

## ARTICLE

# Spatiotemporal Variation in Distribution, Size, and Relative Abundance within a Salish Sea Nearshore Forage Fish Community

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## Abstract

Forage fish are schooling species commonly occurring in both offshore pelagic and nearshore coastal habitats. Beyond use by some species for spawning, the dynamics of nearshore habitat use are not well understood. The objective of our study was to evaluate the spring–summer dynamics of forage fish occurrence in nearshore habitats of the Strait of Juan de Fuca, Washington. We suspected that habitat changes resulting from removal of two large dams on the Elwha River (2009–2011) may have altered fish presence and abundance. Monthly beach seine sampling in four regions along 40 km of shoreline was conducted from April to September between 2006 and 2019. We caught nearly 600,000 fish, comprising 82 different species. Nine species of forage fish accounted for 81.7% of all fishes caught; most were classified as postlarvae and juveniles based on size. There were spatial differences in the forage fish assemblage between two of our sites but no discernable year effects and no obvious impact of dam removal on forage community composition. Three species represented 78.8% of the catch: Pacific Herring *Clupea pallasii*, Pacific Sand Lance *Ammodytes hexapterus*, and Surf Smelt *Hypomesus pretiosus*. We used a Bayesian generalized linear mixed model to evaluate spatial and temporal variability in the probability of occurrence of these species. Each species exhibited a unique pattern of intra-annual, interannual, and regional fluctuations. Pacific Herring occurrence progressively increased monthly, Pacific Sand Lance occurrence decreased, and Surf Smelt probability of occurrence peaked in June. Temporal variations in distribution and abundance of these species are likely driven by life history differences and biological requirements. We speculate that specific characteristics of each region, including proximity to spawning areas, spawn timing, extant current patterns, and ecosystem processes, drove variations in distribution between species.

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Forage fish are abundant, pelagic, schooling species found worldwide in most marine ecosystems (Alder et al. 2008; Cury et al. 2011; Pikitch et al. 2014). The term "forage fish" can be broadly applied to a diverse assemblage of species that are, in many cases, related through ecology and not phylogeny. Middle trophic levels in marine food webs are inherently dominated by forage fish, which are critical to the transfer of energy from primary or secondary producers to higher trophic levels (Casini et al. 2004; Szoboszlai et al. 2015; Albo-Puigserver et al. 2017; Staudinger et al. 2020).

Forage fish are primarily planktivorous (Alder et al. 2008; Engelhard et al. 2013) and are a critical component of marine ecosystems as they are consumed by a large variety of fish, birds, and mammals (Bishop and Green 2001; Gende and Sigler 2006; Miller and Brodeur 2007; Pikitch et al. 2012; Brodeur et al. 2014; Staudinger et al. 2020). Especially in adult stages, forage fish are commonly associated with pelagic habitats, but some species also utilize nearshore or benthic habitats during portions of their life histories (Cury et al. 2000; Penttila 2007; Eggers et al. 2015; Kanstinger et al. 2016). Many species of forage fish are also economically important as the focus of live bait, reduction, and directed (food) fisheries (Bargmann 1998; Sweetnam 2007; Engelhard et al. 2013).

Worldwide, many populations of forage fish have dropped to low levels of abundance (Essington et al. 2015; MacCall et al. 2016). These declines contribute to a variety of direct and indirect effects, including reduced fisheries and decreased predator abundance, effects that can propagate through the food web affecting various consumers at higher trophic levels (Pearson et al. 1999; Kaplan and Leonard 2012; Atkinson et al. 2014). Declining forage fish abundance is a potential factor associated with dramatic decreases in some populations of marine mammals, seabirds, and high-trophic-level fish, such as Pacific salmon *Oncorhynchus* spp. (Cooney et al. 2001; MacLeod et al. 2007; Cury et al. 2011; Beamish et al. 2012; Pikitch et al. 2012, 2014). Therefore, forage fish management can play a key role in the conservation of other important species.

Declines in abundance of forage fish populations are attributed to both natural stressors, such as large-scale climate events (i.e., El Niño; Zebdi and Collie 1995; Williams 1999; Reum et al. 2011), and anthropogenic factors, such as harvest and habitat degradation (Toft et al. 2007; Shaffer et al. 2017). Forage fish conservation efforts have focused primarily on managing fishing pressure to increase numbers (Essington et al. 2015; McClatchie et al. 2017). Less attention has been given to other anthropogenic factors, such as habitat loss and change (Penttila 2007; Toft et al. 2007; Kanstinger et al. 2016; Staudinger et al. 2020). Nevertheless, habitat degradation and loss have had extensive impacts on forage fish in nearshore intertidal and shallow subtidal ecosystems (Miller et al. 1980; Greene et

al. 2015; Sheaves et al. 2015; Brown et al. 2018). These habitats play a key role in the life cycle of many forage fish species for spawning, feeding, migration, rearing, and refuge from predation (Robards et al. 1999a; Beck et al. 2003; Bradbury et al. 2008; Kanstinger et al. 2016; Munsch et al. 2016).

Human modification of nearshore areas has been extensive globally and includes construction of bulkheads along the shore, erection of piers and docks, dredging and filling, removal of riparian vegetation, and pollution (Airolidi and Beck 2007; West et al. 2008; Sobocinski et al. 2010; Dethier et al. 2016; Gittman et al. 2016). Changes to critical nearshore habitats are a global issue that will continue to create negative outcomes for forage fish and are expected to increase as more people occupy coastal areas (Lotze et al. 2006). For example, the availability and suitability of intertidal and shallow subtidal spawning habitats of both Pacific Herring *Clupea pallasii* and Atlantic Herring *Clupea harengus* are being impacted by human activities in coastal areas (Penttila 2007; Kanstinger et al. 2016). Moreover, nearshore regions are also susceptible to climate variability, extreme storm events, and rising sea levels (Flint 1985; Hay et al. 2008). In addition to direct human-derived effects in marine waters and along shorelines, nearshore habitats can be affected by in-river changes that alter sediment dynamics or flow near river mouths through deposition or scour (Day et al. 2000; Syvitski 2005; Slagel and Griggs 2008; Ralston et al. 2021). Dams in the lower portions of rivers are one specific modification that can generate such effects by blocking sediments that help build a variety of habitats such as beaches, spits, and wetlands (Day et al. 2000; Wilcox et al. 2014; Warrick et al. 2019); conversely, their removal can help rebuild beaches and estuarine habitats.

The Salish Sea includes the inland marine waters of both Washington and southern British Columbia and is rich in nearshore habitat. Anthropogenic factors affect the quantity and quality of much of this habitat (Toft et al. 2007; Fresh et al. 2011; Dethier et al. 2016). Restoration efforts that include armoring removal and construction of piers that allow passage of light have been made within the Salish Sea (Clancy et al. 2009; Sawyer et al. 2020). Additionally, in the Strait of Juan de Fuca, the removal of two large dams on the Elwha River was undertaken beginning in 2009 to provide fish passage and restore natural sediment processes in the river and nearshore (Gelfenbaum et al. 2015; Magirl et al. 2015; Randle et al. 2015; Warrick et al. 2015; Eidam et al. 2016). Dam removals were initiated in 2009 and concluded in September 2011. This action resulted in the release and redistribution of stored sediment to the nearshore area near the mouth of the Elwha River over several years (Warrick et al. 2009, 2019; Miller et al. 2011). These changes have been associated with changes in fish community structure in the

estuary and in the nearshore area adjacent to the river mouth (Foley et al. 2017; Rubin et al. 2017; Shaffer et al. 2017; Lincoln et al. 2018).

A number of forage fish species use nearshore ecosystems of the Salish Sea during portions of their life history, particularly as nursery habitat (Penttila 2007; Munsch et al. 2016). Studies of forage fish use of these nearshore habitats have focused primarily on reproductive ecology and habitat associations (Penttila 2007; Haynes and Robinson 2011; Quinn et al. 2012; Shaffer et al. 2012, 2020), especially for Pacific Herring, Pacific Sand Lance *Ammodytes hexapterus*, and Surf Smelt *Hypomesus pretiosus*. These three species are the most commonly occurring forage fish in this region (Emmett et al. 1991; Penttila 2007; Greene et al. 2015). Pacific Herring spawn in subtidal vegetation (Haegele et al. 1981; Hay et al. 2009), and several smelt species utilize fine-grain beaches to deposit eggs (Therriault et al. 2002b; Penttila 2007; Quinn et al. 2012; Shelton et al. 2014a). Pacific Sand Lance primarily spawn in intertidal and subtidal areas of mixed sand and gravel (Robards et al. 1999a; Selleck et al. 2015). Although they do not spawn in nearshore areas, American Shad *Alosa sapidissima*, Eulachon *Thaleichthys pacificus*, and Longfin Smelt *Spirinchus thaleichthys* migrate through or stage in nearshore areas prior to migrating into rivers to spawn (Emmett et al. 1991; Penttila 2007; J. K. Gaydos and J. Zier, paper presented at the Proceedings of the Salish Sea Ecosystem Conference, 2014). All three of the most common forage fish species rear for varying periods in nearshore areas during the postlarval and juvenile stages (Emmett et al. 1991; Penttila 2007; Haynes and Robinson 2011; Quinn et al. 2012; Greene et al. 2015).

In coastal shelf ecosystems including the Salish Sea, variation in abundance of forage fish species has been related to commercial harvest (Bargmann 1998; Stick et al. 2014; Essington et al. 2015), decadal climatic indices (Cury et al. 2000; Reum et al. 2011; Greene et al. 2015), and biological processes (Lasker 1985; Freon et al. 2005). While broadly acknowledged, quantitative descriptions of within-year and interannual variation in forage fish assemblages in nearshore coastal habitats remain limited. In particular, researchers are building an understanding of spatial and temporal variability in the structure of these assemblages, as well as factors that may affect their distribution and abundance during residence in nearshore ecosystems (Weitkamp et al. 2012; Munsch et al. 2016; Shaffer et al. 2020).

Most studies in nearshore areas have been short term (<3 years) in nature (Emmett et al. 1991; Toft et al. 2007; Quinn et al. 2012; Rice et al. 2012; Shaffer et al. 2012). Longer-term data (>5 years) on forage fish use of nearshore ecosystems associated with shoreline areas show variable regional trends in forage fish catch over time and linkages between anthropogenic activities and forage fish abundance (Greene et al. 2015; Shaffer et al. 2020).

Nearshore ecosystems in the Salish Sea are subject to various disturbances, including coastal development, winter storms, and climate variability (Krueger et al. 2010; Munsch et al. 2015; McInnes et al. 2017). Such disturbances can affect nearshore substrates and marine plants that provide habitat and food for nearshore species (Dean et al. 2000; Rice 2006; Toft et al. 2007; Quinn et al. 2012). While forage fish species are often discussed as a group, we hypothesized that individual species within forage fish communities will respond differentially to environmental conditions affecting these habitats over multiyear time periods.

