# Introduction

Climate models predict that the effects of environmental change will be felt most acutely in the Arctic, with far-reaching and cascading ecological consequences. Shifts in climate include a predicted increase in sea surface temperatures more than in temperate latitudes, while mean annual temperatures will outpace global averages, rising 3–10°C over the next 80 years (IPCC 2014). Effects of climate change are much broader than just temperature; precipitation is expected to increase 30–50% and observed mean annual sea-ice spatial extent has decreased 3.5–4.1% per decade since 1979 (IPCC 2014). The persistent presence of sea ice and its effect upon the local ecosystem is unique to the Arctic Ocean. The reduction of Arctic sea ice has increased coastal erosion rates, which has increased suspended sediment load and reduced benthic and water column primary production (Bonsell and Dunton 2018). The reduction in primary productivity and increase in temperatures has direct implications on the ecological responses of many cool-temperature reliant taxa (e.g., calanoid copepods and amphipods) and fishes such as Arctic Cod *Boreogadus saida* that prey upon such species (Bradstreet and Cross 1982; Gradinger and Bluhm 2004). As a result of such dependence, changes in Arctic environmental conditions are expected to impact regional fish abundance.

Fish abundance is affected by environmental conditions such as water temperature and salinity and as such, individual fish exhibit behaviors to optimize growth and survival (Cushing 1990; Monaghan 2008). Such parameters may vary by life stage, especially for diadromous fishes (Werner and Gilliam 1984). As poikilotherms, fish have internal temperatures that are regulated by their environment, which causes surrounding water temperatures to affect their rate-dynamic parameters (Pauly 1980). Conditions outside of the optimal thermal range can be lethal, but it is often difficult to determine sub-optimal or sub-lethal effects (Coutant 1987). Within estuarine areas, salinity can fluctuate greatly, and subsequent osmoregulation can incur a substantial energetic cost (Bœuf and Payan 2001). Both marine and diadromous fishes (e.g., gadids and salmonids, respectively) living outside of their optimal salinity limits can experience substantial reductions in growth or higher natural mortality (Arnesen et al. 1993; Dutil et al. 1997). These environmental conditions may be reflected in the presence and abundance of individual fish species and in fish community composition (Jackson et al. 2001; Collie et al. 2008).

Due to the dynamic nature of resources and conditions in the Arctic, some Arctic fishes adopt life-history strategies to increase chances of encountering habitats with favorable conditions (Craig 1984; Power 1997; Roux et al. 2016). Arctic whitefish species such as Arctic Cisco *Coregonus autumnalis*, Broad Whitefish *C. nasus*, Least Cisco *C. sardinella*, and Humpback Whitefish *C. pidschian* are amphidromous, tolerant of moderate levels of salinity, and capable of far-ranging migrations (Bond and Erickson 1985; de March 1989; Fechhelm et al. 1993). Arctic Cisco in Alaskan waters are hatched in the Mackenzie River, Northwest Territories, Canada, and transported >500 km east as juveniles via easterly winds pushing surface currents (von Biela et al. 2013; Zimmerman et al. 2013), while Broad Whitefish, Least Cisco, and Humpback Whitefish spawning populations occur in rivers across northern Alaska (Craig 1984, 1989; Fechhelm et al. 1994). Juvenile whitefishes spend summer months feeding in the estuaries and deltas along the coastal Beaufort Sea and overwinter in deep-water pools or areas of upwelling in local rivers, especially the Colville River (Craig et al. 1985; Fechhelm et al. 1999; Seigle and Gottschalk 2013). Arctic gadids, predominantly Arctic Cod, are also ecologically important and support the Arctic marine ecosystem with their prevalence and high energetic content (Elliott and Gaston 2008; Harter et al. 2013; Thorsteinson and Love 2016). Arctic Cod play a key linkage between abundant zooplankton such as calanoid copepods and amphipods and higher trophic organisms such as Black Guillemot *Cepphus grille*, ringed seals *Pusa hispida*, and beluga whales *Delphinapterus leucas* (Bradstreet and Cross 1982; Harter et al. 2013). Arctic Cod also undertake migratory behavior ostensibly to encounter habitats with favorable conditions during winter months (Vestfals et al. 2019). Pacific salmon have also been documented as Arctic species, with a natal population in the Mackenzie River in Canada (Irvine et al. 2009). Arctic anadromous species undergo movements to find suitable habitat and conditions in this dynamic region, and subsequently make up a substantial portion of the fish community structure/species composition in the nearshore Alaskan Arctic.

In addition to supporting a robust ecosystem, the nearshore fishes of the Alaskan Arctic also provide subsistence food for local indigenous communities (Fechhelm et al. 2007; Thorsteinson and Love 2016). While there are no commercial fisheries in Arctic federal waters, subsistence fisheries in the nearshore Alaska Arctic are important social and nutritional contributions to local Inupiaq communities (Fechhelm et al. 2007; NPFMC 2009). Those these fisheries have limited economic impact, ecological changes to Arctic fish communities would have substantial social ramifications for biological and human communities (Moerlein and Carothers 2012).

Assessing long-term trends and spatial patterns of species composition is imperative for understanding how a fish community responds to changes in environmental variables, especially in nearshore populations (Neves et al. 2016). Further, examining species composition in a multivariate framework provides a more comprehensive understanding of changes occurring to all species at once, rather than to one or two species individually (Fechhelm et al. 1995). Previous studies in Prudhoe Bay and the Alaska Arctic have been focused upon single species or lacking long-term monitoring, which may not capture temporal community changes (Fechhelm et al. 1993, 1999; Thedinga et al. 2013; Streever et al. 2016).

In this study, we assessed the effects of how the fish community is changing in response to shifts in environmental conditions within a nearshore semi-estuarine ecosystem in Prudhoe Bay, Alaska, at one of the only long-term monitoring projects of Arctic fishes. We hypothesized that ongoing shifts in Arctic environmental conditions would bring about measurable changes in fish populations during 2001–2018. To quantify changes in fish community metrics we assessed 1) species richness and rare species presence over time, 2) effects of environmental variables upon species composition and 3) species composition and abundance changes over time. Given the substantial importance of nearshore Arctic fishes to terrestrial and marine ecosystems and to local subsistence users, it is important to understand how fishes respond to their changing environment.

