# Introduction

Climate models predict that the effects of climate change will be felt most acutely in the Arctic, with sea surface temperatures predicted to rise more than in temperate latitudes, and mean annual temperatures predicted to 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 already been decreasing 3.5–4.1% per decade since XXXX (IPCC 2014). The consequences of these large-scale changes are far-reaching and cascading. For example, the persistent presence of sea ice and its effect upon the local ecosystem is unique to the Arctic Ocean. The reduction of sea ice in the Beaufort Sea has increased coastal erosion rates, increasing suspended sediment load, and consequently decreased benthic and water column primary production (Bonsell and Dunton 2018). The decreased primary productivity has direct implications on the ecological responses of many ice-associated taxa (e.g., calanoid copepods and amphipods) and fishes like Arctic Cod *Boreogadus saida* that prey upon such species (Bradstreet and Cross 1982, Gradinger and Bluhm 2004). As a result, changes in the environmental conditions impact the Arctic regions, specifically nearshore areas, which support a variety of fishes and invertebrates.

Fish exhibit behaviors to seek environmental conditions such as water temperature and salinity that 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 by the presence and abundance of fish species because fish community composition can be a function of a temperature and other abiotic factors for marine and freshwater species (Jackson et al. 2001; Collie et al. 2008).

Due to the dynamic nature of resources and conditions in the Arctic, some Arctic fishes adopt certain life history strategies to increase chances of encountering habitats with favorable conditions (Craig 1984; Power 1997; Roux et al. 2016). Arctic whitefish species like Arctic Cisco *Coregonus autumnalis*, Broad Whitefish *Coregonus nasus*, Least Cisco *Coregonus sardinella*, and Humpback Whitefish *Coregonus 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 born 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 many rivers across northern Alaska (Craig 1984, 1989; Fechhelm et al. 1994). The juvenile life stage of these 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). Gadids, predominantly Arctic Cod, are also ecologically important and support the Arctic marine ecosystem with their prevalence and high energetic content (Gradinger and Bluhm 2004; Elliott and Gaston 2008; Harter et al. 2013; Majewski et al. 2016; 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; Thorsteinson and Love 2016). Arctic Cod also undertake migratory behavior ostensibly to increase changes of encountering habitats with favorable conditions (Vestfals et al. 2019). Even Pacific salmon have also been documented as Arctic species, with a natal population in the Mackenzie River in Canada (Irvine et al. 2009). Together, these species make up a substantial portion of the fish community structure/species composition in the Alaskan Arctic.

Studying the species composition of catches offers robust insights to changes occurring to all species at once, rather than examining one or two species individually. By analyzing the abundance and proportions in a multivariate framework, there are additional insights about how simultaneous interactions occur between species, particularly between populations that may have inferred competition (Fechhelm et al. 1995). Long-term trends and spatial patterns of species composition is useful for understanding how the fish community responds to environmental variables, especially in nearshore populations (Neves et al. 2016).

Nearshore fishes of the Alaskan Arctic support a robust ecosystem and provide subsistence food for local indigenous communities, yet exist in a changing environment. In this study, we assessed the effects of environmental variables upon the abundance of various fish species present within a nearshore semi-estuarine ecosystem of the Alaskan Arctic to demonstrate how the fish community is changing in response to shifts in climate and environmental conditions. 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 / absence over time, 2) effects of environmental variables upon species composition and 3) species composition changes over time.

# Methods

## Study Area

This study was conducted along the coast near Prudhoe Bay, Alaska, 2001–2018. 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 water depth contour less than 5 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. In addition, 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 (Figure 1) along the coast were established for daily fish monitoring. 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 two fyke nets set side-by-side, 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, the 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, though modified 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. All 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). Fish were released offshore away from the cod-end openings to minimize recapture. Field sampling protocols were essentially unchanged from 2001 to 2018.

## Environmental Data Sources

Environmental variables examined were water temperature (°C) and salinity (ppt) measured near the top of the water column, 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. Daily Sagavanirktok River discharge data were collected by a United States Geological Survey (USGS) gaging station upriver from the river mouth, near Pump Station 3. Wind data was 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 directionality 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 the formula:

## Data Analysis

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. All 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:

Total number of species was defined as the number of unique species across all sites combined for each biweek period. The variable is the biweekly sampling period that was assigned as four events evenly distributed during 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 also tested against null models and 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 binomial Generalized Linear Models (GLMs):

where was the mean value of species *j*, and was the effect for each Station *s*. 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. Response variables for multivariate analyses were species catch per unit effort (CPUE) that were fourth-root transformed then standardized to percent of the maximum transformed catch. To prevent rare species from dominating multivariate analyses, we restricted analysis 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 allows for the multivariate analysis of quantitative environmental variables upon the responding species assemblages (Oksanen et al. 2018).

Next, we conducted a multivariate Mantel-type test (vegan command: bioenv()) on the biweekly catch matrix of Bray-Curtis distances with a Euclidean distance metric and Spearman correlation method. This resulted in 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 square-root transformed environmental variables, for each variable and combined variables. Biweekly periods that had gaps in 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 was the East-West wind vector (-1 = 270° West wind; 1 = 90° East wind). 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:

where was each of the three multi-dimensional scaling axes. 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:

where is the biweekly CPUE of species k at each station. Changes in variability of catches over time was determined using the annual coefficient of variation (CV) defined as . The annual CV was then 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 not 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 of 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 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) over 2001–2018 showed a significant increase per 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 *Liparis* spp. both increased in abundance during a season (estimate = 0.72, SE = 0.222, p = 0.001, and estimate = 3.00, SE = 0.990, p = 0.002, respectively).