Our study evaluated spatial and temporal variability in the dominant species in the forage fish community over a 14-year period in nearshore habitats of the Strait of Juan de Fuca, which connects the Pacific Ocean with protected environments of the Salish Sea. Study objectives were to assess monthly, interannual, and spatial variability in forage fish abundance and community composition. We hypothesized that time (month and year) and space (as defined by region along the Strait of Juan de Fuca) would influence the occurrence of species at specific locations. We also considered several factors that potentially drive this variability that operate on a variety of spatial and temporal scales.

## METHODS

*Study species.*—We focused on the nine most common forage fishes found in nearshore habitats of the Salish Sea (Pacific Herring, Pacific Sand Lance, Surf Smelt, Northern Anchovy *Engraulis mordax*, American Shad, Night Smelt *Spirinchus starksi*, Pacific Sardine *Sardinops sagax caerulea*, Longfin Smelt, and Whitebait Smelt *Allosmerus elongatus*). In terms of abundance, distribution, and accessibility, Pacific Herring was arguably the most important forage fish present (Meyer and Adair 1978; Penttila 2007). This herring species supports a number of commercial fisheries, primarily in British Columbia, and has been historically important to Washington fisheries as well (Stick et al. 2014). Several other forage fish species were present, including Pacific Sand Lance (Haynes and Robinson 2011; Selleck et al. 2015) and Northern Anchovy (Therriault et al. 2002a). Several osmerid smelt species also occurred, including Surf Smelt and Night Smelt (Healey 1980; Emmett et al. 1991; Quinn et al. 2012). Additional species such as juvenile salmonids and rockfishes *Sebastes* spp. may function as forage fish during the short periods they spend in inland marine waters during migration (Szoboszlai et al. 2015; Wells et al. 2017), but since the designation only applies to some life history stages, these were not included as forage fish for analysis.

*Study area.*—Our study encompassed sampling locations along an area of approximately 40 km of the Strait

of Juan de Fuca on the Washington State coast (USA). Sampling was conducted monthly from April through September during 2006–2008, 2010–2012, and 2014–2019. We sampled 23 beach seine sites divided among four regions (Appendix Table A.1). From west to east, these regions were designated as Elwha, Port Angeles, Green Point, and Sequim (Figure 1).

Within each region, comparable sampling sites were selected for ability to sample, general geomorphic similarity (following the classification of McBride et al. 2009), and common features of low nearshore gradient, substrate, presence of similar vegetation, exposure, and proximity to historical high-density forage fish spawning sites. Across regions, most sampling sites were bluff-backed beaches. The Elwha, Green Point, and Sequim regions roughly correspond to marine drift cells, a unit of sediment processing associated with beaches (Johannessen and MacLennan 2007; Shaffer et al. 2012; Warrick et al. 2019). All regions are exposed to the same broad ocean conditions, such as onshore current flow, and degree of nutrient upwelling but vary in the degree of exposure to wind and waves.

The Elwha region included five sites east and west of the Elwha River mouth and was directly affected by significant river-derived sediment input (Warrick et al. 2019). The region is highly exposed to wind and waves. Sites west of the river mouth were embayments, while those east of the mouth were bluff-backed beaches, one with partial armoring. The Port Angeles region included six beach sites on spits or below bluffs, all with heavy anthropogenic modification and backed by bank-stabilizing

material within a protected area of Port Angeles harbor. The Green Point region is located 15 km east of the Elwha River, and sampling sites were all backed by natural, eroding coastal bluffs (feeder bluffs) and were highly exposed to wind and waves; the four Green Point sites were most similar to the Elwha sites (Shaffer et al. 2012). Finally, the Sequim region included eight sampling sites located 30 km east of Green Point in an area with feeder bluffs (seven sites) and spits (one site) and devoid of armoring in the sample areas; due to the protection afforded by Dungeness Spit, this region is less exposed to wind and waves. As an area resource for use by migrating fish, kelp and eelgrass beds exist in each of the sampling areas. However, beach seine sampling was conducted inshore of these beds where they exist, and our quantitative analyses focused entirely on catch in the immediate nearshore intertidal and subtidal.

*Sampling protocol and quantifying catch.*—To characterize the nearshore forage fish community, we used beach seine sampling with a slightly modified Puget Sound protocol (Miller et al. 1990; Simenstad et al. 1991) in which the net was deployed about 33 m from and parallel to shore. A line attached to each end of the net was used to pull the net to shore, with both ends hauled in at the same pace from each side. When the net was about 10 m from shore, the two ends were pursed together (“round haul”) to force fish into the bag. We used a 37-m Puget Sound beach seine (Hahn et al. 2007), which ranged from a width of 2 m at the end of the wings to 3.1 m at the bag. Mesh size was 3 cm in the wings and 3.2-mm knotless nylon in

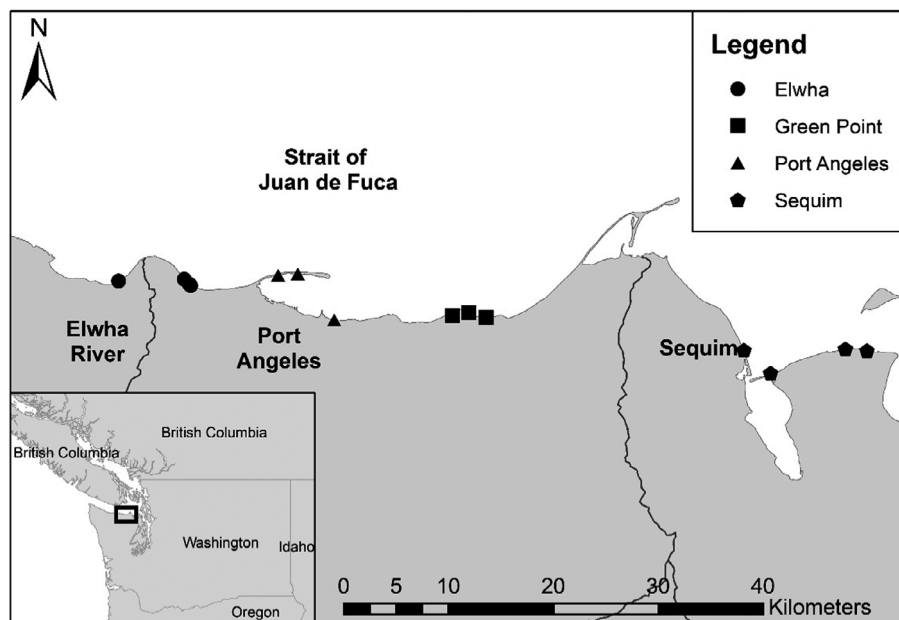


FIGURE 1. Study area within the Strait of Juan de Fuca along the coast of Washington, with sampling locations indicated.

the bag. Our unit of sampling was a seine haul, which under ideal conditions represented an area of about 1,200 m<sup>2</sup>. When calculating metrics such as catch per unit effort (CPUE), a seine haul was used as the denominator and considered a standardized unit. Sampling was conducted generally during ebb neap tides and morning hours.

For each set, fish were removed from the net as quickly as possible and immediately processed. All fish caught were identified to species and enumerated. For hauls with a catch of less than 21 individuals of a species, the fork length of all individuals was measured; when hauls contained more than 20 fish of a given species, a random sample of 20 individuals was measured and the rest were counted prior to release. Although we strived to hand count all catches, large single or multiple species catches (generally >500 individuals) were volumetrically subsampled and processed as above. Catches of Surf Smelt, Pacific Herring, and Pacific Sand Lance were counted by size-class (<50 mm, 50–120 mm, >120 mm), with 20 individuals measured in each size-category, which loosely corresponded with postlarval, juvenile, and adult stages, respectively. Sampled fish were released at the capture site immediately after species identification and measurement. All sampling was conducted under valid federal and state permits.

To examine spatial and temporal variability in fish assemblages, fish catch was summarized by functional group (general associations of fish type, i.e., forage fish, flatfish, salmonids, etc.) and individual species on overall, annual, and regional scales. Due to variability in the data and the occurrence of catches containing both zero and large numbers of individual species and taxonomic groups, we used a coefficient of variation to examine dispersion around mean values. To characterize community structure, we calculated percent of overall catch comprised of different fish groupings by sampling region and overall. We developed forage-fish-specific indices of species richness ( $S$ ), species diversity (Shannon–Weiner  $H'$ , natural log base  $e$ ), and species evenness (Pielou's index  $J'$ ) by year and sampling region, as well as CPUE by region and year. We defined CPUE as the number of fish in a given category caught per beach seine set. Distribution of CPUE among years was plotted by year and region, with the overall annual mean used to represent average density of forage fish. We also plotted the relative proportion of sizes caught for the focal forage fish species, along with size distributions by region and capture date within the sampling period. The change in size distribution within classes was plotted using violin plots of forage fish length.

*Analytical approach.*—Multivariate techniques complemented our qualitative measures (Weitkamp et al. 2012). To visualize changes in forage community composition across sites and before and after removal of the Elwha River dams, we conducted a nonmetric multidimensional

scaling (MDS) on standardized, square-root-transformed catch data. We used analysis of similarities (ANOSIM; a multivariate analog for analysis of variance) to test for the influence of both site and year on this transformed data. The effects of environmental variables were assessed using the BEST function in PRIMER-E to determine the environmental matrix with the highest correlation to the forage fish assemblage. To incorporate the potential influence of large-scale climate events, we included available regional values for Pacific decadal oscillation (annual sum value May–September) and Oceanic Niño Index (El Niño) (sources described in Peterson et al. 2014). These processes affect productivity in local waters (upwelling), which in turn affects bottom-up processes in the Salish Sea, which can be important drivers of forage fish abundance (Reum et al. 2011; Boldt et al. 2019). Additionally, we used annual averages of site-specific temperature and salinity values taken in conjunction with our seasonally restricted sampling activity as local factors that could affect the forage fish assemblage. Salinity was included as a surrogate for variations in regional freshwater inflow, while temperature variations could indicate effects of both local and regional (upwelling and freshwater inflow) conditions. Multivariate analyses were based on pairwise Bray–Curtis similarity coefficients calculated between regions. Bray–Curtis similarity coefficients are widely used in ecological studies because they are unaffected by changes in scale or the number of variables used and produce a value of zero when both values being compared are zero (joint absence problem) (Clarke 1993; Legendre and Legendre 1998). In this application, similarity coefficients ranged from 0 (no catches in common) to 1 (identical catches).

Forage fish species tend to school and thus are often captured in groups. Due to the prevalence of zero catch and of high variation in number caught for a given species in any particular beach seine set, Bayesian model analyses were performed on probability of occurrence rather than abundance. We estimated this probability for each of the three principal forage fish species to determine the influence of spatial and temporal factors on occurrence. For these estimates, we used a Bayesian binomial generalized linear mixed model with a logit-link. In brief, we estimated the probability of catching at least one Surf Smelt, Pacific Herring, or Pacific Sand Lance at each site for each month and year. As the most important local environmental change during the study period was removal of the Elwha River dams, we assessed the effect of dam removals by estimating a pre- and postdam removal effect for each region (hereafter, the dam-region effect,  $D$ ). We used a modified before-after-control-impact design (Smith et al. 1993) to assess changes to the forage fish community resulting from dam removals and subsequent changes to sediment distribution. For these analyses, 2006–2011 represented before dam removal (specifically encompassing

the periods before dam removal and during active dam removal) and 2012–2019 the period following the restoration action (after removal efforts were completed for both dams). The Elwha region served as the impact region, and the other three regions functioned as controls. We compared the dam–region effect across regions to assess whether responses to dam removal in the Elwha region were similar to or different from the changes in adjacent regions. We also include random month  $M$  and year  $Y$  effects to account for monthly and annual changes not associated with dam removal. Thus, our logistic model accounted for monthly, interannual, and region-to-region variability in forage fish occurrence, along with measurement error.

