included only site as a predictor (Fig. 6). Across all sites, the estimated Chinook salmon abundance was greatest at Cornet Bay, >7× greater than at the next-greatest site, Edgewater, and >150× greater than the lowest abundance site, Family Tides, based on median posteriors.

The model weight for chum salmon was distributed more evenly among multiple models (Table 2), but the most weight was associated with a model that included predictors for the presence of eelgrass and sampling period (23% of the model weight; Fig. 7). Sites with eelgrass had >10× higher abundance of chum salmon, compared to sites without eelgrass, based on posterior medians. Chum abundance varied by sampling period, but the effect of eelgrass was consistent across all periods. The greatest abundances of chum were observed during spring months (April–June), as compared to summer/fall months (July–September).

Discussion

Human activities have heavily modified coastal ecosystems, with effects spanning from individual species to entire habitats (Lotze et al. 2006). One of the primary influences along shorelines is the imposition of artificial structures, which have both direct and indirect impacts on physical, biological, and social ecosystem components (Airoldi & Beck 2007; Gittman et al. 2016; Sutton-Grier et al. 2018). As a result, there are tremendous resources invested in coastal habitat restoration intended to improve biodiversity and ecosystem services. In the Pacific Northwest, heavy investment in coastal habitat restoration commonly holds salmon and forage fish foremost in mind (Kinney et al. 2016; Katz et al. 2019). However, resources and evidence for near- and long-term effectiveness of these efforts are often lacking (Borja et al. 2010; Narayan et al. 2016). Here we evaluated the consequences of the removal of shoreline armor for salmonids and forage fish, revealing that—contrary to our expectations—positive relationships between the abundance of these fishes and restored shorelines are largely non-existent 3–7 years following restoration.

We found differences among the four species in our study in terms of the factors that best explained the nearshore abundances we observed, suggesting that these species interact differently with nearshore habitats, or that use of nearshore subtidal habitats is driven by different factors for each species. Many of the differences we observed can potentially be attributed to the different life histories of each species. Broadly speaking, juvenile salmon use of Puget Sound nearshore habitats is transient (they are migrating through to the open ocean) while smelt and herring are more resident in Puget Sound. In some locations, it is known that chum salmon linger for longer periods than Chinook salmon while rearing in nearshore habitats as juveniles (Fresh et al. 2005). For forage fishes, nearshore subtidal habitat remains important to juveniles for weeks to months, or for surf smelt, their entire lives, following hatching from spawning areas on beaches and in nearby subtidal areas (Penttila 2007; Lewandoski & Bishop 2018; Sharpe et al. 2019). While both smelt and herring spawn in nearshore habitats at known locations, smelt deposit their eggs in beach gravel while herring use rooted vegetation for attaching their eggs. These different uses of nearshore habitat by these four species may in part explain the lack of uniform responses to shoreline habitat features.

While shoreline structure was associated with forage fish abundance, the effects were inconsistent: smelt abundance was patchy and either highest at armored or reference sites, while higher abundances of herring were found associated with reference shorelines. Shoreline structure was not a factor in salmonid abundance at all. Overall, abundances at restored shorelines were not similar to abundances at reference shorelines. The lack of an observed relationship between shoreline restoration and the abundance of nearshore fishes in this study may indicate a lack of association between beach restoration and processes that govern fish use of subtidal habitats. Restoration activities aimed at supporting nearshore fishes expect armor removal to reverse the negative impacts of armor placement, that is, increase the amount of shallow-water habitat, delivery of terrestrial insects as prey for salmonids, and spawning habitat for beach-spawning fishes (Francis 2018); these restoration effects have been observed in beach and intertidal monitoring programs. However, effects on fishes are ultimate impacts of restoration activities, which depend upon proximate changes to processes and structures. Our results suggest that achieving these ultimate impacts for subtidal zones may depend upon additional factors beyond the local restoration activities themselves, at least in the near term.