## Effects of Environmental Variables Upon Species Composition

For 2001–2018, water conditions at the sampling stations varied among biweekly periods, years, and stations. For example, 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). Wind speed ranged from 10.5–36.1 kph (mean = 17.1 kph, SD = 3.84), with a mean direction of 42.9° (i.e., Northeast). The discharge from the Sagavanirktok River ranged from 39.3 to 327.7 m3/s (mean = 135.1 m3/s, SD = 54.1). 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). Annual water temperature increased significantly over 2001–2018 (linear regression, estimate = 0.08, SE = 0.021, p = 0.001), but there were not significant changes in annual salinity (linear regression, estimate = 0.06, SE = 0.096, p = 0.53) or wind speed (linear regression, estimate = 0.05, SE = 0.028, p = 0.109) over the same time period. The East-West wind directionality shifted to become more easterly from 2001–2018 (estimate = 0.02, SE = 0.008, p = 0.015), and there was also an increase in Sagavanirktok River discharge (linear regression, estimate = 65.17, SE = 31.83, p = 0.045).

Results from a multivariate Mantel-type test upon the biweekly catch matrix showed that the optimal subset of parameters describing species composition were 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).

Both of the nMDS centroids of stations 214 and 230 (eastern stations) and stations 218 and 220 (western stations) were outside of the 95% CI ellipse for each group (Figure 5). While there was substantial overlap in species composition among all four stations, there was a clear divide between eastern and western stations. 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 similarity percentage analysis differences. 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 *Liopsetta glacialis* 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) shows slight effects of water temperature (R2 = 0.017) and salinity (R2 = 0.020) upon species composition, even after spatio-temporal variables have been isolated.

## Species Composition and Abundance Changes

To assess changes in species composition over time, we modeled nMDS axes by year, station, and biweekly period. Results from this model showed the 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 axis 1, there was a significant non-linear increase from 2001–2018. 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 slightly lowest at one optimal breakpoint. Given this tepid evidence, we concluded that the overall time series of the nMDS axes showed no structural change.

The linear models of each individual species CPUE showed significant associations in abundance. There were six species that significantly changed in abundance 2001–2018: Broad Whitefish and Saffron Cod *Eleginus gracilis* increased in abundance (estimate = 44.3, p < 0.001; estimate = 13.6, p = 0.014, respectively), while Arctic Cod (estimate = -813.7, p = 0.041), Fourhorn Sculpin (estimate = -18.1, p = 0.005), Humpback Whitefish (estimate = -3.9, p = 0.018), and Least Cisco (estimate = -90.3, p < 0.001) decreased in abundance (Table 2). Water temperature significantly affected the abundance of Arctic Flounder (estimate = 128.7, p < 0.001), Broad Whitefish (estimate = 148.8, p < 0.001), Dolly Varden (estimate = -45.9, p < 0.001), Fourhorn Sculpin (estimate = 43.5, p = 0.033), Saffron Cod (estimate = 50.4, p = 0.004). Salinity significantly affected the abundance of Arctic Cisco (estimate = 161.9, p < 0.001), Capelin (estimate = 1.0, p = 0.003), Dolly Varden (estimate = -7.9, p = 0.013), Humpback Whitefish (estimate = -5.4, p = 0.002), Least Cisco (estimate = -61.0, p < 0.001), Pacific Herring (estimate = 0.4, p <0.001), and Saffron Cod (estimate = 17.6, p = 0.002). The annual variability of catches increased for Dolly Varden (estimate = 0.03, p = 0.035) and decreased for Saffron Cod (estimate = -0.04 , p = 0.029).

# Discussion

The Arctic Ocean represents 34% of the world's coastline (Lantuit et al. 2012), yet is among the least-studied marine ecosystems in the world due to inaccessibility, inclement weather, and high proportion of shallow coastal shelves that are not accessible by deep-drafted, ocean-research vessels (Eakins and Sharman 2010). As nearshore Arctic regions have undergone changes in environmental conditions, it is imperative to know how fish species composition is also changing. However, determining such effects can be difficult in the dynamic environment of the Arctic, where solar energy and temperature vary widely between seasons. This study assesses one of the only long-term monitoring projects of Arctic fishes, especially in nearshore locations. The confluence of dynamic environmental conditions and unchanging protocols meant that we were able to provide the first determination of how the nearshore fish community has responded to changing conditions and establishes a baseline for future regional fish studies. Previous studies in Prudhoe Bay and the Alaska Arctic have been focused upon single species or lacking long-term monitoring, which may misrepresent how a community changes over time. In this study, we documented changes in environmental conditions and likely corresponding shifts in species composition.

## Changes in Environmental Conditions

Several of the environmental variables examined in this study have significantly changed. Water temperature, discharge from the Sagavanirktok River, and the proportion of easterly winds have significantly increased, with no detectible changes in salinity or wind speed. Many of the variables examined are entwined and difficult to disentangle, especially salinity. For example, salinity in Prudhoe Bay is affected by strong easterly or westerly winds as upwelling or intrusions cause marine waters to either retreat or advance shoreward. Similarly, while discharge from the Sagavanirktok River was ultimately not important to many of the models regarding species assemblage structure, it is difficult to separate the effects of salinity and freshwater discharge. As salinity was deemed important to many examinations of variables influencing species assemblage structure, we posit that future changes to wind patterns and regional precipitation will affect fishes by altering local salinity.