Formally, let  $X_{i,j,k,q}$  be the true presence of taxon  $i$  in year  $j$  and month  $k$  in dam–region  $q$ , such that

$$\text{logit}(X_{i,j,k,q}) = Y_j + M_k + D_q + \eta_{j,k}, \quad (1)$$

where stochasticity in the probability of sampling at least one individual of a species that is attributable to random forces is  $\eta_{j,k} \sim N(0, 1/\phi^2)$ , with a diffuse gamma prior for the variance parameter,  $\phi^2 \sim \text{gamma}(1.5, 1.5)$ .

This process model (1) was linked to an observation model where the observed occurrence of individuals was  $Z_{i,j,k,q}$ :

$$Z_{i,j,k,q} \sim \text{Bernoulli}(X_{i,j,k,q}). \quad (2)$$

We used diffuse independent normal priors for year  $j$  and month  $k$  effects,  $Y_j \sim N(0, 1/\delta^2)$  and  $M_k \sim N(0, 1/\epsilon^2)$ , and diffuse gamma priors for the associated precision estimates,  $\delta^2 \sim \text{gamma}(1.5, 1.5)$  and  $\epsilon^2 \sim \text{gamma}(0.01, 0.01)$  for Surf Smelt and Pacific Herring and  $\epsilon^2 \sim \text{gamma}(1.5, 1.5)$  for Pacific Sand Lance. During model evaluation, a range of prior distributions for year and month effects were examined for each species. The prior distributions had minimal consequences for parameter estimates but substantial effects on model estimation speed and efficiency (i.e., Markov chain–Monte Carlo [MCMC] mixing). The chosen prior distributions improved model estimation without substantively affecting the biological interpretation. Finally, we used a diffuse independent normal prior for the dam–region effect  $D$ ,  $D_q \sim N(0, 1/10^7)$ . We used MCMC methods as implemented in JAGS (Plummer 2003) to estimate the model, with a burn-in of 5,000 iterations, 25,000 monitored iterations, and three replicate MCMC chains from random starting points. We performed standard model convergence checks (Appendix Figure A.1; Gelman–Rubin statistics; Gelman et al. 2003).

We estimated the effects of year and month on probability of occurrence for each of the three dominant forage fish species using these models. In addition, we calculated the difference between estimated dam–region effects  $D_q$

following and prior to removal of the Elwha River dams. This calculation represented the change in predicted probability of occurrence for each species in each region following dam removal after controlling for annual, monthly, and random process variation. All analyses were conducted in R (version 3.3.1; R Core Team 2016).

## RESULTS

Catches of fish in the nearshore habitats we sampled were highly variable, ranging from 0 to 32,000 individual fish in a single set. Over the 12 study years, a total of 575,801 individual fish were caught, comprising 82 different species arrayed amongst eight functional groups (Table 1). Annual catch ranged from 17,710 (2018) to 92,677 (2014) individual fish, with the annual number of species ranging from 45 (2007) to 55 (2011, 2016). The largest number of species caught was in the Sequim region ( $n = 66$ ), and the largest number of individual fish caught was in the Green Point region ( $n = 188,114$ ).

With the exception of American Shad, all species were native to the northeastern Pacific Ocean. Most measured fish were small, averaging 86.8 mm ( $\pm 43.5$  mm SD) over all species, regions, and years. Catch of individual species was extremely variable, with coefficients of variation ranging from 100.8 for gadids in the Port Angeles region to 515.7 for forage fish in the Port Angeles region. Surf Smelt was caught in all years and regions, while Whitebait Smelt was present in only 2 years and in one region.

We categorized species into eight groups based on taxonomic and functional similarities (Table 1): flatfish (order Pleuronectiformes), forage fish, gadids, hexagrammids, salmonids, sculpins (family Cottidae), surfperches (family Embiotocidae), and other. The most specious group was "other," with 21 identifiable species; however, this group accounted for less than 3% of the total number of fish caught over all sites and years. Within the "other" group, Tubesnout *Aulorhynchus flavidus* was the most abundant and was present in up to 32% of the sets (in the Green Point region). Each functional group was represented in 5.6% to 96.0% of all sets over the study period (Table 1).

Forage fish were represented by nine species (see Figures 2, A.2) and were numerically the most dominant group, accounting for 81.7% of the catch in all regions and years combined (Table 1). Diversity of forage fish varied considerably between years and regions (Table 2), with  $H'$  ranging from 0.01 in 2006 to 1.30 in 2011 in the Elwha region alone. Overall, the lowest diversity of forage fish occurred in the Port Angeles region, but this area also had the lowest abundance (Tables 1, 2). The highest forage fish diversity occurred in 2010 and 2011, which also corresponded to two of the lowest annual average forage fish catches per set we recorded (Figure 2). Species evenness was generally lowest in the Green Point region and highest

TABLE 1. Total number of individuals, percent of total beach seine catch comprised of various fish groupings (see Results for grouping definitions), and likelihood of catch (percent of sets with a representative) presented by sampling region.

Fish groupings	Total number of individuals (n)	Percent of total catch (%)	Likelihood of catch (%)
<b>Elwha</b>			
Flatfish	2,076	1.3	38.7
Forage fish	138,163	84.5	90.0
Gadids	7,074	4.3	42.4
Hexagrammids	1,088	0.7	16.6
Salmonids	13,453	8.2	54.6
Sculpins	496	0.3	38.4
Surfperches	747	0.5	31.7
Other	483	0.3	50.6
<b>Green Point</b>			
Flatfish	2,553	1.4	52.7
Forage fish	178,438	94.9	96.0
Gadids	2,407	1.3	37.8
Hexagrammids	69	0.0	11.4
Salmonids	922	0.5	47.8
Sculpins	691	0.4	45.3
Surfperches	1,473	0.8	43.3
Other	1,561	0.8	68.2
<b>Port Angeles</b>			
Flatfish	3,642	4.2	27.8
Forage fish	63,655	73.6	58.5
Gadids	94	0.1	5.6
Hexagrammids	695	0.8	28.8
Salmonids	10,302	11.9	55.7
Sculpins	2,414	2.8	68.2
Surfperches	3,132	3.6	21.3
Other	2,571	3.0	55.5
<b>Sequim</b>			
Flatfish	1,198	0.9	20.5
Forage fish	89,913	65.3	60.4
Gadids	465	0.3	13.1
Hexagrammids	2,489	1.8	36.3
Salmonids	14,366	10.4	66.1
Sculpins	1,762	1.3	54.2
Surfperches	20,080	14.6	61.4
Other	7,329	5.3	65.5

in the Sequim region (Table 2). Nearly two-thirds of all evenness values were less than 0.50, reflecting the dominance of a few species and propensity for large catches of individual species within the forage fish samples.

Annual forage fish CPUE varied by nearly an order of magnitude, with 2012 representing the lowest and 2016 the highest CPUE (Figure 2). Three species of forage fish

consistently occurred and were generally abundant across regions, months, and years: Surf Smelt, Pacific Herring, and Pacific Sand Lance. Together, these three species comprised 78.8% of the catch among all species and 98.0% of the catch among forage fish. Green Point had consistently high catches of Surf Smelt, with 898 individuals per haul on average (Figure 3), and Surf Smelt were present in 95.6% of sets. Catch of Pacific Sand Lance in the Green Point region was very low (0.9 per haul on average and present in 13.7% of sets). Both Pacific Sand Lance and Surf Smelt were common in the Elwha region, at 175 and 216 individuals per average haul, respectively. The Port Angeles and Sequim regions had low average CPUEs for all forage fish. Of the forage fish caught in these regions, Surf Smelt were most common in Port Angeles (99 individuals/set on average and present in 40.6% of sets), while Pacific Sand Lance were most common in Sequim (87 individuals/set on average). Of the other six forage fish species, most were caught occasionally as isolated individuals or in small groups over several years (Figures 3, A.3). One notable exception to this pattern was Northern Anchovy, which was absent from most catches but showed up in considerable numbers in 2010, driven by captures in the Green Point region in September of that year.

Based on literature describing the life history of each species, we grouped Surf Smelt, Pacific Herring, and Pacific Sand Lance into three size-classes that generally corresponded to the postlarval, juvenile, and adult stages (Robards et al. 1999a, 1999b; Therriault et al. 2002a, 2002b, 2009). Most individuals of all three species were classified by size as postlarval or juvenile. Relatively few adults were caught and these were mostly Surf Smelt (Figures 4, 5). Many adult Surf Smelt were gravid as evidenced by the extrusion of gametes with handling. We often caught all three size-classes of Surf Smelt at the same time, especially at Green Point (Figure 5). Adult-sized Pacific Herring (>120 mm) were captured almost exclusively in the Elwha region. Postlarval Pacific Herring (<50 mm) were relatively abundant compared with juveniles, especially in the Sequim and Port Angeles regions (Figure 5). Yet the CPUE of Pacific Herring was lowest in Port Angeles, at only 7.4 individuals on average (Figure 3). Other forage fish species were also mostly juveniles based on life history information, size, and morphological characteristics. Within size-classes, we observed seasonal development of postlarvae and juveniles as evidenced by increases in average size, particularly among Surf Smelt and Pacific Herring (Figure 6). Sizes within the adult class remained stable for all three focal forage fish species, with early season evidence of postlarval and juvenile recruitment into larger size-classes for Pacific Herring and Pacific Sand Lance (Figures 5, 6).

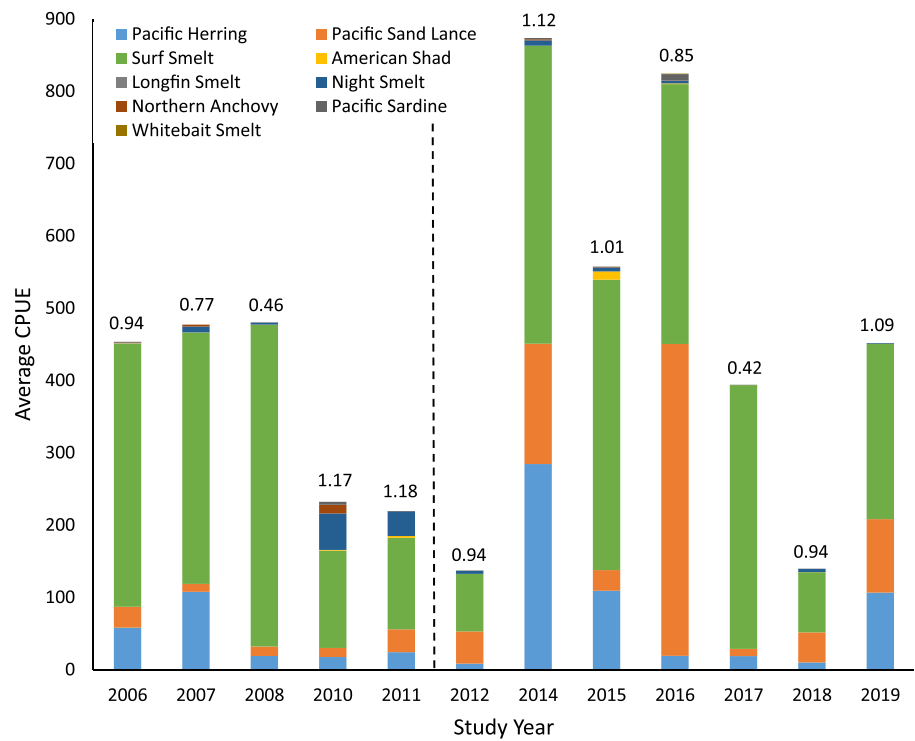


FIGURE 2. Average annual catch per unit effort (CPUE) of forage fish species at sites in the Strait of Juan de Fuca. The dashed line indicates the initiation of dam removal (in 2011 after annual sampling was complete). The numbers over the bars show the Shannon–Weiner diversity ( $H'$ ) of forage fish species for each year.