# Methods

## Study Area

This study was conducted in the Arctic Ocean along the coast near Prudhoe Bay, Alaska, 2001–2018 (Figure 1). Prudhoe Bay is a semi-estuarine bay of the Beaufort Sea formed near the mouth of the Sagavanirktok River delta. The immediate surrounding coastal waters are shallow, with the 6-m depth contour less than five km from most parts of natural, unaltered shore and several barrier islands are within 15 km of shore (Ross 1988). Much of the terrestrial environment around Prudhoe Bay has developed infrastructure for the extraction and processing of oil, with many permanent structures inland from the coast. Several oil extraction and processing facilities have been constructed on man-made islands that are connected to shore with gravel causeways and bridge breaches (Ross 1988).

## Fish Sampling

Four stations spaced approximately 27 km apart along the coast were established for daily fish monitoring (Figure 1). From west to east, these sites are identified as Site 220 (1 km west of the West Dock causeway), Site 218 (West Beach drilling pad), Site 214 (Niakuk drilling pad), and Site 230 (eastern side of the Endicott Causeway). Fish monitoring occurred at each of the four sampling locations using side-by-side fyke nets, each with an opening of 1.8 m by 1.7 m, opening towards the coastline, with a 60-m block net leading to shore. A 15-m blocker wing was attached to the outer edge of each cod end. Using this bi-directional sampling method, fyke nets intercepted and caught fish moving along the shoreline in either direction. All lead nets and wings were constructed from 2.5-cm stretch mesh, while the fyke net mesh consisted of 1.27-cm stretch mesh. Three consecutive throats were located behind each 1.7-m frame opening, with the outermost throat having a functional width of 11.4 cm. Net specifications were consistently used during the study, with a modification in 2009 to add a vertical metal bar to the fyke net funnel to prevent entry by marine mammals.

Sampling sites were operated from approximately 01 July through 01 September each year, with the precise dates of installation and removal for each site varying annually. Each net was checked daily unless conditions prevented sampling, and fish were identified to and enumerated by species according to Mecklenburg et al. (2002), George et al. (2009), and Thorsteinson and Love (2016). Length measurements were collected for a subsample of pre-determined species using protocols established in Priest et al. (2018) and Green et al. (2018), and fish were released offshore away from the cod-end openings to minimize recapture. Field sampling protocols, including sampling sites, were essentially unchanged from 2001 to 2018.

## Environmental Data Sources

Environmental variables examined were water temperature (°C), salinity (ppt), discharge for the Sagavanirktok River (m3/s), and wind speed and directionality (km/h; east/west). Water temperature and salinity data were collected daily during each sampling event at each site near the fyke net cod ends using a calibrated handheld YSI 30 salinity / conductivity / temperature meter (YSI Inc., Yellow Springs, Ohio) at the bottom, mid-water column, and just below the surface. For data analyses, measurements taken near the top of the water column were used. Daily Sagavanirktok River discharge data were collected by a United States Geological Survey (USGS) gaging station approximately 170 km upriver from the river mouth, near Pump Station 3. Wind data were collected hourly by the National Weather Service (NWS) at the Deadhorse Airport meteorological data collecting site (PASC) located 12 km inland from Prudhoe Bay. Wind direction was recorded as cardinal direction (0–360) and averaged using the circular mean, then converted from polar to cartesian coordinates to get the East-West unit vectors, using:

## Data Analyses

Abundance data were recorded by net site and side for each species; however, both net sides were aggregated for analyses. Fish abundance data were pooled and scaled by combined sampling effort for biweekly catch per unit effort (CPUE) by species. All environmental variables were assessed in a correlation matrix, with no variables that were highly correlated (>0.5). All significance testing was done at the α = 0.05 level, and data were imported and analyzed using the statistical program R (R Foundation, https://www.R-project.org, Version 3.6.0).

## Species Richness and Rare Species Presence

To investigate trends in annual and seasonal species richness, Generalized Additive Models (GAMs) were used from package “mgcv” in R. This addressed potential curvature in the models, as GAMs are amenable to non-linear response curves commonly found in ecological response scenarios (Guisan et al. 2002). Expected values of species richness were modeled as:

where was defined as the number of unique species across all sites combined for each biweekly period. The variable was the biweekly sampling period that was assigned as four events evenly distributed throughout the sampling season (i.e., period 1 = start date–July 15, period 2 = July 16–31, period 3 = August 1–15, and period 4 = August 16–end date). Top-fitting models were determined using Akaike’s Information Criterion (AIC) and the “dredge” function from the R package “MuMIn”. Smoothing functions were restricted to k=3 to prevent overfitting of the model, and were tested against null models as well as models without any smoothing terms.

To determine whether there were changes in the presence of “rare” species (defined as species ≤ 100 individuals caught in all samples combined), each rare species was assessed using Generalized Linear Models (GLMs) of binomial logistic regression. The expected mean value of species *j*, was estimated as:

where was the sample year, was the effect for each Station *s*, and was the biweekly sampling period (1–4).

## Effects of Environmental Variables Upon Species Composition

To determine the effects of environmental variables upon species assemblage structure, we began with a dissimilarity matrix of the multivariate catch data using Bray-Curtis distances. The Bray-Curtis dissimilarity matrix was reduced to three dimensions using non-metric multidimensional scaling (nMDS) using k=3 to get stress < 0.2. Response variables for multivariate analyses were CPUE values for each species which were fourth-root transformed, while explanatory environmental variables were square-root transformed. Both response and environmental variables were standardized to the percent of the maximum transformed catch or environmental variable. To prevent rare species from dominating multivariate analyses, we restricted analyses to the species whose abundance was greater than 100 fish, all catches combined (Poos and Jackson 2012). Multivariate analyses were conducted using the “vegan” package in R, which allowed for the multivariate analysis of quantitative environmental variables upon the responding species assemblages (Oksanen et al. 2018).

A multivariate Mantel-type test (vegan command: bioenv()) was conducted on the biweekly catch matrix of Bray-Curtis distances with a Euclidean distance metric and Spearman correlation method to find the optimal subset of environmental variables describing species composition. Multivariate models after this included only these parameters and the spatial-temporal variables year and station. Significance testing of environmental variables was conducted using vector and factor fitting upon MDS1 & MDS2 (vegan command: envfit()). The similarity percentile (vegan command: simper()) was calculated to determine which species contributed to the Bray-Curtis dissimilarity using pairwise comparisons between each sample year, station, and biweekly period (Clarke 1993; Oksanen et al. 2018).