As the Arctic climate changes with a predicted increase in water temperature, an increase in precipitation, increased oceanic turbidity, and decreased sea ice cover, this will force a selection which species are likely to become more or less abundant. If such shifts in conditions continue, we expect generalist species adapted to a wide range of conditions (including new and old conditions) to proliferate. The nearshore Arctic environment of Prudhoe Bay is naturally a seasonally dynamic environment, shifting from months of darkness to months without sunsets, shorefast ice for most of the year warming to up room temperature, and salinity that ranges from complete freshwater to entirely marine. With competition and limited resources, we expect increases in abundance of species that are better suited for these new conditions with declines in abundance of species that are stenohaline and stenothermal (e.g., Arctic Cod).

## Shifts in Species Richness

A basic determination of whether species composition is changing is to examine trends in species richness across time. The species richness in Prudhoe Bay, Alaska is significantly increasing at a rate of approximately one additional species per decade. Species richness is also not static within a season but increases nonlinearly, with less of an increase towards the end of the season. Species richness is highest later in the ice-free season though it is unclear what would happen if the duration of ice-free months were to continue expanding. Given large-scale climatic changes in the region, the trend of increasing species richness is likely to continue or potentially increase as species distributions change.

While all species captured as a part of this study are local to the region, studies in lower latitudes of Arctic Alaska have documented species expanding their range northward (Mueter and Litzow 2008). It is plausible to expect that given current fish distribution trends in the Chukchi Sea that such species will eventually reach the Beaufort Sea affecting the species richness and composition in Prudhoe Bay. In addition, once fish distribution is established reliably at Point Barrow, there could be a rapid range expansion eastward as the coastal Alaskan Beaufort Sea is all the same latitude and similar habitat. Of the 14 rare species captured in this study, three showed significant changes over time. The two rare species that are significantly increasing in abundance (Slimy Sculpin and Burbot) are both 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. The rare species that has declined (Bering Cisco) is anadromous and has not been captured since a single sample in 2015.

## Species Composition

The species composition of Prudhoe Bay fishes shows strong evidence of being influenced by environmental variables, despite existing in a fluctuating environment. All of the variables tested (year, biweekly period, station, water temperature, and salinity) were highly significant which was expected given that the Mantel test filtered for variables that had a likely effect upon species composition as well as significance being common at such high dimensionality. The top PERMANOVA model only explained approximately half of the variation of the biweekly catches. Variability of ecological community composition is thought to be indicative of stressors acting upon the populations (Warwick and Clarke 1993). In Arctic fishes, the natural environment likely contributes a high-degree of such variability.

The nMDS ordination and associated analyses showed clear effects from environmental and spatio-temporal variables upon species composition. The environmental vector of salinity most greatly affected species composition which is expected given the diametric salinity requirements of freshwater and marine. As each sampling station had a unique salinity profile (Figure 4), it is also unsurprising that differences between stations are distinct in the nMDs ordination (Figure 5). The other vector that strongly influenced species composition was the biweekly period, which aligns with results from modeling how species richness shifts over the course of the season (Figure 2).

## Effects of Individual Species

Differences in the species composition of Prudhoe Bay among stations and over time was affected by several species. The species composition differences between the eastern stations (stations 230 and 214) and western stations (stations 218 and 220) were influenced by several species that were amphidromous (Round Whitefish, Threespine Stickleback, Ninespine Stickleback). Similarly, the species that were each most correlated with each nMDS axis (Threespine Stickleback, Round Whitefish, Arctic Flounder) are all tolerant of a wide variety of estuarine conditions. Together, these indicate 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.

The species composition of Prudhoe Bay changed over time because of shifts in catches of individual species. Due to the multivariate aspect of species composition, it is difficult to ascertain precisely which species caused these changes. However, of the 17 species examined for linear trends over time, six species showed significant trends 2001–2018, with Broad Whitefish and Saffron Cod significantly increasing and Arctic Cod, Fourhorn Sculpin, Humpback Whitefish, and Least Cisco significantly decreasing in abundance. Saffron Cod has been increasing in abundance over time, is positively associated with increased water temperature and salinity, and the variability of abundance has been decreasing over time.

## Unexamined Variables

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. Researchers are currently processing high-resolution shorefast ice imagery that will cover Prudhoe Bay (pers. comm. A. Mahoney, University of Alaska Fairbanks Geophysical Institute). However, preliminary modeling efforts 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 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. Nearshore areas are important habitats that provide a wide diversity of trophic contributions, increased nursery production of juvenile fishes (Beck et al. 2001), and ontogenetic migration corridors (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. Changes to environmental conditions or to the community structure of populations would likely have a detrimental effect upon the juveniles of many species.

It is important to note that we assumed that trends in catches at the fyke nets were truly reflective of local abundance and not a function of changing sampling efficiency. For example, changes in assemblage structure at different wind conditions were reflective of fish distributional movement patterns and not the fyke nets selecting for certain species. Further, we assumed that by pooling samples to a biweekly sampling period that we would account for any short-term fluctuations. Lastly, our geographic spread of sample sites, while constrained to inshore regions, attempted to mitigate effects from any potential inshore/offshore or East/West species distribution. By having four sample sites spread across broad spatial and temporal sampling units, we made our samples representative of 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 moderate observed changes in species composition in this study demonstrate a fish community with adept ability to sustain populations. It is unknown whether the Arctic fish community will be able to continue to have such resilience as the pace of environmental change increases further.