TABLE 2. Diversity indices of forage fish catch by sampling year and region.

Region	Sampling year											
	2006	2007	2008	2010	2011	2012	2014	2015	2016	2017	2018	2019
Species richness ( $S$ )												
Elwha	3	5	6	6	6	5	6	6	7	6	6	4
Green Point	4	5	5	6	6	5	6	5	6	4	5	6
Port Angeles	5	5	3	6	5	3	5	6	5	3	5	3
Sequim	3	4	3	4	5	4	5	4	3	3	3	4
Species diversity (Shannon–Weiner $H'$ )												
Elwha	0.01	0.76	0.71	0.74	1.30	0.56	1.07	0.85	0.36	0.06	0.95	0.57
Green Point	0.06	0.16	0.06	0.99	0.66	0.50	0.67	0.05	0.20	0.17	0.49	0.05
Port Angeles	0.56	0.99	0.56	0.98	1.10	0.95	0.28	0.42	0.28	1.00	0.77	0.40
Sequim	0.53	0.98	0.71	0.80	1.04	0.54	0.13	0.58	0.70	0.71	0.30	0.76
Species evenness (Pielou's index $J'$ )												
Elwha	0.01	0.47	0.40	0.41	0.72	0.35	0.60	0.47	0.19	0.03	0.53	0.41
Green Point	0.04	0.10	0.04	0.55	0.37	0.31	0.37	0.03	0.11	0.12	0.31	0.03
Port Angeles	0.35	0.62	0.51	0.55	0.69	0.86	0.18	0.24	0.18	0.91	0.48	0.36
Sequim	0.49	0.71	0.65	0.58	0.65	0.39	0.08	0.42	0.64	0.65	0.28	0.55

The multivariate assemblage analyses showed consistent forage fish assemblage differences between regions (ANO-SIM: global  $R=0.367$ , significance level = 0.1%), and the MDS shows that these compositional differences are especially pronounced between Sequim and Green Point, while the forage assemblage was highly variable in the Elwha



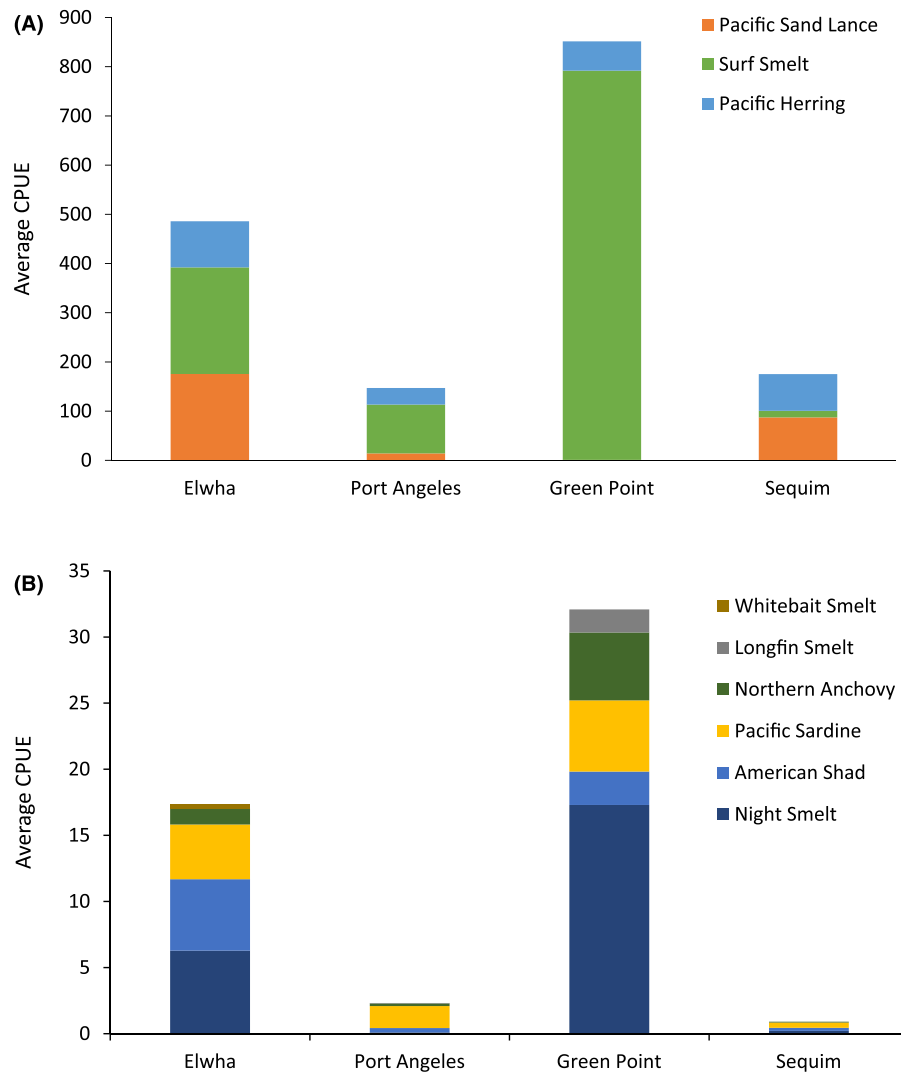


FIGURE 3. Average CPUE of individual forage fish species in each region within the Strait of Juan de Fuca, showing CPUE for (A) the dominant three species caught (Pacific Herring, Surf Smelt, and Pacific Sand Lance) and (B) the remaining forage fish species encountered. Note the different y-axis scales.

and Port Angeles regions (Figure 7A). There were no discernable year effects (ANOSIM:  $R=0$ ,  $P=81\%$ ), and there was no obvious difference in forage community composition pre- and postdam removal (Figure 7B). The explanatory power of the environmental factors we considered on the forage fish assemblage was very low (ANOSIM:  $r<0.05$ ) for all combinations with the best model, including all variables (Pacific decadal oscillation, Oceanic Niño Index, temperature, and salinity;  $r=0.046$ ). Thus, the environmental covariates we evaluated did not explain the spatial differences in forage fish community composition.

Our model for probability of occurrence showed considerable interannual and within-season variability for the three main forage fish species (Figure 8). Each species

exhibited a unique pattern in interannual fluctuations. Pacific Herring exhibited the most annual variability in probability of occurrence and Pacific Sand Lance the least (with the exception of 2012, in which they were exceptionally common). Surf Smelt and Pacific Herring had similar annual patterns of occurrence, with Pacific Sand Lance showing opposite annual probabilities (higher likelihood of occurrence when Surf Smelt and Pacific Herring were low). We found no other trending patterns in annual probability of occurrence for these species.

Within a year, month-to-month changes in probability of occurrence differed among the three dominant species (Figure 8). For Surf Smelt, probability of occurrence peaked in June, when it was almost 50% higher than in the other 5 months. Pacific Herring encounter rates

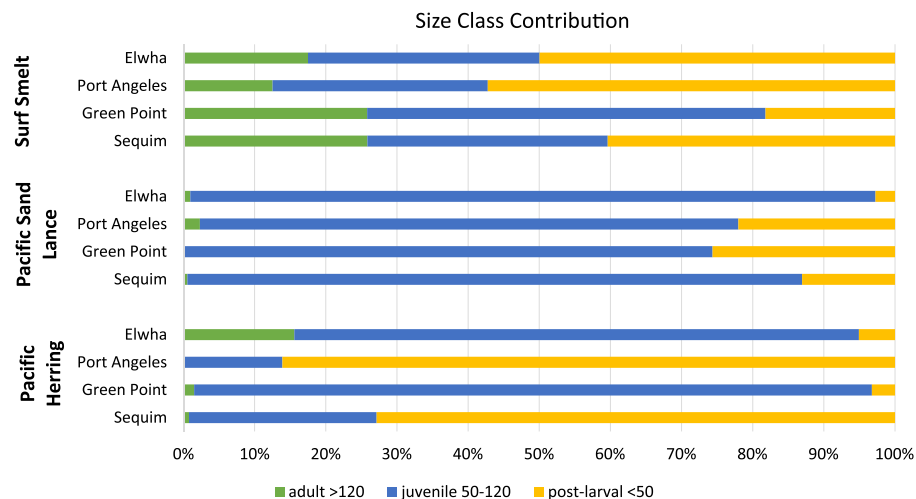


FIGURE 4. Percent of each dominant forage fish species by region and size-class for adult (>120 mm), juvenile (50–120 mm), and postlarval (<50 mm) fish.

increased through the sampling season (Figure 8), with low mean probability of occurrence in April and May (~20% and 25%) and higher rates (~70%) in August and September. Conversely, Pacific Sand Lance was less likely to occur as the year progressed, with the lowest encounter rates in August (Figure 8).

Diversity measures of forage fish populations showed no broad effects of habitat change resulting from dam removal in the Elwha region or reference regions after 2011 (Table 2; Figure 2). Overall abundance of forage fish increased slightly in the entire study area (Figure 2), with both positive and negative effects depending on the individual species. Surf Smelt were more likely to occur following dam removal, with small increases in occurrence (5–15%) in all four regions (Figure 9). Pacific Herring and Pacific Sand Lance were ~10% more likely to occur in the Elwha region following dam removal. For Pacific Herring, probability of occurrence increased ~1.5 times in the Port Angeles region but decreased ~25% in the Sequim region. In contrast, probability of occurrence for Pacific Sand Lance was ~20% higher in the Sequim region but ~10% lower in the Green Point region following dam removal (Figure 9).