The most parsimonious model of environmental variables on the species CPUE dissimilarity matrix was determined by Permutational Analysis of Variance (PERMANOVA) using the standardized and transformed environmental variables. Biweekly periods with varying levels of effort were accounted by standardizing for sampling effort (CPUE); biweekly periods with no data coverage in environmental monitoring were excluded from analyses. The full model for PERMANOVA was:

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where was the Bray-Curtis dissimilarity matrix of transformed and standardized CPUE for all non-rare species, and were the surface water measurements, and was the East-West wind vector (-1 = 270° West wind; 1 = 90° East wind); variables , , and were the same as defined for previous models. The top fitting PERMANOVA model was determined using backward stepwise model selection, with improved model fit defined as a reduction in residual R2 using marginal results (vegan command adonis()).

## Species Composition Changes Over Time

To assess how species composition changed over time, models of the nMDS time-series data were evaluated using nested linear effects models (station effects by year) compared to Generalized Additive Models:

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where was each of the three multi-dimensional scaling axes and variables , , and were the same as defined for previous models. The smoothing parameter was tested against a model without smoothed effects, measured using the proportion of explained deviance. The optimal number of breakpoints in the time series was tested using the Chow Test for structural breaks (Bai and Perron 2003) using package “strucchange” (Zeileis et al. 2015).

The effect of whether individual species have changed over time or in response to water temperature and salinity was investigated using linear regression:

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where is the biweekly CPUE of species k at each station and variables , , , , and were the same as defined for previous models. Changes in variability of catches over time was determined using the annual coefficient of variation (CV) defined as , and the annual CV was evaluated in a linear model by year for each species. Linear models were not adjusted for Bonferroni corrections.

# Results

## Fish Sampling

From 2001 to 2018, a total of 1,784,593 fish were captured in fyke nets and identified to one of 31 fish species (Table 1). Fishes that could only be identified to genus (*n*=76), were hybrids (*n*=22), or could not be identified (*n*=2), were excluded from analyses. Of the 31 species used in analyses, 14 were rare species and 17 were non-rare species (Table 1). Total catch per species per biweekly samples (aggregated catch) ranged from 0 to 324,692 fish. The seven most abundant species accounted for approximately 92% of all fish recorded in this study, with the most common species (Arctic Cod) accounting for 33% of the total catch. Six species (Arctic Cisco, Arctic Flounder *Liopsetta glacialis*, Broad Whitefish, Fourhorn Sculpin *Myoxocephalus quadricornis*, Least Cisco, and Rainbow Smelt *Osmerus mordax*) were present in all biweekly station samples.

## Species Richness and Rare Species Presence

Species richness in the aggregated samples (year by biweekly period by station) ranged from 9 to 17, with a mean of 13.1 species present. Species richness increased significantly from 2001 to 2018 (GAM; t value = 3.386, p = 0.001) and over the season (GAM, k = 3: F = 62.85, edf = 1.83, p < 0.001). The rate of increase in species richness was not constant among biweekly periods, as there was a greater increase in species richness early in the season (biweekly period 1) compared to the late season (biweekly period 4; Figure 2). While the rate of species richness trends varied among stations, the increasing trend in species richness over years and during the season occurred at all stations.

Results from the binomial presence GLM of rare species (*n* = 14) from 2001 to 2018 showed significant increases each year for Slimy Sculpin *Cottus cognatus* (estimate = 0.48, SE = 0.220, p = 0.028) and Burbot *Lota lota* (estimate = 0.23, SE = 0.079, p = 0.003) and a significant decrease for Bering Cisco *Coregonus laurettae* (estimate = -0.10, SE = 0.043, p = 0.019; Figure 3). Two additional species showed a significant trend in presence over the course of the season: Chum Salmon *Oncorhynchus keta* and unidentified snailfish *Liparis* spp. both increased in abundance as biweekly periods (intra-seasonal duration) increased (estimate = 0.72, SE = 0.222, p = 0.001, and estimate = 3.00, SE = 0.990, p = 0.002, respectively).

## Effects of Environmental Variables on Species Composition

From 2001 to 2018, environmental conditions at the four sampling stations varied temporally and spatially. Water temperature ranged from 2.1 to 12.7° C (mean = 8.1° C, SD = 1.98) and salinity ranged from 0.14 to 28.7 ppt (mean = 11.4 ppt, SD = 7.40). Annual water temperature increased significantly over 2001–2018 (linear regression, estimate = 0.08, SE = 0.021, p = 0.001), but there was no significant change in salinity among years (linear regression, estimate = 0.06, SE = 0.096, p = 0.53). Among the stations, water temperature fluctuated substantially but was highest on average at station 230 and lowest at station 220, while salinity was highest on average at station 220 and lowest at station 230 (Figure 4). Discharge from the Sagavanirktok River ranged from 39.3 to 327.7 m3/s (mean = 135.1 m3/s, SD = 54.1), with a significant increase in discharge from 2001–2018 (linear regression, estimate = 65.17, SE = 31.83, p = 0.045). Wind speed ranged from 10.5 to 36.1 kph (mean = 17.1 kph, SD = 3.84), with a mean direction of 42.9° (i.e., Northeast). There were no significant changes in wind speed (linear regression, estimate = 0.05, SE = 0.028, p = 0.109) over 2001–2018, while the East-West wind directionality shifted to become more easterly over the same time period (estimate = 0.02, SE = 0.008, p = 0.015). Results from a correlation of environmental variables showed that the most correlated variables were salinity and Sagavanirktok River discharge (-0.28).

Results from a multivariate Mantel-type test upon the biweekly catch matrix showed that the optimal subset of parameters describing species composition were comprised of biweekly period, water salinity, and water temperature (correlation 0.391). As a result, only these three parameters and the spatial-temporal variables year and station were used in the subsequent nMDS assessments and PERMANOVA models. The nMDS was fit using k=3 with convergent stress of 0.156. Analysis of the nMDS by environmental vectors revealed that species composition had significant temporal associations for biweekly periods and years (R2 = 0.442, p < 0.001; R2 = 0.048, p = 0.003, respectively). Species composition was associated with water salinity (R2 = 0.571, p < 0.001), while water temperature was marginally significant (R2 = 0.021, p = 0.058). We also found that species composition was significantly different among stations (R2 = 0.306, p < 0.001).