# Literature Cited

Arnesen, A. M., E. H. Jørgensen, and M. Jobling. 1993. Feed intake, growth and osmoregulation in Arctic charr, Salvelinus alpinus (L.), following abrupt transfer from freshwater to more saline water. Aquaculture 114:327–338.

Bai, J., and P. Perron. 2003. Computation and analysis of multiple structural change models. Journal of Applied Econometrics 18(1):1–22.

Beck, M. W., K. L. Heck, K. W. Able, D. L. Childers, D. B. Eggleston, B. M. Gillanders, B. Halpern, C. G. Hays, K. Hoshino, T. J. Minello, R. J. Orth, P. F. Sheridan, and M. P. Weinstein. 2001. The Identification, Conservation, and Management of Estuarine and Marine Nurseries for Fish and Invertebrates. BioScience 51(8):633–641.

von Biela, V. R., C. E. Zimmerman, B. R. Cohn, and J. M. Welker. 2013. Terrestrial and marine trophic pathways support young-of-year growth in a nearshore Arctic fish. Polar Biology 36(1):137–146.

Bœuf, G., and P. Payan. 2001. How should salinity influence fish growth? Comparative Biochemistry and Physiology - Part C Toxicology and Pharmacology 130(4):411–423.

Bond, W. A., and R. N. Erickson. 1985. Life History Studies of Anadromous Coregonid Fishes in Two Freshwater Lake Systems on the Tuktoyaktuk Peninsula, Northwest Territories Canadian Technical Report of Fisheries and Aquatic Sciences. Canadian Technical Report of Fisheries and Aquatic Sciences 1336.

Bonsell, C., and K. H. Dunton. 2018. Long-term patterns of benthic irradiance and kelp production in the central Beaufort Sea reveal implications of warming for Arctic inner shelves. Progress in Oceanography 162:160–170.

Bradstreet, M. S. W., and W. E. Cross. 1982. Trophic Relationships at High Arctic Ice Edges. Arctic 35(1):1–12.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure (1988):117–143.

Collie, J. S., A. D. Wood, and H. P. Jeffries. 2008. Long-term shifts in the species composition of a coastal fish community. Canadian Journal of Fisheries and Aquatic Sciences 65(7):1352–1365.

Coutant, C. C. 1987. Thermal preference: when does an asset become a liability? Environmental Biology of Fishes 18(3):161–172.

Craig, P. C. 1984. Fish use of coastal waters of the Alaska Beaufort Sea: a review. Transactions of the American Fisheries Society 113(3):265–282.

Craig, P. C. 1989. An introduction to anadromous fishes in the Alaskan Arctic. Biological Papers of the University of Alaska (24):27–54.

Craig, P. C., W. B. Griffiths, L. Haldorson, and H. McElderry. 1985. Distributional Patterns of Fishes in an Alaskan Arctic Lagoon. Polar Biology 4:9–18.

Cushing, D. H. 1990. Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. Advances in Marine Biology 26:249–293.

Dutil, J.-D., Y. Lambert, and E. Boucher. 1997. Does higher growth rate in Atlantic cod (Gadus morhua) at low salinity result from lower standard metabolic rate or increased protein digestibility? Canadian Journal of Fisheries and Aquatic Sciences 54:99–103.

Eakins, B. W., and G. F. Sharman. 2010. Volumes of the World’s Oceans from ETOPO1. Page NOAA National Geophysical Data Center, Boulder, CO.

Elliott, K. H., and A. J. Gaston. 2008. Mass-length relationships and energy content of fishes and invertebrates delivered to nestling Thick-billed Murres Uria lomvia in the Canadian Arctic, 1981-2007. Marine Ornithology 36(1):25–34.

Elmqvist, T., C. Folke, M. Nystrom, G. Peterson, J. Bengtsson, B. Walker, and J. Norberg. 2003. Response diversity, ecosystem change, and resilience RID C-1309-2008 RID F-2386-2011. Frontiers in Ecology and the Environment 1(9):488–494.

Fechhelm, R. G., J. D. Bryan, W. B. Griffiths, W. J. Wilson, and B. J. Gallaway. 1994. Effect of Coastal Winds on the Summer Dispersal of Young Least Cisco (Coregonus-Sardinella) from the Colville River to Prudhoe Bay, Alaska - a Simulation-Model. Canadian Journal of Fisheries and Aquatic Sciences 51(4):890–899.

Fechhelm, R. G., P. S. Fitzgerald, J. D. Bryan, and B. J. Gallaway. 1993. Effect of salinity and temperature on the growth of yearling Arctic cisco (Coregonus autumnalis) of the Alaskan Beaufort Sea.

Fechhelm, R. G., W. B. Griffiths, J. D. Bryan, B. J. Gallaway, and W. J. Wilson. 1995. Application of an in Situ Growth Model: Inferred Instance of Interspecific Trophic Competition between Anadromous Fishes of Prudhoe Bay, Alaska. Transactions of the American Fisheries Society 124(1):55–69.

Fechhelm, R. G., L. R. Martin, B. J. Gallaway, W. J. Wilson, and W. B. Griffiths. 1999. Prudhoe Bay causeways and the summer coastal movements of Arctic Cisco and Least Cisco. Arctic 52(2):139–151.

Gradinger, R. R., and B. A. Bluhm. 2004. In-situ observations on the distribution and behavior of amphipods and Arctic cod (Boreogadus saida) under the sea ice of the High Arctic Canada Basin. Polar Biology 27(10):595–603.

Green, D. G., J. T. Priest, K. P. Gatt, and T. M. Sutton. 2018. Beaufort Sea Nearshore Fish Monitoring Study: 2018 Annual Report:56.