## DISCUSSION

Forage fish are dominant fish species in nearshore habitats around the world (Vahteri et al. 2009 [Finland]; Montecarlo and Abunal 2013 [Philippines]; Akel and Philips 2014 [Egypt]; Kanstinger et al. 2016 [Baltic]). In the north-eastern Pacific Ocean, studies along intertidal and shallow subtidal shorelines have found species groups dominated by either forage fish or juvenile salmonids (which can be classified as forage fish in certain circumstances), with

strong spatial and temporal trends in their abundance (Fresh et al. 1979; Emmett et al. 1991; Trevorrow 1998, 2001; Penttila 2007; Toft et al. 2007; Rice et al. 2012; Snauffer et al. 2014; Greene et al. 2015; Rubin et al. 2017). In this study, the prevalence of forage fish species was consistent with findings from these previous studies. In nearshore ecosystems of the Strait of Juan de Fuca, we found a diverse fish assemblage numerically dominated by forage fish. Despite representing only 12.5% of all species caught, forage fish represented more than 82% of all individuals caught over the 9 years we sampled.

In the northeast Pacific Ocean, several interacting factors are likely important determinants of the dominant species group present; habitat preferences, food availability, and proximity to spawning areas are especially relevant at the spatial scales we sampled. Local habitat factors, such as substrate type, exposure, and presence and type of marine vegetation, help determine the prevalence of individual species (Dean et al. 2000; Hamilton and Konar 2007). Beyond local drivers, species prevalence can also be affected by regional factors. Similar to the mixed oceanic and riverine species assemblage at the mouth of the Columbia River (Weitkamp et al. 2012), the assemblage in the Strait of Juan de Fuca is a mix of ocean and inshore species and various size-classes, reflecting its role as a transition zone connecting the Pacific Ocean and the Salish Sea (Miller et al. 1980). The forage fish community in this study was comprised of both persistent and ephemeral components. Three species, Pacific Herring, Surf Smelt, and Pacific Sand Lance, were most abundant and occurred broadly and consistently during the course of our study, allowing for further assessment of distribution patterns. The capture of other oceanic (i.e., Northern Anchovy, Pacific Sardine, Night Smelt, and Whitebait

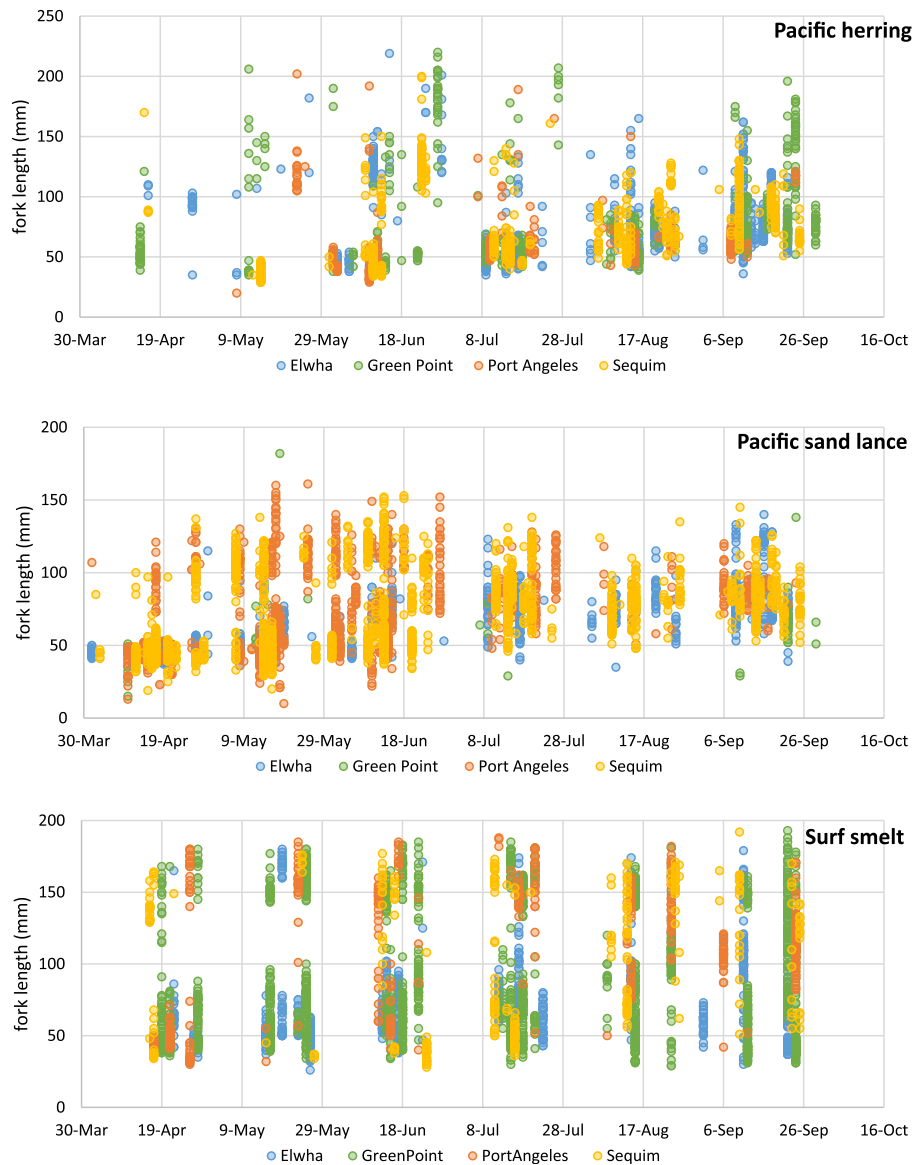


FIGURE 5. Size distributions of measured individuals by region and capture date within a year for Pacific Herring, Pacific Sand Lance, and Surf Smelt.

Smelt) and coastal forage fish species (i.e., Longfin Smelt) typical of interior basins of the Salish Sea (Miller et al. 1980; Penttila 2007; Therriault et al. 2009; Quinn et al. 2012) contributed to community diversity but were not common enough for further spatial or temporal analyses. While the presence of Northern Anchovy in 2010 was noteworthy, it did not coincide with especially poor ocean conditions or elevated ocean conditions like those of 2014–2016 as we would have expected based on Duguid et al. (2019). Variation in diversity indices by region reflected both infrequent catch of uncommon species and extreme dominance of individual species within other regions (e.g., Surf Smelt in the Green Point region; Figure 3).

These same species, Pacific Herring, Surf Smelt, and Pacific Sand Lance, were most prevalent in recent studies of nearshore fish communities in inland portions of the northeastern Pacific Ocean (Fresh 2006; Shaffer et al. 2012) and of pelagic fish assemblages in Puget Sound (Rice et al. 2012; Greene et al. 2015; Shaffer et al. 2020). Intriguingly, the dominance of these three species is not reflected in beach seine collections in the central Strait of Juan de Fuca between 1976 and 1979 (Miller et al. 1980), though this study occurred in more varied and broadly distributed habitats. During that period, the three dominant species were Pacific Staghorn Sculpin *Leptocottus armatus*, English Sole *Parophrys vetulus*, and Sand Sole *Psettichthys melanostictus*, although Pacific Sand Lance

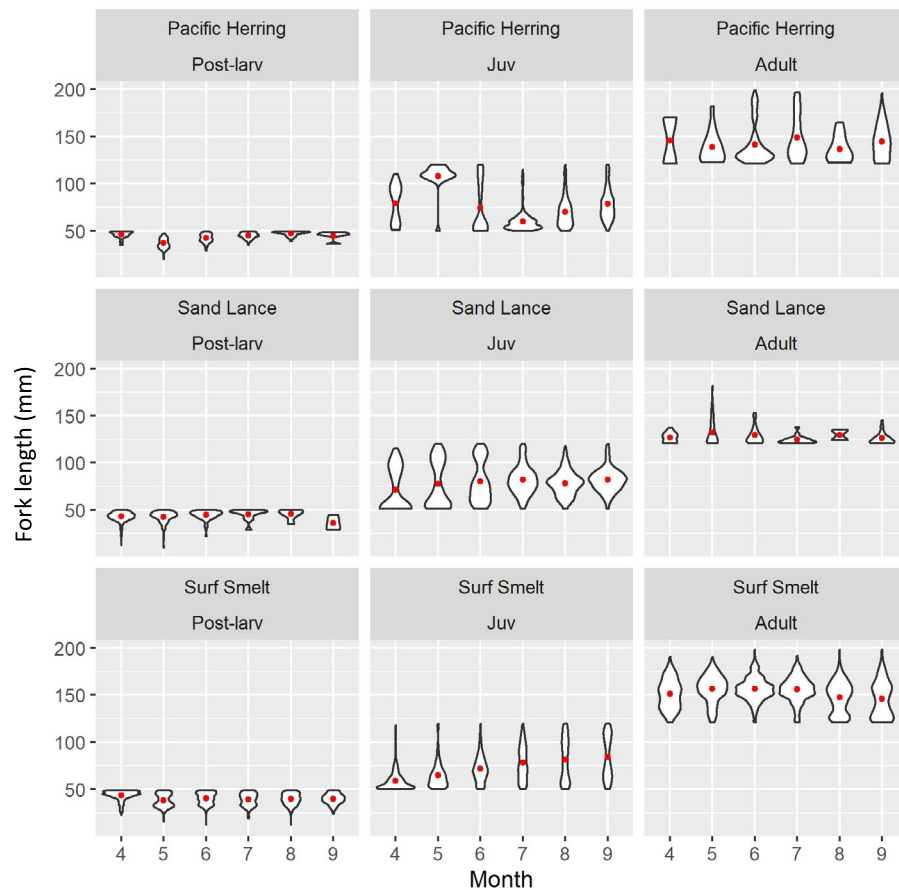


FIGURE 6. Violin plots of measured forage fish fork length (mm) within size-classes (adult > 120 mm, juvenile = 50–120 mm, and postlarval < 50 mm) for Pacific Herring, Pacific Sand Lance, and Surf Smelt.

was among the most abundant species. However, our three dominant forage fish species were common and abundant in tow-net collections that sampled nearshore pelagic habitats from that period (Miller et al. 1980). The difference may not indicate a shift in species inhabiting the Strait of Juan de Fuca, but an increased use of shallow nearshore habitats by these species or could be reflective of differences in sampled habitats between the two studies.

The size distributions observed in our samples reveal how different class structures of each species occupied nearshore habitats during the sampling time frame. While we observed some adults, most of which were Surf Smelt, most individuals we caught were postlarvae and juveniles. Changes in the size distribution over the sampling months showed growth within size-classes and recruitment from smaller size-classes into larger ones, particularly in April and May. This suggested that shallow shoreline habitats in the Strait of Juan de Fuca were functioning as nursery grounds or predation refugia for smaller individuals, functions commonly ascribed to nearshore ecosystems globally

(Paterson and Whitfield 2000; Hay et al. 2001; Beck et al. 2003; McLusky and Elliott 2007; Munsch et al. 2016). The nearshore area in the Strait of Juan de Fuca may be important for other functions throughout the year; we did not target locations or months when spawning activity may occur in the area, particularly for Pacific Herring and Pacific Sand Lance.