While there was substantial overlap in species composition among all stations, there was a clear divide between eastern (214 and 230) and western (218 and 220) stations. The nMDS centroids of the eastern stations and the western stations were outside of the 95% CI ellipse for each group (Figure 5). The top five species accounting for the difference between eastern and western sites were Round Whitefish *Prosopium cylindraceum*, Threespine Stickleback *Gasterosteus aculeatus*, Pacific Herring *Clupea pallasii*, Ninespine Stickleback *Pungitius pungitius*, and Arctic Grayling *Thymallus arcticus*, contributing 37.1% of the differences from the similarity percentage analysis. Pearson correlations between species catch and the three nMDS axes identified the dominant species affecting species composition: Threespine Stickleback was the species most associated with axis 1 (correlation = 0.753), Round Whitefish was the species most associated with axis 2 (correlation = -0.697), and Arctic Flounder was the species most associated with axis 3 (correlation = 0.756).

The marginal PERMANOVA model containing year, station, biweekly period, water temperature, and salinity explained 46.8% of the sample variation. There were significant associations between the species composition and each of the five variables: year (marginal R2 = 0.029, pseudo-F = 13.6, p = 0.001), station (marginal R2 = 0.087, pseudo-F = 13.8, p = 0.001), biweekly period (marginal R2 = 0.110, pseudo-F = 17.6, p = 0.001), water temperature (marginal R2 = 0.012, pseudo-F = 5.7, p = 0.001), and salinity (marginal R2 = 0.020, pseudo-F = 9.5, p = 0.001). The sequential (Type I) sums of squares PERMANOVA model (Station + biweekly + Year + water temperature + salinity) showed effects of water temperature (R2 = 0.017) and salinity (R2 = 0.020) upon species composition, even after spatio-temporal variables were isolated.

## Species Composition and Abundance Changes

Model selection results of the nMDS axes time series showed that nMDS axes 1 and 2 were best fit with a non-linear GAM framework (measured by percent deviance explained), while nMDS axis 3 was best fit with a linear model. For axes 1 and 2, there was a significant non-linear increase and decrease from 2001–2018, respectively. For axis 2, there was a significant non-linear decrease from 2001–2018. For axis 3, there was no significant change over the same time period. Results from the F-statistic (Chow test statistic) showed that of the 12 station/axis combinations, three showed weak support of structural breaks, with the Bayesian Information Criterion for these three slightly lowest at one optimal breakpoint. Based on these results, it was concluded that the overall time series of the nMDS axes showed no structural change.

The linear models of the CPUE for each individual species showed significant associations in abundance. Six species changed significantly in abundance over time from 2001–2018: Broad Whitefish and Saffron Cod *Eleginus gracilis* increased in abundance while Arctic Cod, Fourhorn Sculpin, Humpback Whitefish, and Least Cisco decreased in abundance (Table 2). Water temperature significantly affected the abundance of Arctic Flounder, Broad Whitefish, Dolly Varden *Salvelinus malma*, Fourhorn Sculpin, and Saffron Cod. Salinity also significantly affected the abundance of Arctic Cisco, Capelin *Mallotus villosus*, Dolly Varden, Humpback Whitefish, Least Cisco, Pacific Herring, and Saffron Cod. The annual variability of catches increased for Dolly Varden and decreased for Saffron Cod.

# Discussion

Our analyses found several changes in measurements of fish species composition as well as significant associations between environmental conditions and the fish populations of Prudhoe Bay, Alaska. Assessing the shifts in environmental conditions and commensurate changes in species composition provides insight into a region undergoing substantial climatic changes (IPCC 2014). Local and regional increases in some environmental drivers (e.g., temperature, river discharge, eastern winds) and reductions in others (e.g., ice cover), result in changes in species abundances and proportions. With shifts in conditions, generalist species adapt to a wide range of conditions (including new and old conditions) to proliferate (Wilson et al. 2008; Fossheim et al. 2015; Kortsch et al. 2015). With competition and limited resources, we expect increases in abundance of species that are better suited for these new conditions (e.g., Saffron Cod) with declines in abundance of species that are stenohaline and stenothermal (e.g., Arctic Cod; Fechhelm et al. 1992, 1993, 1995; Laurel et al. 2016; Vestfals et al. 2019). Specifically, continued increases in temperature, river discharge, and eastern winds may select for a fish community that is more reflective of estuarine conditions and more anadromous in composition. This study found several changes in fish species composition as well as significant associations between environmental conditions and the fish populations of Prudhoe Bay, favoring more generalist species.

Our study found that species richness increased significantly from 2001-2018 in Prudhoe Bay, Alaska, at a rate of approximately one additional species per decade. Species richness increased nonlinearly throughout the sampling season, tapering off at the end of the season when species richness is highest and ice coverage is lowest. This is likely due to the typical wind patterns and reduced ice cover (increasing fetch) during mid- to late-August, causing nearshore increases in salinity and catch of marine fishes. We identified a total of 31 unique species in this study, representing 10% of the approximately 310 fish species known to inhabit the Arctic Ocean (Mecklenburg et al. 2011; Reist et al. 2006). The increase in number of species caught is due to shifts in distributions of Arctic fish species and increases in local ranges, as species from lower latitudes of Arctic Alaska expand their range northward. It is plausible to expect that given documented northward distribution shifts of species from lower latitudes of Arctic Alaska, there is the potential for further increases in species richness in the Beaufort Sea (Grebmeier et al. 2006; Mueter and Litzow 2008). Increasing species richness is probable as spatial distributions of species expand northward and marine water temperatures increase (Hiddink and ter Hofstede 2008). Changes to both inter- and intra-annual species richness have potential to affect the Prudhoe Bay species composition.

Though no major changes in species composition because of increased rare species abundance are likely, three rare species showed significant changes over time. The two rare species that increased in abundance (Slimy Sculpin and Burbot) are freshwater species, demonstrating either a potential shift in acceptable nearshore environmental conditions or possibly an expansion in the freshwater populations as individuals search for new habitat. Spatial range expansion by freshwater fishes into the marginal estuarine habitat could be reflective of favorable recruitment conditions in local rivers (Lehodey et al. 2006). Alternatively, the increase in river discharge could be displacing and transporting freshwater fishes into the Sagavanirktok River delta. The rare species that has declined (Bering Cisco) is anadromous and has not been captured since a single sample in 2015.