Guisan, A., T. C. Edwards, and T. Hastie. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecological Modelling 157:89–100.

Harter, B. B., K. H. Elliott, G. J. Divoky, and G. K. Davoren. 2013. Arctic Cod (Boreogadus saida) as Prey: Fish Length-Energetics Relationships in the Beaufort Sea and Hudson Bay. Arctic 66(2):191–196.

IPCC. 2014. Climate Change 2014 Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Page 151 *in* C. W. Team, R. K. Pachauri, and L. Meyer, editors. IPCC. Geneva, Switzerland.

Irvine, J. R., R. W. Macdonald, R. J. Brown, L. Godbout, J. D. Reist, and E. C. Carmack. 2009. Salmon in the Arctic and How They Avoid Lethal Low Temperatures. Atlantic 5(5):39–50.

Jackson, D. A., P. R. Peres-Neto, and J. D. Olden. 2001. What controls who is where in freshwater fish communities – the roles of biotic, abiotic, and spatial factors. Canadian Journal of Fisheries and Aquatic Sciences 58(1):157–170.

Lantuit, H., P. P. Overduin, N. Couture, S. Wetterich, F. Aré, D. Atkinson, J. Brown, G. Cherkashov, D. Drozdov, L. Donald Forbes, A. Graves-Gaylord, M. Grigoriev, H. W. Hubberten, J. Jordan, T. Jorgenson, R. S. Ødegård, S. Ogorodov, W. H. Pollard, V. Rachold, S. Sedenko, S. Solomon, F. Steenhuisen, I. Streletskaya, and A. Vasiliev. 2012. The Arctic Coastal Dynamics Database: A New Classification Scheme and Statistics on Arctic Permafrost Coastlines. Estuaries and Coasts 35(2):383–400.

Majewski, A. R., W. Walkusz, B. R. Lynn, S. Atchison, J. Eert, and J. D. Reist. 2016. Distribution and diet of demersal Arctic Cod, Boreogadus saida, in relation to habitat characteristics in the Canadian Beaufort Sea. Polar Biology 39(6):1087–1098.

de March, B. G. E. 1989. Salinity tolerance of larval and juvenile broad whitefish (Coregonus nasus). Canadian Journal of Zoology 67:2392–2397.

Monaghan, P. 2008. Early growth conditions, phenotypic development and environmental change. Philosophical Transactions of the Royal Society B: Biological Sciences 363(1497):1635–1645.

Mueter, F. J., and M. A. Litzow. 2008. Sea Ice Retreat Alters the Biogeography of the Bering Sea. Ecological Applications 18(2):309–320.

Neves, L. M., T. P. Teixeira-Neves, G. H. Pereira-Filho, and F. G. Araújo. 2016. The farther the better: Effects of multiple environmental variables on reef fish assemblages along a distance gradient from river influences. PLoS ONE 11(12):1–23.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O’hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, H. Wagner, and M. J. Oksanen. 2018. Vegan: community ecology package.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. ICES Journal of Marine Science 39(2):175–192.

Peterson, G., C. R. Allen, and C. S. Holling. 1998. Ecological Resilience, Biodiversity, and Scale. Ecosystems 1:6–18.

Poos, M. S., and D. A. Jackson. 2012. Addressing the removal of rare species in multivariate bioassessments: The impact of methodological choices. Ecological Indicators 18:82–90. Elsevier Ltd.

Priest, J. T., D. G. Green, B. M. Fletcher, and T. M. Sutton. 2018. Beaufort Sea Nearshore Fish Monitoring Study: 2017 Annual Report. Fairbanks, Alaska.

Ross, B. D. 1988. Causeways in the Alaskan Beaufort Sea. Anchorage, Alaska.

Roux, M. J., L. A. Harwood, X. Zhu, and P. Sparling. 2016. Early summer near-shore fish assemblage and environmental correlates in an Arctic estuary. Journal of Great Lakes Research 42(2):256–266.

Seigle, J. C., and J. M. Gottschalk. 2013. Fall 2012 subsistence fishery monitoring on the Colville River. Fairbanks, Alaska.

Sheaves, M., R. Baker, I. Nagelkerken, and R. M. Connolly. 2014. True Value of Estuarine and Coastal Nurseries for Fish: Incorporating Complexity and Dynamics. Estuaries and Coasts 38(2):401–414.

Thorsteinson, L. K., and M. S. Love. 2016. Alaska Arctic Marine Fish Ecology Catalog.

Vestfals, C. D., F. J. Mueter, J. T. Duffy-Anderson, M. S. Busby, and A. De Robertis. 2019. Spatio-temporal distribution of polar cod (Boreogadus saida) and saffron cod (Eleginus gracilis) early life stages in the Pacific Arctic. Polar Biology 42(5):969–990. Springer Berlin Heidelberg.

Warwick, R. M., and K. R. Clarke. 1993. Increased variability as a symptom of stress in marine communities. Journal of Experimental Marine Biology and Ecology 172(1–2):215–226.

Werner, E. E., and J. F. Gilliam. 1984. The Ontogenetic Niche and Species Interactions in Size-Structured Populations. Annual Review of Ecology and Systematics 15:393–425.

Zeileis, A., F. Leisch, K. Hornik, C. Kleiber, B. Hansen, and E. C. Merkle. 2015. R package strucchange - Testing, Monitoring, and Dating Structural Changes Description. CRAN.