Evaluating variation in the nearshore fish community depends on the temporal scope as well as the spatial scale of sampling. In our analyses, exploration of the effects of year, time of year within our sampling window, and sample region on probability of catch and relative abundance showed species-specific differences for Pacific Herring, Pacific Sand Lance, and Surf Smelt, suggesting that unique characteristics in life history and species biology affect distributional patterns. Pacific Herring showed the most variability in abundance and probability of occurrence between years. This species was most abundant in 2014 (Figure 2) but most likely to be caught in 2007 (Figure 8). Patterns in probability of occurrence were markedly similar across years between Pacific Herring and Surf

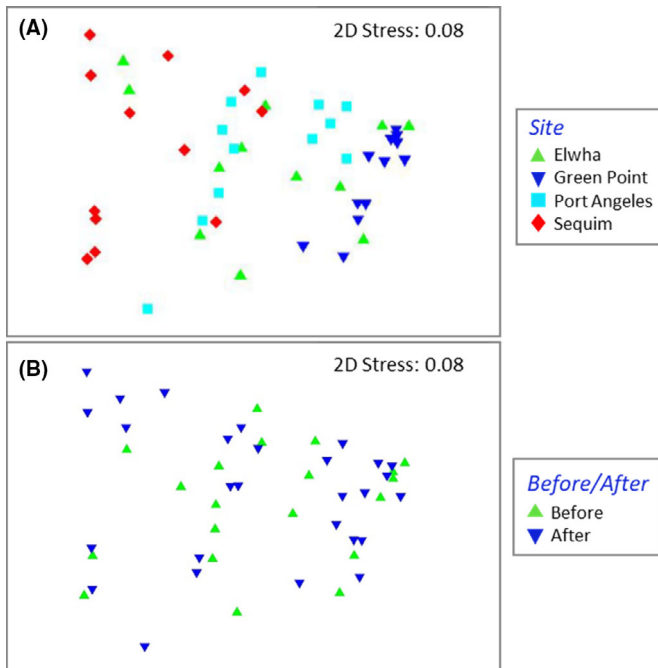


FIGURE 7. Nonmetric multidimensional scaling plots of forage fish community relatedness by (A) site and (B) study year coded as before or during dam removal and after dam removal.

Smelt, with decreases for both species in 2008 and 2012. Conversely, Pacific Sand Lance had the highest probability of occurrence in 2012, an outlier amidst consistent capture probabilities for this species. This could be attributed to the influx of sediment over gravel immediately after dam removal (Rubin et al. 2017), a situation conducive to the burrowing habits of Pacific Sand Lance (Bizzaro et al. 2016). The patterns in probability of occurrence did not necessarily match those in average abundance, as determined by CPUE; there were isolated hauls with a large number of individual species that coincided with a low regional or monthly probability of occurrence.

Sampling spanning up to 3 years in nearshore studies is common (Penttila 2007; Toft et al. 2007; Duffy et al. 2010; Foley et al. 2017), but sampling regimens that span only 2 or 3 years would miss the exceptional variability of forage fish communities that we found and could affect subsequent conclusions. For example, if sampling had been limited to 2006–2007, we would have concluded that Surf Smelt absolutely dominate and that forage fish CPUE is consistently around 500. Thus, our longer data set captured much greater variation in both productivity and species evenness, providing a more complete view of fish community structure. Similarly, sampling in only one or two of the regions would have provided a much different view of the forage fish community. Without sampling in the Green Point region we could not have seen patterns in

the presence of Surf Smelt. Our ability to monitor over a decadal time scale also helps separate the annual variations in demographics of these populations from isolated obscure changes we might observe in short studies (Sandström et al. 2005).

Spatially, we found significant and consistent regional differences in forage fish occurrence of the three primary species caught. Factors that could account for spatial variability in forage fish density between years, months, and regions are complex and depend on processes operating at multiple scales. Thus forage fish occurrence at any particular site will be influenced by local- or site-scale habitat attributes like vegetation and substrate (Toft et al. 2007; Munsch et al. 2016), as well as factors operating at the regional scale, including ocean current patterns, amount of anthropogenic influence, exposure to wind and waves, and presence of riverine influences (Beamer and Fresh 2012; Albo-Puigserver et al. 2017).

Our observations of Surf Smelt distribution appeared tied to regional factors. Given the consistent regional differences, we hypothesized that Surf Smelt abundance in regions of the central Strait of Juan de Fuca was driven primarily by spawning habitat availability. Surf Smelt prefer a mix of coarse sand and gravel for spawning (MacLennan et al. 2010), which is available in all of our regions. Overall, we found an increased probability of encountering Surf Smelt in June coincident with the smelt spawning cycle. We saw abundant Surf Smelt in a variety of size-classes in the Green Point and Elwha regions known to be spawning areas for Surf Smelt (Nabors 2008; Shaffer et al. 2012) but rarely observed them in the Sequim region with no known spawning, despite the physical similarities to other sampling locations. This suggests that Surf Smelt are spawning and rearing in the same area; that is, Surf Smelt populations are local. In the nearby San Juan Islands, a similar pattern was observed, with Surf Smelt most likely to be found in regions associated with spawning areas (Beamer and Fresh 2012). Surf Smelt showed clear increases in average size across the sampling season, particularly within the juvenile size-class, further supporting the concept of local residence and growth.

Spatial patterns were less clear for Pacific Sand Lance, but they were in markedly low numbers and had lower probability of encounter from the Port Angeles and Green Point regions compared with the Sequim and Port Angeles regions. The likelihood of catching Pacific Sand Lance generally decreased monthly across the sampling season. Captured individuals were almost exclusively of a juvenile size. There are documented intertidal spawning areas for Pacific Sand Lance in bays in the Sequim and Port Angeles regions (Bargmann 1998) and also likely significant subtidal spawning areas in the strait (Selleck et al. 2015; Baker et al. 2019). However, this is a winter-

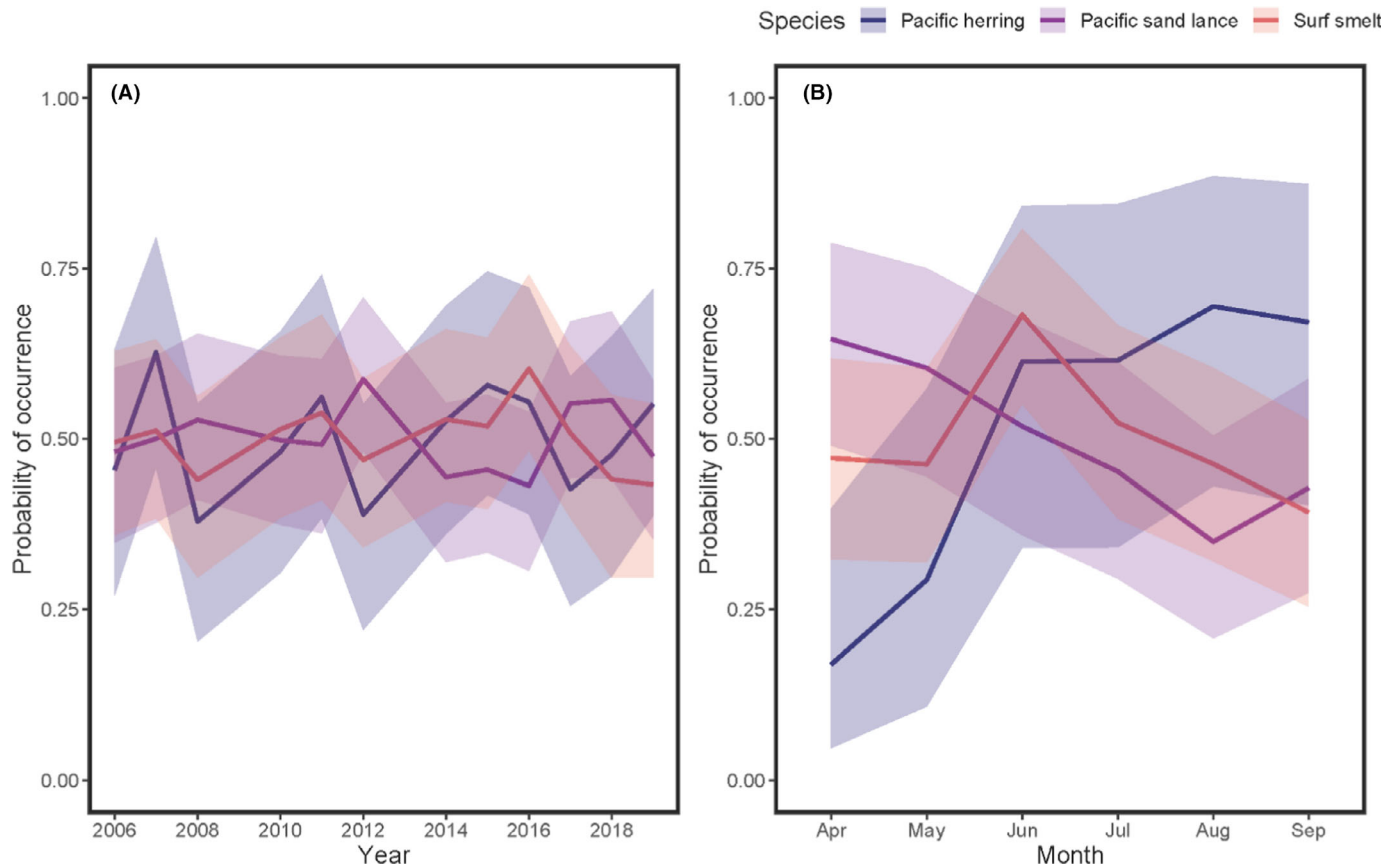


FIGURE 8. Probability of occurrence of Surf Smelt, Pacific Herring, and Pacific Sand Lance by (A) year and (B) month. Lines represent medians, and error bars represent 95% credible intervals.

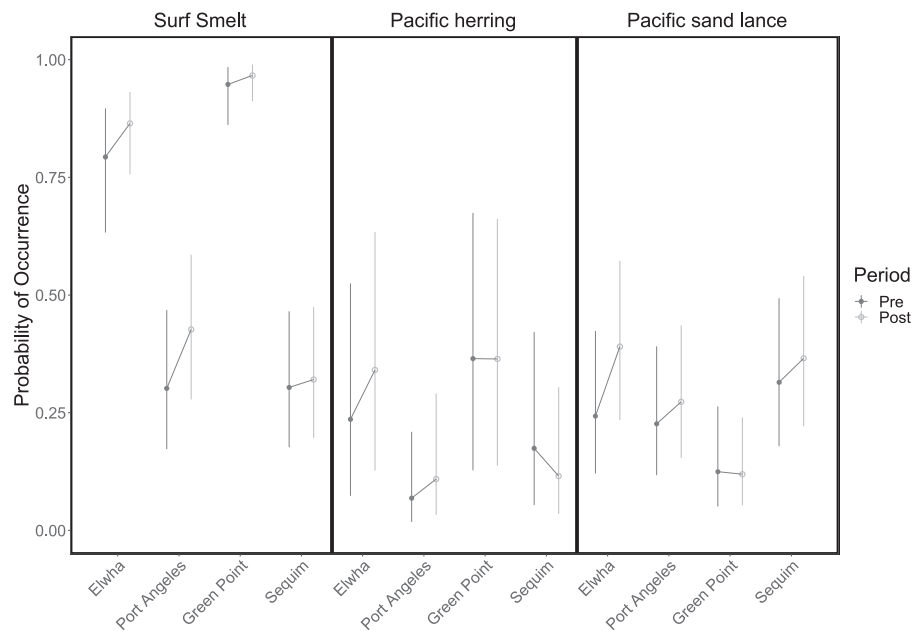


FIGURE 9. Predicted effect of dam removal (pre = before or during removal, post = after removal) on the probability of occurrence of Surf Smelt, Pacific Herring, and Pacific Sand Lance in each of the four regions. Points represent medians, and error bars represent 95% credible intervals.



spawning species (Robards et al. 1999b) and juveniles seem to recruit regularly to nearshore areas (Bizzarro et al. 2016) in a seasonal pattern similar to that seen in nearshore surface waters of northern Puget Sound (Fresh 1979; Haynes and Robinson 2011; Selleck et al. 2015; Baker et al. 2019). The juvenile size-class of captured individuals contained both small and large juveniles in April and May, but June to September samples had stable average juvenile sizes, supporting the idea of fresh influxes of juveniles rather than local growth. In the nearby San Juan Islands, Baker et al. (2019) noted an increase in Pacific Sand Lance occurrence in odd years that was not apparent in our collections.