In addition to increasing species richness, the species composition of Prudhoe Bay fishes showed strong evidence for being influenced by spatio-temporal and environmental variables, despite existing in a dynamic environment. Prevailing theories of life-history responses to environmental changes posit that changes to water conditions will result in observable changes to fish populations (Lehodey et al. 2006). While several environmental variables significantly changed over the course of the study, it is especially notable that annual water temperature became approximately 1.4° C warmer. Species compositions models demonstrated that catch abundances were substantially influenced by water temperature. On an individual species level, water temperature positively affects growth parameters of whitefishes and parabolically influences the growth of cool-water adapted Arctic Cod, maximizing Arctic Cod growth around 5 °C (Fechhelm et al. 1992, 1993; Laurel et al. 2016). Our study documented several species that both significantly changed in annual abundance and were associated with water temperature: Broad Whitefish, Fourhorn Sculpin, and Saffron Cod were significantly positively associated with water temperature, while Humpback Whitefish were negatively associated with water temperature. While many species were positively associated with water temperature, further increases could push fish past optimal metabolic conditions or cause detrimental species interactions (e.g., increased trophic competition; Reist et al. 2006).

Increases in water temperature could also be linked to changes in river discharge. The annual freshwater discharge from the Sagavanirktok River significantly increased 25.4 m3/s over the course of the study. While river discharge appeared only to be minorly influential to models of species composition, the amount of freshwater input to nearshore areas strongly affects the levels of other variables (i.e., salinity, temperature) and it is difficult to separate multicollinearity between variables. River discharge affects estuarine species composition and contributes to nearshore productivity by way of terrestrial carbon transfer, extending habitat extents, and providing sediment transport to create barrier islands (Loneragan and Bunn 1999; Costa et al. 2007). Such contributions mean that the significant changes in Sagavanirktok River discharge have the potential to disrupt fish community composition.

We found a significant increase in easterly winds over time and associations between wind direction and species composition. The change towards easterly winds increases the occurrence of marine upwelling events which lowers local water levels and brings nutrient-rich, high-saline water towards nearshore regions (Ross 1988). Easterly winds also facilitate the transport of juvenile Arctic Cisco from the Mackenzie River while hindering movements of fish from the Colville River (Fechhelm and Fissel 1988). Under such wind regimes in Prudhoe Bay, Arctic Cisco abundance would benefit from increased easterly winds while Least Cisco abundance would decrease. Wind direction in Prudhoe Bay also strongly affects local salinity by causing upwelling or intrusions of marine waters to either retreat or advance shoreward.

While salinity did not significantly change over the study, it was very important to all models of species composition. We found that salinity greatly affected species composition, in the expected manner of marine species being associated with higher salinity. The significant increase in river discharge likely influenced the distribution of salinity gradients in estuarine locations by extending or retracting freshwater plumes, which affects osmoregulation and feeding rates (de March 1989; Arnesen et al. 1993; Bœuf and Payan 2001). Salinity is also likely partly responsible for distinct spatial patterns: because each sampling station had a unique salinity profile, differences in species composition among stations were distinct in the nMDS ordination. Similarly, species composition differences between eastern and western stations were influenced by species that were amphidromous and tolerant of estuarine fluctuations. Species that drove changes in species composition are euryhaline and eurythermal, indicating that there does not appear to be a shift toward more predominately marine or freshwater species types, but rather a selection toward species that are more generalist in nature. Anadromous fishes are tolerant of a wide range of conditions and would be expected to be better positioned for increased environmental variability (Fechhelm et al. 1993; Bisson et al. 2009; IPCC 2014). Several species significantly changed in abundance and also were influenced by salinity: Humpback Whitefish and Least Cisco were negatively associated with salinity, and Saffron Cod was positively associated with salinity. Local salinity conditions are also highly dependent upon other variables such as wind direction and river discharge. Thus, because salinity was deemed important to many models influencing species assemblage structure, we posit that any potential future changes to wind patterns and regional precipitation will affect fishes by altering local salinity (Fechhelm et al. 1993).

One variable that was not able to be examined in this study was sea ice (extent and duration). This was primarily due to a lack of fine-scale sea ice data available from the National Snow and Ice Data Center. Sea ice is known to influence distribution of Arctic fish species such as Arctic Cod, and known to affect nearshore turbidity (Bradstreet and Cross 1982; Gradinger and Bluhm 2004; Bonsell and Dunton 2018). Researchers are currently processing high-resolution shorefast ice imagery that will cover Prudhoe Bay (A. Mahoney, University of Alaska Fairbanks Geophysical Institute, personal communication). However, preliminary modeling efforts of coarse-scale ice coverage did not show a relationship between species composition and regional sea ice indices. Future research should examine whether declines in sea ice influence patterns in species abundance.

While the multivariate methods used in this study parsed out the individual effects of each environmental variable, correlation between variables remains a difficult challenge to assign effects. To address issues of correlation, we used a variety of univariate and multivariate approaches to determine whether influence of environmental conditions, as well as a high threshold for multicollinearity. Similarly, multivariate models make it difficult to ascertain precisely which species cause changes between samples and cannot quantify precise effects or even directionality of responses. The variability of the environmental conditions is also likely the reason explaining why the top PERMANOVA model explained approximately half of the variation of the biweekly catches. This high amount of residual variability is likely a relic of the natural environmental fluctuations. Given the considerable environmental fluctuations in the Arctic (e.g., solar insolation, temperature swings, and wind events), it is unsurprising to see high amounts of residual variability in the PERMANOVA models (Anderson 2001).

While this study did not address ages or age-structures of fish species, many of the fish captured were juveniles, with the nearshore environment of Prudhoe Bay providing an important habitat for many early-life stage fishes (Craig 1984; von Biela et al. 2013). Nearshore areas are important habitats that provide a wide diversity of trophic contributions, increased nursery production of juvenile fishes, and ontogenetic migration corridors (Beck et al. 2001; Sheaves et al. 2014). The variety of environmental conditions within the Prudhoe Bay nearshore, comprised of a gradient of temperatures, salinities, and turbidities, ideally allow for juvenile fishes to have access to a range of conditions that optimize their growth (Cyrus and Blaber 1987; Thorpe 1994). Changes to these environmental conditions or to the community structure of populations may have a detrimental effect upon the recruitment of juveniles of many species. Future studies are recommended to assess the impacts of a changing climate upon juvenile recruitment.