Zimmerman, C. E., A. M. Ramey, S. M. Turner, F. J. Mueter, S. M. Murphy, and J. L. Nielsen. 2013. Genetics, recruitment, and migration patterns of Arctic cisco (Coregonus autumnalis) in the Colville River, Alaska, and Mackenzie River, Canada. Polar Biology 36(11):1543–1555.

# 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.



# 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.

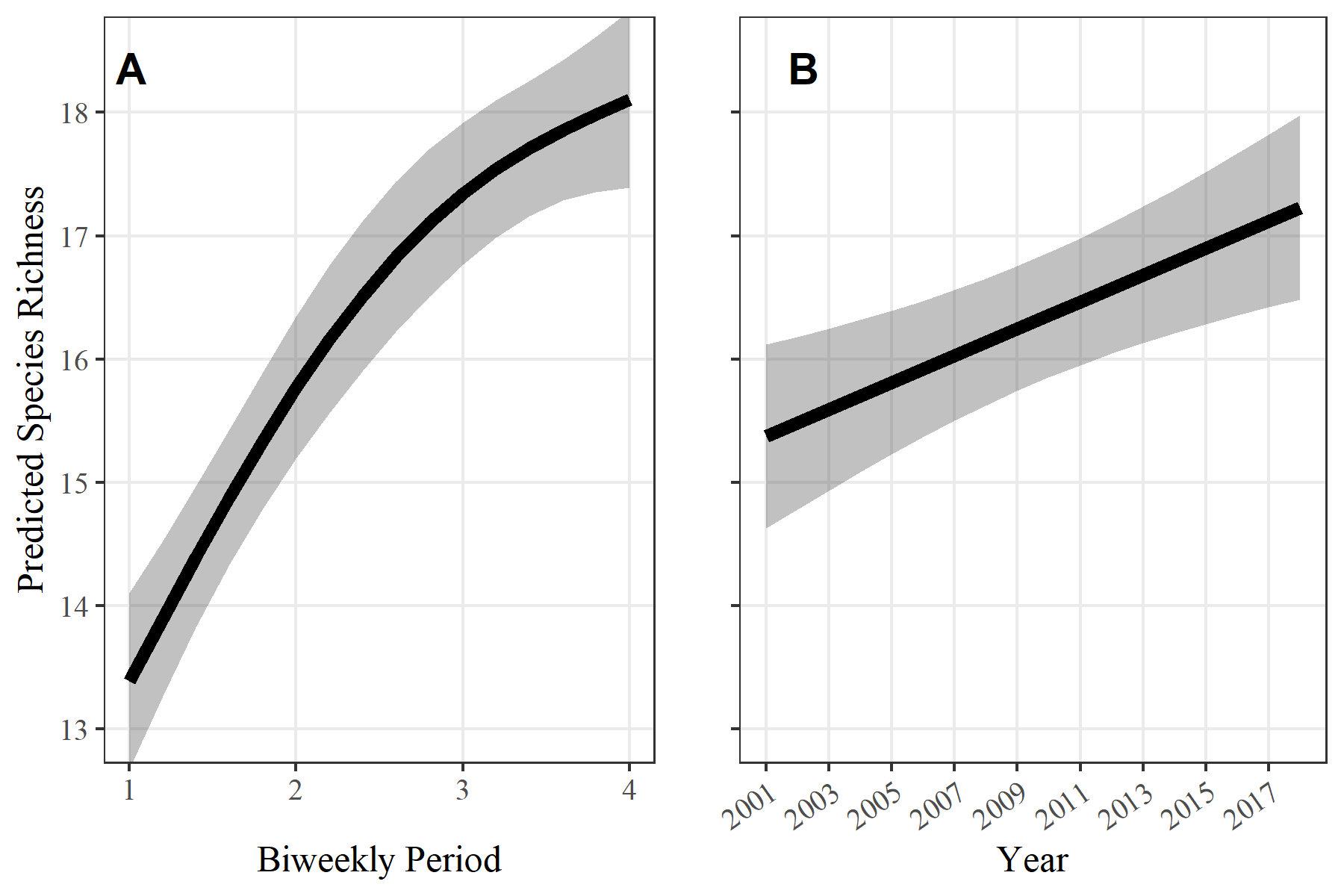


Figure 2. Predicted species richness by biweekly period (A) and year (B) for Prudhoe Bay, Alaska, 2001–2018. Modeled results from a Generalized Additive Model showed a predicted increase in species richness across years and biweekly periods.