For Pacific Herring, catch probability increased dramatically during the 6 months we sampled each year. Pacific Herring spawn in late winter and spring, although there are only a few limited Pacific Herring spawning sites in our sampling area (Penttila 2007; Sandell et al. 2019). These spawning sites in Discovery Bay and Dungeness–Sequim Bay are categorized as critical and declining, respectively, based on their historically low spawning biomass during this study (Sandell et al. 2019). We found virtually no adult Pacific Herring in the Sequim region, however, with adult captures occurring almost exclusively in the Elwha region. There are very large spawning populations of Pacific Herring elsewhere in the Salish Sea, especially in the southern Strait of Georgia (Thompson et al. 2017). The strong currents in the eastern Strait of Juan de Fuca (Yang and Khangaonkar 2010) could transport juvenile Pacific Herring into our study region from considerable distances, and juvenile sizes at capture spanned the 50–120-mm range. Therefore, while our catches of Pacific Herring potentially represent some fish from local spawning populations, it is likely that juveniles recruited from spawning locations outside our sampling regions are included in significant numbers. For Pacific Herring, months with low probability of occurrence generally coincided with low densities based on spawn timing elsewhere in the Salish Sea. Adult distributions within the Salish Sea are well described during the winter and spring spawning periods, but migration patterns and distributions of adults and juveniles through the year remain poorly understood (Seitz et al. 2010) and selective impacts on these life stages could have important management implications (Shelton et al. 2014b). Though reported in fall surveys in the Strait of Georgia (Thompson et al. 2020), we found an unexpectedly high likelihood of catching juvenile Pacific Herring in August and September. The increased occurrence late in the season reflects either protracted dispersal of Pacific Herring from Salish Sea spawning grounds to winter feeding grounds in the North Pacific Ocean or use of overwintering areas within the Salish Sea (Penttila 2007).

Although we do not understand the full range of habitat requirements for each dominant forage fish species

beyond their spawning needs, the importance of local habitat conditions (regional differences) is suggested by the variation in diversity and abundance between regions and the spatial separation in forage community composition in some regions shown in the MDS analysis despite their seeming physical similarities. Forage community composition between the Green Point and Sequim regions was particularly distinct, while Elwha and Port Angeles assemblages were quite variable and overlapped one another as well as the other sites. Clearly, there might be finer site-scale habitat characteristics important to the forage fish that are not reflected in our site selection criteria. In our study, the Port Angeles region has armored feeder bluffs, shows high levels of anthropogenic influence, and was characterized by a diverse fish assemblage but relatively low total abundance of forage fish. The Green Point and Elwha sites both feature exposed beaches backed by feeder bluffs, and Green Point consistently had the highest catch of individuals and was particularly productive for Surf Smelt and Night Smelt compared with other areas. The Elwha region, which is directly affected by river-derived sediment output, had the highest diversity of forage fish and the greatest variation in forage community composition. All regions experienced exposure to broad oceanic conditions, such as a degree of upwelling, sea surface temperature, and onshore currents. Large-scale environmental variables and local temperature and salinity measurements could not explain observed patterns in the forage fish assemblage. Thus, while ocean conditions may explain annual fluctuation in some species like Northern Anchovy, they cannot explain the high variability we observed between sampling regions.

In the Strait of Juan de Fuca, geomorphic habitat type is stable, but local habitat features can change due to anthropogenic factors and natural processes. For example, kelp beds and rocky benches tend to be stable features over the time scale we sampled, and areas dominated by feeder bluffs remain as such (Dethier and Kunze 1997; Warrick et al. 2009, 2015; Foley et al. 2017; Rubin et al. 2017). When physical changes do occur, they are localized and typically driven by bluff erosion events, riverine sediment input, and large debris deposition from winter storms. Sediment and algal communities can be highly variable in composition at small scales (e.g., meters), and sediment composition on beaches, which influences spawning habitat for several forage fish species, can be altered at intra-annual to decadal time scales from these processes. We did observe small-scale (meters) physical changes at some sites with respect to such habitat characteristics as beach slope, sediment composition, and characteristics of attached vegetation that we did not measure. Over the course of 14 years in a dynamic environment such as the Strait of Juan de Fuca, such changes are not unexpected.

Localized changes occurred as a result of anthropogenic and natural ecosystem processes. The most striking and rapid changes to habitat conditions in our study area resulted from sediment changes attributed to the removal of two Elwha River dams approximately halfway through our study (removals conducted 2009–2011; Gelfenbaum et al. 2015; Randle et al. 2015; Warrick et al. 2019), causing some noticeable and persistent changes in localized habitat conditions (Warrick et al. 2009, 2015; Miller et al. 2011; Magirl et al. 2015; Foley et al. 2017). From that action, 4 million metric tons of sediment accumulated at the river delta (Warrick et al. 2015) and in Freshwater Bay near the mouth of the Elwha River, and cobble beaches transitioned to sand and gravel (Miller et al. 2011; Foley et al. 2017). This was a unique case wherein a human perturbation released impounded sediment and restored natural sediment depositional processes to nearshore areas. Briefly, major physical changes that have been documented are a significant increase in the size of the Elwha River delta and associated submarine delta, accretion of sediment on beaches in the Elwha drift cell, alterations in sediment composition in shallow subtidal and intertidal areas, and large pulses of suspended sediment entering the strait, often tied to freshet events. These visibly affected beach and subtidal habitat within our Elwha sampling region.

Some of our results might be explained by the significant sediment process changes that occurred in the Elwha region during the course of our study. In the 7 years that we sampled following dam removal, we observed positive trends in presence for several individual species in the marine nearshore environment. Such changes in spawning and rearing habitat in the Elwha region would have been indicated in our data by increased presence of forage fish. Catch per unit effort for many species was high following dam removal relative to preremoval baselines. We did not explicitly measure subtidal or intertidal habitat changes at study locations or directly assess changes to forage fish spawning habitat. Pacific Sand Lance, Pacific Herring, and Surf Smelt all spawn in intertidal areas where alterations to seasonal and annual sediment delivery could affect location and success of spawning (Parks et al. 2013; Wefferling 2014; Parks 2015). Changes in sediment delivery to the nearshore area could occur both from dam removal and from natural bluff erosion processes, but in this study, dam removal functioned as a proxy for responsive nearshore habitat change in the area immediately adjacent to the river mouth.

In other localized Elwha River estuary and plume fish community studies, fish colonized newly created estuarine habitats rapidly (Shaffer et al. 2017). Fish community response to suspended or deposited sediment in shallow subtidal areas depended on what was present prior to dam removal, what material was deposited, and its persistence (Rubin et al. 2017).

For our study, we found that increased occurrence of the three most common forage fish was seen most strongly in the region most directly affected by the dam removal (the Elwha sampling region), with some increase in the adjacent Port Angeles region. Specifically, our model suggested that of the three most common species we sampled, only Surf Smelt were more common following dam removal than prior to it in all four regions. Overall, the forage community composition did not appear very different pre- and postdam removal (Figure 7B). These results imply that regular use of the areas closest to the Elwha River mouth may have been positively affected by habitat change for Pacific Herring and Pacific Sand Lance, while increases in Surf Smelt occurrence throughout the study area were likely unrelated to dam removals since occurrence increased in all four regions, and overall, these individual species responses were not strong enough to result in a collective change in the forage community following dam removal. While our approach did not explicitly incorporate or measure the innumerable specific habitat features that may have changed in response to the dam removal, it was robust enough to provide a signal if this major environmental perturbation had significant direct or indirect effects on forage fish occurrence. Unfortunately data are not currently available for a more thorough analysis of habitat change resulting from dam removal and the specific impacts on the fish community.

We concluded that the main driver of observed spatio-temporal variability in the present study was likely population dynamics (that is, biological factors) in response to local conditions. Given natural variation in presence and abundance, the most common forage fish species appeared resilient to local habitat change. While consistent population responses to large-scale environmental drivers may be revealed by exploring patterns of forage fish abundance on a larger geographic scale, their transient use of habitats within this study area may reduce the explanatory power of large-scale environmental drivers on the presence and abundance of juvenile stages of forage fish. These were the most prominent functional group of fish across the approximately 40 km encompassed by our study regions. We found that their abundance and occurrence varied on a species-specific basis at regional, local, annual, and monthly scales. While monthly patterns in probability of occurrence can be linked to species-specific life history characteristics and migration behaviors, regional variability likely depends upon habitat heterogeneity. For mobile species, such heterogeneity may also mitigate potential negative impacts of short-term perturbations, such as sediment distribution following dam removal. Thus, the preservation of varied nearshore habitats should be considered in developing management plans geared at forage fish.



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## APPENDIX: ADDITIONAL DATA

TABLE A.1. Number of beach seine sets by year and sampling region in the Strait of Juan de Fuca.