We presumed that trends in project catches were reflective of local abundance and not a function of changing sampling efficiency. For example, we assumed that changes in assemblage structure at different wind conditions were reflective of fish distributional movement patterns in response to wind and not changes in sampling selectivity or efficacy. To counter changes in spatio-temporal sampling efficiency, we pooled samples to a biweekly sampling period (to account for short-term fluctuations and minor gaps in sampling) and grouped eastern and western sampling sites. The geographic spread of sample sites attempted to mitigate effects from any potential inshore/offshore or East/West species distribution by virtue of sampling locations that varied in proximity to river deltas and along isthmuses that extended into Prudhoe Bay. By having four sample sites and biweekly sample periods across broad spatial and temporal sampling units, fish catches were representative of nearly the entire Prudhoe Bay fish species composition.

Resilience of ecological communities to persist during changes to their habitat or environment is a characteristic of healthy communities with high biological diversity and wide response diversity of these species (Peterson et al. 1998; Elmqvist et al. 2003). Thus, despite natural variability and increasing shifts in environmental conditions, the observed changes in species composition in this study demonstrate a fish community able to respond to increased stressors. However, as the pace of environmental change increases further, it is less clear whether the Arctic fish community will continue to have such resilience if variability of ecological community composition increases (Warwick and Clarke 1993). If population variability increases, such warnings could indicate imminent sudden changes in community organization or collapses in abundances (Scheffer et al. 2001; Hunt et al. 2002; Carpenter et al. 2011). Continued monitoring of nearshore Beaufort Sea fish populations will allow for insight into how future species communities might organize and respond to perturbations in their natural environment.

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# Tables

Table 1. Total catch by species, mean catch and range per biweekly period, and percent present in biweekly catch per station. Species that are only included in rare species analysis (<100 total catch) are marked with †.



Table 2. Regression coefficients and significance levels for year, water temperature, salinity, and the annual coefficient of variation (CV) for each species, Prudhoe Bay, Alaska, 2001–2018.



# Figures



70.2°

70.3°

70.4°

148.5°

148.0°

Figure 1. Map of study sample locations, Prudhoe Bay, Alaska. Projection is in Alaska Albers, NAD83.

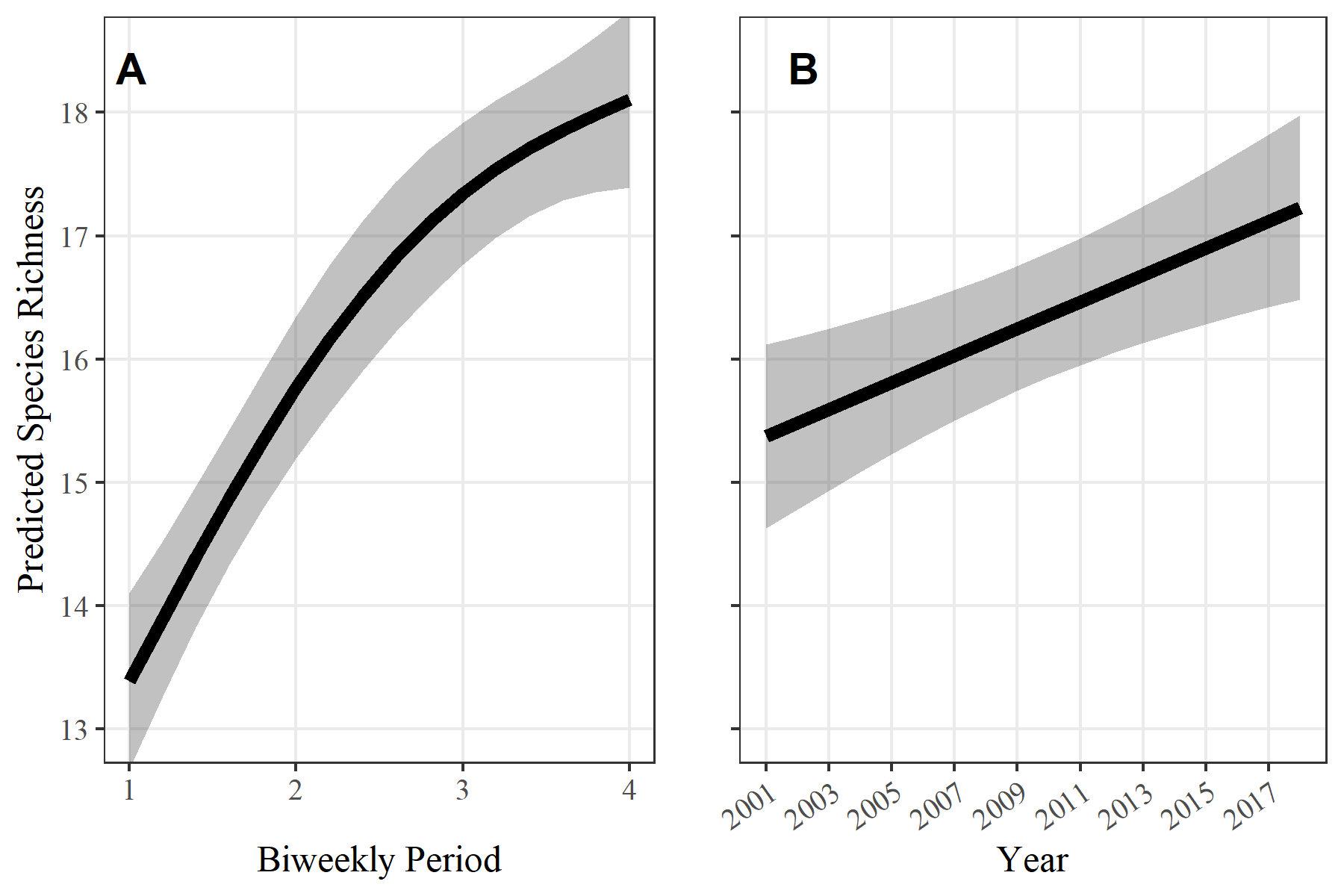


Figure 2. Predicted species richness by biweekly period (A) and year (B) for Prudhoe Bay, Alaska, 2001–2018. Modeled results from a Generalized Additive Model showed a predicted increase in species richness across years and biweekly periods.