We hypothesized that disruption of geomorphic, structural habitat, and food web dynamics by armor, and restoration of those dynamics via armor removal, would be reflected in patterns of abundance associated with shoreline structure. In part this is because, among other deleterious effects, installation of shoreline armor is associated with decreased terrestrial (for Chinook) and epibenthic (for chum) prey in the diets of salmonids in intertidal habitats (Toft et al. 2007; Duffy et al. 2010). However, we found inconsistent effects of shoreline structure on fish

abundance, and no greater abundance of fish adjacent to restored shorelines as compared to armored, suggesting that prey availability associated with armor or its removal is unlikely to drive use of subtidal habitats among these fishes, at least at the spatial scale common to armor removal projects in Puget Sound. There is substantial overlap in planktonic diet between these four species of the sizes we observed (Fresh et al. 1981; Kemp & Beauchamp 2014; Fladmark et al. 2016), so they may be expected to respond similarly to prey availability. However, there is a high degree of water movement in Puget Sound, and strong tidal currents may transport planktonic prey such that local shoreline effects on prey availability are muted. In addition, armor or its removal may differentially affect different prey types, only increasing delivery of terrestrial prey that would primarily be accessed by Chinook salmon; however, we found no relationship between restored shorelines and Chinook abundance. It may be that the effects of restoration, and the associated effects on prey supply or delivery, attenuate with distance from shore, such that prey and dietary differences may be less pronounced in subtidal habitats, preventing detection of an effect. Alternatively, the distribution and abundance of these fishes may be driven less by factors that affect foraging and growth, and more by those that determine predation risk and mortality. While we did not measure prey availability directly, we found no suggestion that restoration-associated prey increases drive local patterns of subtidal fish abundance.

The lack of associations between fish abundance and shoreline restoration found here may also be linked to distance decay in responses to the removed armor. Shoreline armor impacts are increasingly pronounced the lower (more waterward) the armor is relative to the shoreline (Toft et al. 2007). Thus, armor that is higher up on beaches may have fewer deleterious effects from which subtidal habitats at restoration sites can potentially recover, resulting in little observable difference in fish abundance between armored and unarmored shorelines. A related possible explanation is that the linear distances in absolute terms between the armor and/or restoration and the subtidal habitats we sampled here are sufficiently large to preclude measurable effects that are more pronounced in intertidal zones. Whether due to distance-dependence alone or in combination with shifts in distance-dependent ecological factors, a ripe area of future inquiry centers on determining how the distribution of fish across intertidal and subtidal nearshore habitats interacts with attenuation of armor-removal signals to impact individual- and population-level growth and survival rates.

Importantly, the lack of a positive association between restored shorelines and fish abundance in our findings may reflect a mismatch between the spatial and/or temporal scales of the restoration projects and the scale at which fish population abundance is measurably affected. The scale at which we surveyed fish populations for this study, on the order of 30 m of shoreline, was chosen to match the scale of restoration projects, as the primary question at hand is, do small-scale restoration projects affect populations of fish using nearshore habitats? Local-scale habitat influences are likely active, but the landscape context within which individual restoration activities occur may be as or more important. Small amounts of armor

or intact shoreline habitat may be more influential for fish with longer nearshore residence times, or for fishes that are obligate on a particular habitat type, than for those that are more mobile and able to pass through potentially degraded areas. Thus, the signal of armor or restoration may be lost in the noise of the surrounding spatial matrix. Instead, responses by nearshore fishes may accumulate over many individual restoration projects in a larger geographic area and be discernible only at larger scales. Larger-scale influences on subtidal fish communities have been previously observed (Toft et al. 2021), including upland habitat features and effects that vary across spatial scales, and investigations into the influence of watershed features and other landscape-scale patterns are warranted.

There also may be a temporal lag in biotic responses to physical changes associated with restoration. Following the disturbance created by a restoration project, there may be a prolonged settling period before responses by organisms and food webs are apparent. Our suite of study sites spanned between 3 and 7 years post-restoration. Effects of armor removal are observable 4 years post-restoration (Toft et al. 2021) and rapid responses to restoration have been observed for juvenile salmon in tidal marshes (Ellings et al. 2016) Interestingly, the site with consistently highest abundance and occurrence of all focal species was also the most mature restoration site, Cornet Bay; however, restoration age was not correlated with abundance either across or within species. It may be that not enough time has passed for subtidal zones in our sites to resettle, and for habitat structure and function to respond to the restoration. It is possible that the effects of armor removal from open marine shorelines are less detectable in shorter time periods because fish are more broadly dispersed across these habitats compared to aggregating habitats, like spawning river deltas. Temporal lags in subtidal habitat responses to restoration may necessitate longitudinal studies to determine project effectiveness.