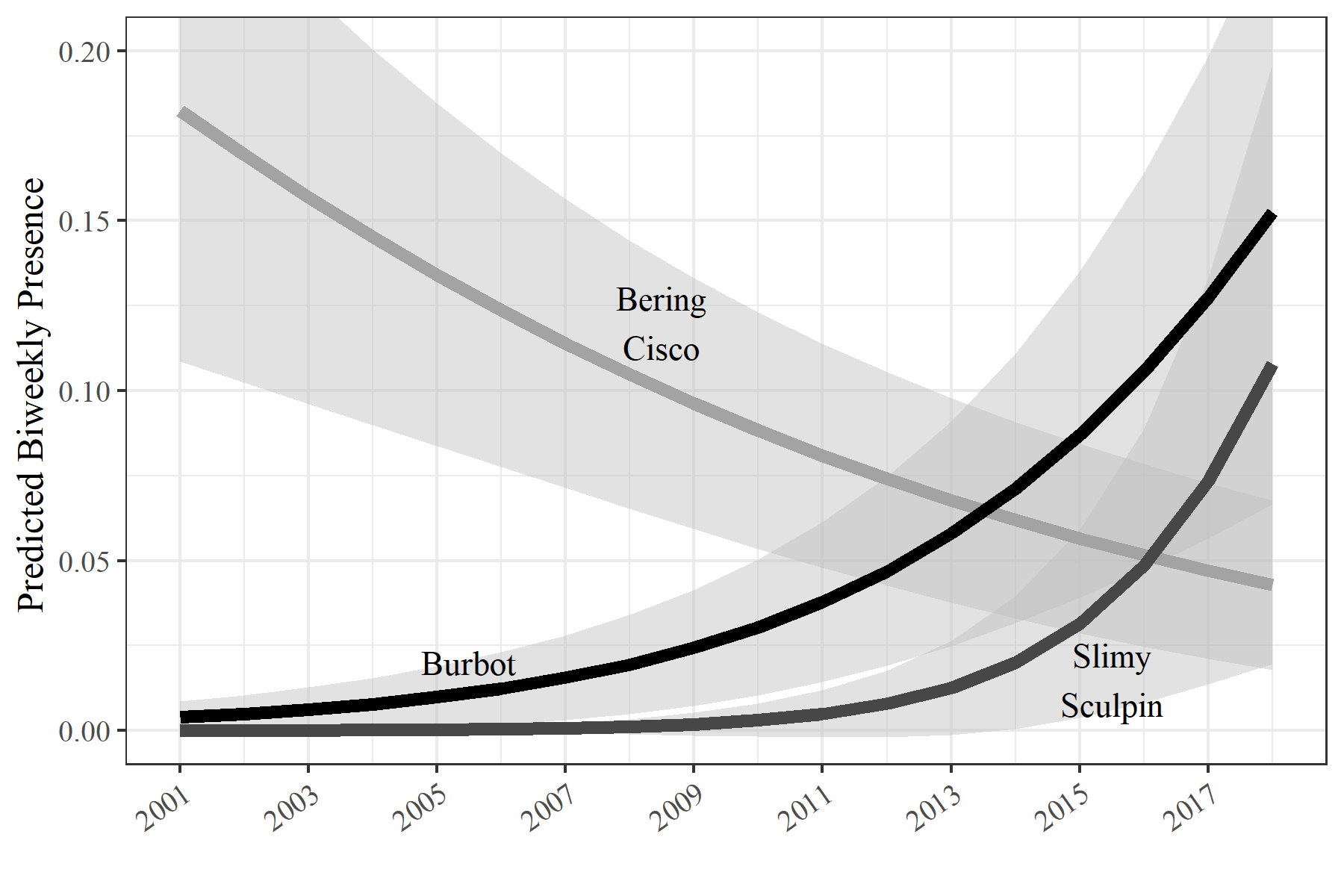


Figure 3. Predicted proportion of presence in a biweekly sample from a binomial Generalized Linear Model, Prudhoe Bay, Alaska, 2001–2018, all stations are combined. Only the three significant species are displayed. Standard error bars are shown as shaded.