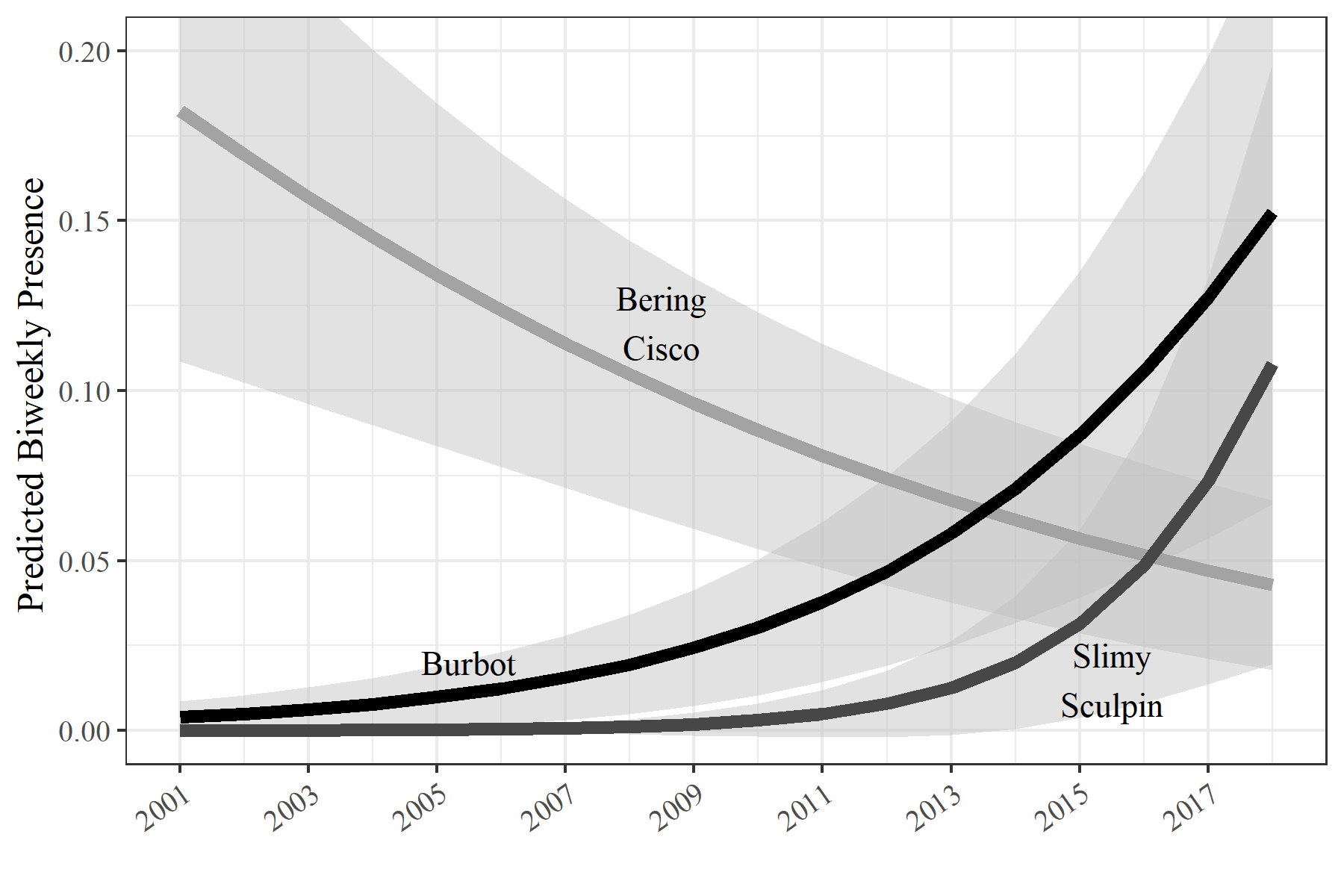


Figure 3. Predicted proportion of presence in a biweekly sample from a binomial Generalized Linear Model, Prudhoe Bay, Alaska, 2001–2018, all stations are combined. Only the three significant species are displayed. Standard error bars are shown as shaded areas.