Study year and total	Elwha	Green Point	Port Angeles	Sequim	Total set count
2006	14	8	24	43	89
2007	25	22	36	41	124
2008	21	19	35	47	122
2010	20	20	36	42	118
2011	21	15	30	38	104
2012	30	22	36	47	135
2014	22	19	37	38	116
2015	21	19	36	47	123
2016	26	16	42	43	127
2017	26	17	42	40	125
2018	17	8	35	29	89
2019	28	16	42	43	129
Total set count	271	201	431	498	1,401

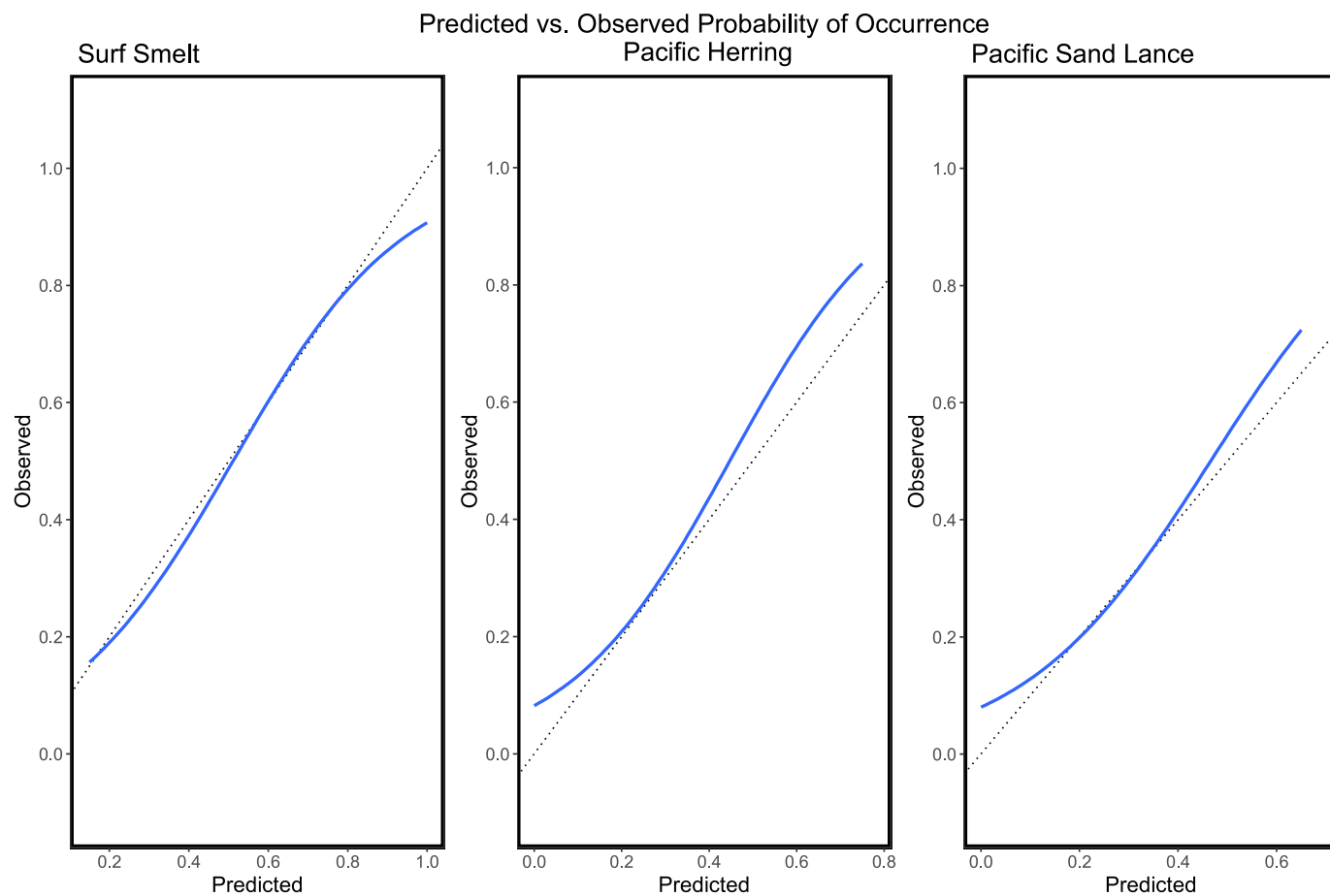


FIGURE A.1. Posterior predictions for probability of occurrence for Surf Smelt, Pacific Herring, and Pacific Sand Lance. The  $x$ -axis values represent the predicted probability of occurrence for each observation on the  $y$ -axis (presence = 1, absence = 0). In each panel, the dotted line represents the one-to-one line and the blue line represents a smoothed quasibinomial fit to the points.

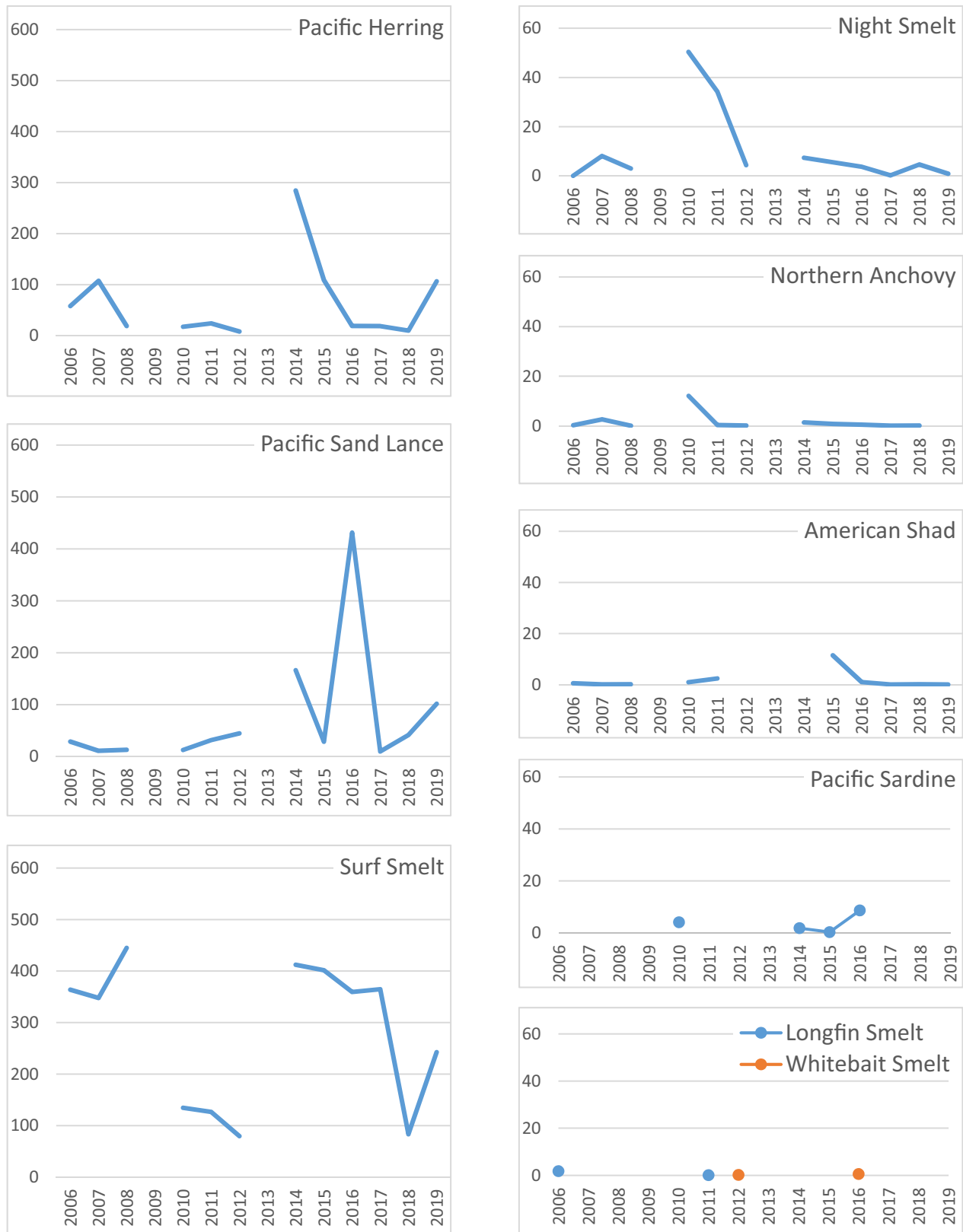


FIGURE A.2. Average annual CPUE of individual forage fish species at sites in the Strait of Juan de Fuca.

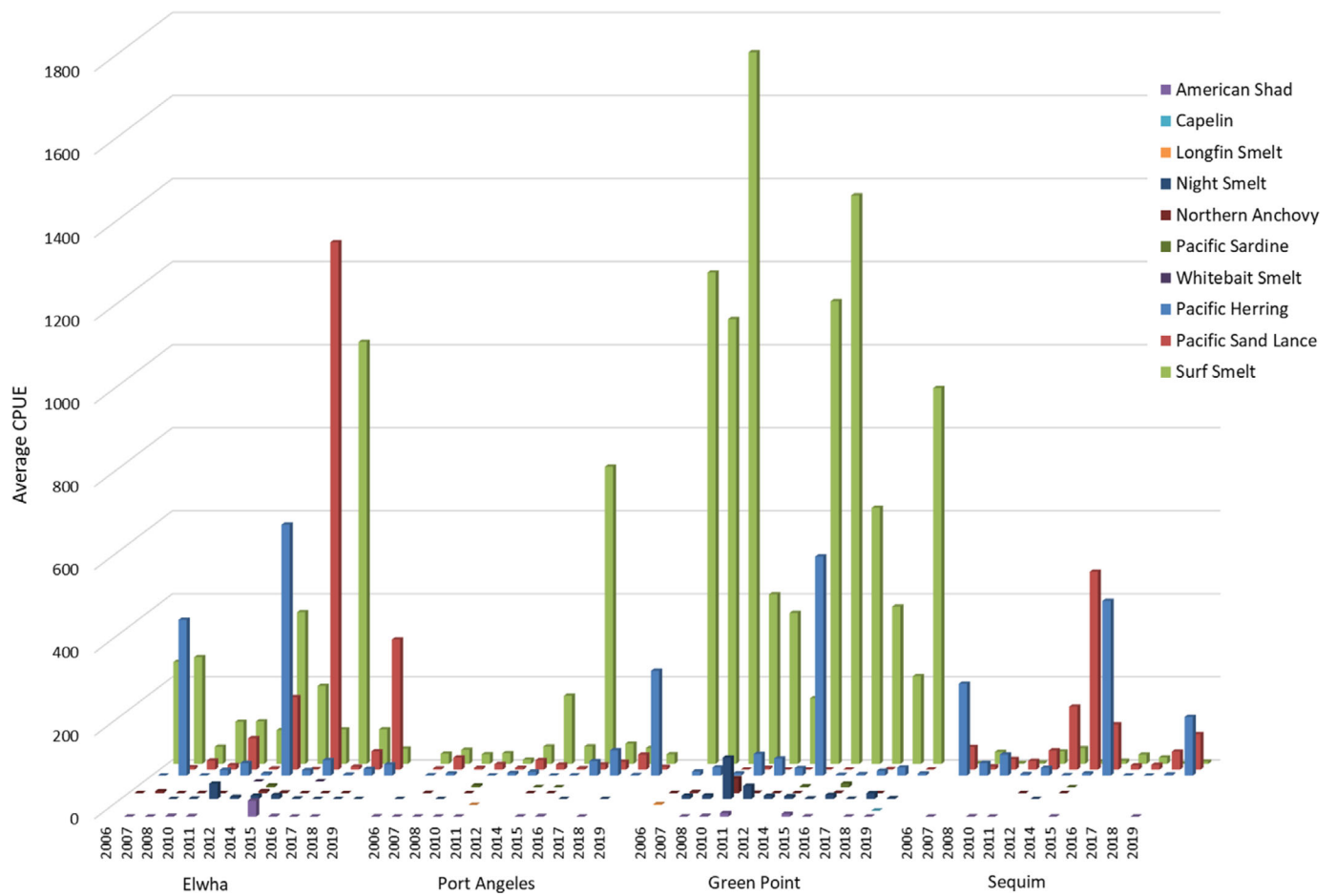


FIGURE A.3. Average CPUE of individual forage fish species in each study year and region within the Strait of Juan de Fuca.