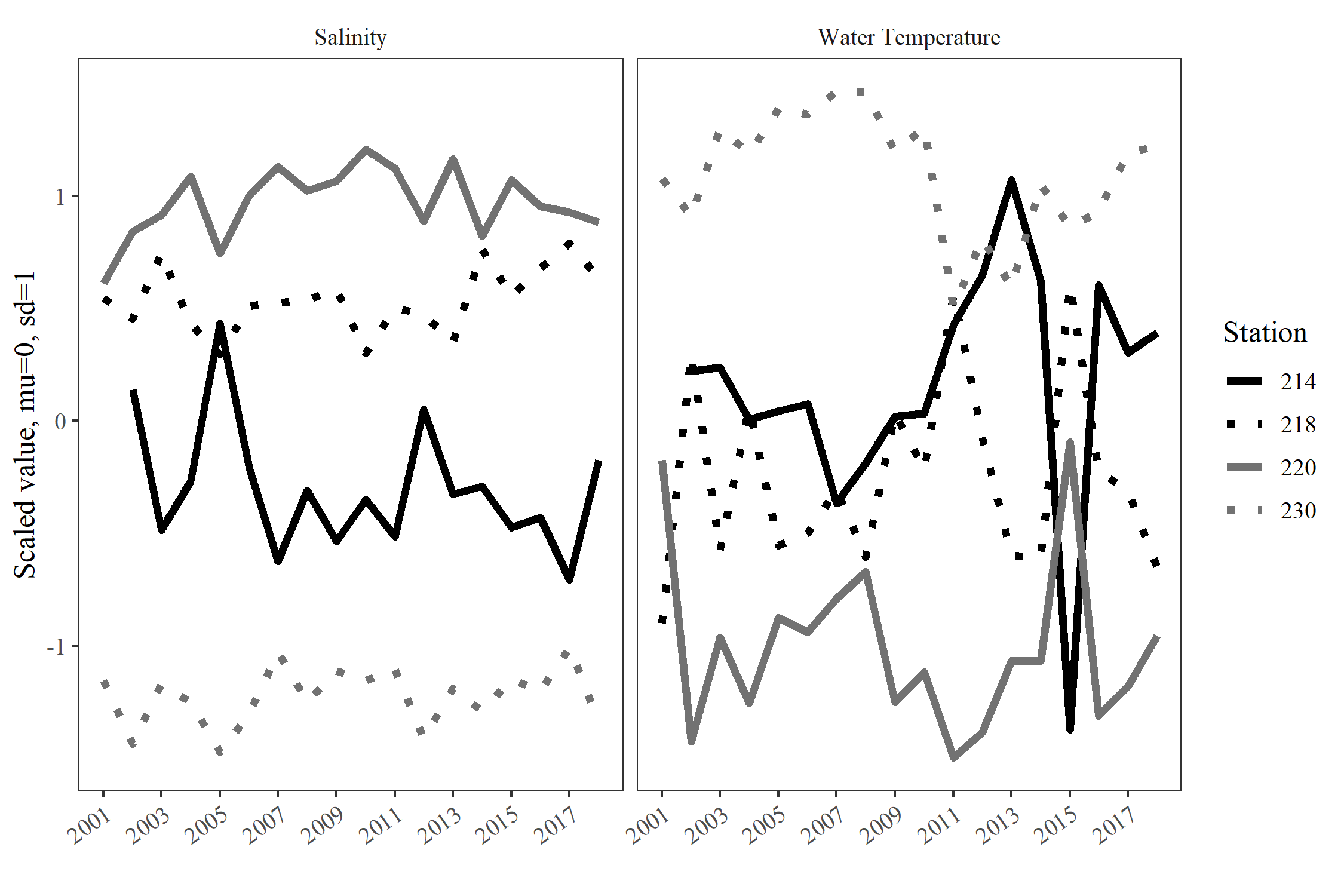


Figure 4. Annual trends of salinity and water temperature by station, Prudhoe Bay, Alaska, 2001–2018, scaled to µ=0 and σ=1.

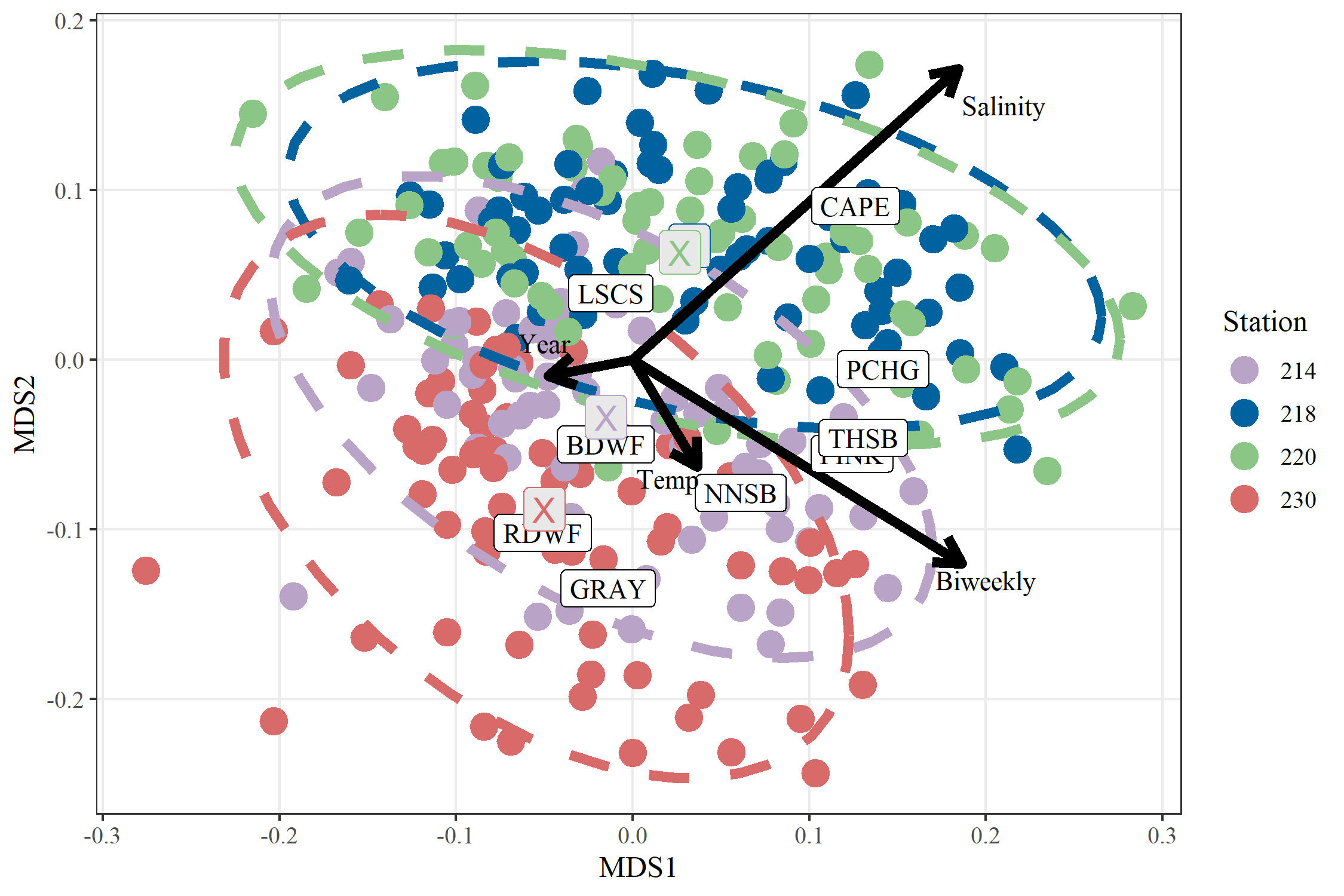


Figure 5. Non-metric multidimensional scaling (nMDS) ordination of fish species composition from Prudhoe Bay, Alaska, 2001–2018. Dashed ellipses are 95% confidence intervals; “X” labels mark centroids for each station. Environmental vectors of salinity, water temperature, biweekly period, and year are 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*.