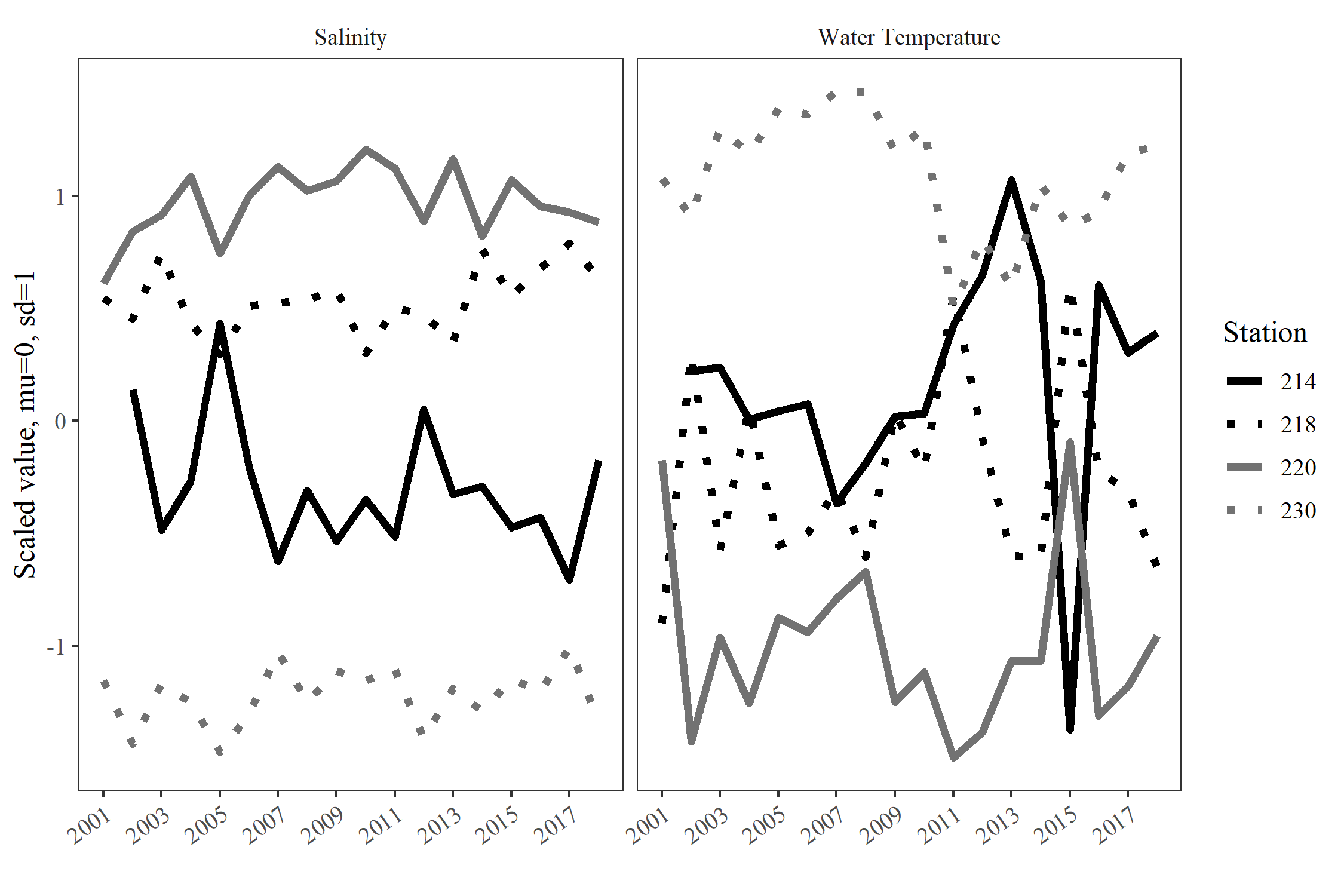


Figure 4. Annual trends of salinity and water temperature by station, Prudhoe Bay, Alaska, 2001–2018, scaled to µ=0 and σ=1.

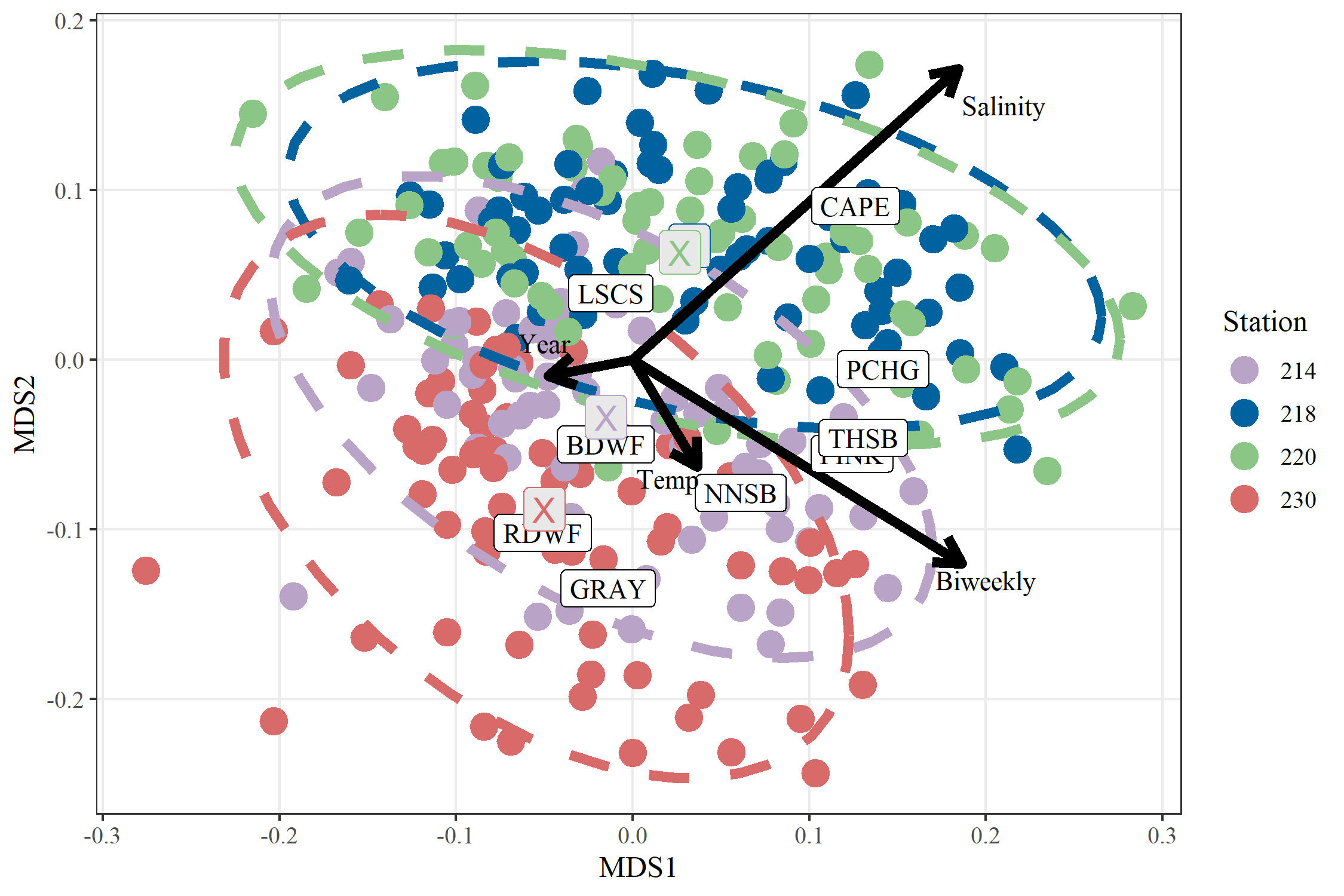


Figure 5. Non-metric multidimensional scaling (nMDS) ordination of fish species composition from Prudhoe Bay, Alaska, 2001–2018. Dashed ellipses are 95% confidence intervals; “X” labels mark centroids for each station. Environmental vectors of salinity, water temperature, biweekly period, and year are orthogonal to the gradient contours, pointing towards the direction of maximum association with the ordination. Displayed are the top nine species that were associated with nMDS axes 1 and 2, positioned according to their ordination score. Species codes are as follows: BDWF = Broad Whitefish *Coregonus nasus*, CAPE = Capelin *Mallotus villosus*, GRAY = Arctic Grayling *Thymallus arcticus*, LSCS = Least Cisco *Coregonus sardinella*, NNSB = Ninespine Stickleback *Pungitius pungitius*, PCHG = Pacific Herring *Clupea pallasii*, PINK = Pink Salmon *Oncorhynchus gorbuscha*, RDWF = Round Whitefish *Prosopium cylindraceum*, THSB = Threespine Stickleback *Gasterosteus aculeatus*.