Aside from shoreline structure, the presence of eelgrass was associated with the abundance of nearshore fishes in our study. Chum salmon were on average 10-fold more abundant at sites with eelgrass than without, and eelgrass was included in the best models for herring and smelt abundance. There are many reasons why eelgrass beds may be positively associated with nearshore fish abundance, including prey availability, predator avoidance, and other factors that cause eelgrass beds to be valuable nursery habitat (Beck et al. 2001; Semmens 2008; Kennedy et al. 2018). Previous work has shown various patterns in terms of use of different nearshore habitat types by the fish studied here, some of which match the present findings. In the Skeena River delta, Chinook salmon were more often found in eelgrass habitats (Sharpe et al. 2019) and in the Skagit River delta, Chinook salmon, herring and surf smelt were all more abundant in eelgrass habitat (Rubin et al. 2018). In the Fraser River estuary, herring and smelt were more abundant in eelgrass habitat than Chinook and chum salmon (Chalifour et al. 2019). The positive associations we found between eelgrass and nearshore fishes echo previous findings and suggest that restoration activities aimed at benthic habitat enhancement may have direct benefits for these threatened species in Puget Sound.

Survey site was also associated with the abundance of all our focal species, save chum salmon. Survey site may serve, in our

models, as an aggregate of abiotic and biotic factors we did not directly measure and that may be important determinants of nearshore fish abundance and distribution. For example, habitat association models have found a significant influence of temperature and dissolved oxygen on Chinook salmon abundance, and that turbidity is a predictor of chum abundance (Chalifour et al. 2019; Sharpe et al. 2019). Similar models for herring and smelt have found local temperature and salinity, respectively, to be predictors of abundance (Sharpe et al. 2019). Smelt have been more commonly observed in nearshore areas with bare substrates (Smith et al. 2016). We did not include these environmental parameters in our models, but they may vary by survey site and therefore influence the patterns we observed.

Beyond environmental factors, the locations of our survey sites on the landscape may be important for understanding the distribution of these species in nearshore environments more directly. For example, juvenile Chinook salmon move through nearshore habitats as they migrate from their natal rivers and streams to the Pacific Ocean, and are often found in basins some distance from where they spawned or, for hatchery fish, were released (Hayes et al. 2019); sites where we found higher abundances of Chinook salmon (Cornet Bay and Turn Island) are closer to major spawning rivers (Puyallup and Skagit/Snohomish Rivers). Herring also spawn annually at fixed nearshore sites around the Salish Sea, and survey sites closest to those spawning areas had higher abundances of herring (Cornet Bay and Family Tides). Surveys of recreational fishing have shown that smelt aggregate on certain beaches during spawning events, including near two of our sites where we observed smelt in higher abundance (Dockton and Cornet Bay; Lowry et al. 2015). The presence of survey site in our best models of nearshore fish abundance is important in practical terms; understanding that these species are not uniformly distributed along shorelines can help prioritize protection and restoration activities. Annual monitoring would help identify the degree of persistence in site differences.

Restoring the ecosystem characteristics and benefits provided by coastal and estuarine ecosystems is a priority likely to continue to attract scientific, economic, and social resources. The present findings add to a growing body of work encouraging evidence-based restoration efforts that target the underlying influences on patterns of ecological variation in systems subject to a range of anthropogenic pressures (Cooke et al. 2018). In addition, a global challenge is scaling up local restoration activities (Tan et al. 2020). While studies of local-scale dynamics are useful, there is a need to study the cumulative effects and effects at scale of armor and its removal (Heery et al. 2017). Effectiveness monitoring of coastal restoration projects is a rapidly developing field, and this work points to the need for more rigorous and standardized monitoring frameworks for coastal restoration (Gilby et al. 2021), as have been developed for freshwater restoration projects (Bennett et al. 2016). This work also highlights the need for long-term monitoring to capture the temporal scale of shoreline dynamics.

Acknowledgments

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Supporting Information

The following information may be found in the online version of this article:

Supplement S1. Supplementary methods.

Supplement S2. R script for Bayesian generalized linear model.

Supplement S3. Raw lampara net survey data.

Figure S1. 89% credible intervals based on four MCMC chains of 5,000 draws each for a model of subtidal fish abundance with a single predictor for period.

Table S1. Posterior distributions of regression coefficients from the best-fit models for each species.