# 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 1979 (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, which has increased 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 such as 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, including 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 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 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). 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 been documented as Arctic species, with a natal population in the Mackenzie River in Canada (Irvine et al. 2009). These species undergo movements to find suitable habitat and conditions in the dynamic Arctic, and subsequently make up a substantial portion of the fish community structure/species composition in the nearshore Alaskan Arctic.

Nearshore fishes of the Alaskan Arctic support a robust ecosystem and provide subsistence food for local indigenous communities yet exist in a changing environment (Fechhelm et al. 2007; Thorsteinson and Love 2016). 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). Furthermore, 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). In this study, we assessed the effects of environmental variables upon the abundance of various fish species present within a nearshore semi-estuarine ecosystem in Prudhoe Bay, Alaska 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 over time, 2) effects of environmental variables upon species composition and 3) species composition and abundance changes over time.

# Methods

## Study Area

This study was conducted in the Arctic Ocean 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 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. 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), 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 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 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:

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 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 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 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 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 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 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 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 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 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) over 2001–2018 showed significant increases 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 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 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 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 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 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) 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 for these three 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 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 (Table 2). Salinity significantly affected the abundance of Arctic Cisco, Capelin *Mallotus villosus*, Dolly Varden, Humpback Whitefish, Least Cisco, Pacific Herring, and Saffron Cod (Table 2). The annual variability of catches increased for Dolly Varden and decreased for Saffron Cod.

# 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). With the predicted changes in sea-surface temperatures, precipitation, and sea-ice coverage, it is imperative to understand how biodiversity is responding in the Arctic region. 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). This study assessed one of the only long-term monitoring projects of Arctic fishes to examine how the nearshore fish community has responded to changing conditions.

## The Changing Environment

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. Our analyses found significant changes in several of the environmental variables examined in this study. Water temperature became approximately 1.4° C warmer, discharge from the Sagavanirktok River increased 25.4 m3/s, and the wind direction became more easterly over time. Water temperature affects growth parameters of whitefishes (Fechhelm et al. 1992, 1993) and Arctic Cod (Laurel et al. 2016). Similarly, changes in river discharge influence the distribution of salinity gradients in estuarine locations which affects osmoregulation and feeding rates (de March 1989; Arnesen et al. 1993; Bœuf and Payan 2001). The change towards easterly winds increases the occurrence of marine upwelling events which lowers local water levels and bring 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). Together these significant changes in the environmental conditions have real effects upon the Prudhoe Bay species composition.

## Species Richness is Becoming Richer

We identified a total of 31 unique species in this study (Table 1), which represent 10% of the 310 fish species known to inhabit the Arctic Ocean (Mecklenburg et al. 2011; Reist et al. 2006). Because species richness in Prudhoe Bay, Alaska is significantly increasing at a rate of approximately one additional species per decade, we expect the number of species caught to continue to increase, caused by both existing Arctic fish species as well as by species from lower latitudes of Arctic Alaska that are expanding their range northward (Mueter and Litzow 2008). It is plausible to expect that given current fish distribution trends in the Chukchi Sea, such species will eventually reach the Beaufort Sea, affecting the species richness and composition in Prudhoe Bay. If large-scale climatic changes continue in the region, the trend of increasing species richness is likely to continue as the spatial distributions of species change. During the sampling season, species richness increases nonlinearly, tapering off at the end of the season when species richness is highest and ice coverage is lowest.

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.

## Environmental Effects on Species Composition

We hypothesized that ongoing shifts in Arctic environmental conditions would bring about measurable changes in fish populations during 2001–2018. In addition to increasing species richness, the species composition of Prudhoe Bay fishes shows strong evidence of being influenced by environmental variables, despite existing in a dynamic environment. All variables tested (year, biweekly period, station, water temperature, and salinity) were highly significant.

The nMDS ordination and associated analyses showed clear effects from environmental and spatio-temporal variables on species composition. We found that salinity greatly affected species composition. The differences in species composition among stations were distinct in the nMDS ordination (Figure 5), likely because each sampling station had a unique salinity profile (Figure 4). 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. Biweekly period also strongly influenced species composition, which corresponds with the increase in species richness over the season (Figure 2).

The PERMANOVA models also demonstrated the importance of environmental condition on species composition. The top PERMANOVA model explained approximately half of the variation of the biweekly catches. The high amount of residual variability is likely a relic of the natural environmental vicissitude. Water temperature and salinity explained 1.2% and 2.0% of the marginal variation (R2) of species composition, demonstrating that substantial amounts of the biweekly variation of catches can be attributed to these conditions.

## Effects of Individual Species over Time

The species composition of Prudhoe Bay changed over time because of shifts in catches of individual species, however, due to the multivariate aspect of species composition, it is difficult to ascertain precisely which species caused these changes. Of the 17 species examined for univariate linear trends over time, six species showed significant changes in abundance 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 (Table 2). Of these species with annual changes, Broad Whitefish and Fourhorn Sculpin were significantly positively associated with water temperature, Humpback Whitefish were negatively associated with water temperature, Least Cisco was negatively associated with salinity, and Saffron Cod was positively associated with both water temperature and salinity. Declines over time for these species were likely a result of shifts in environmental conditions.

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. 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; Laurel et al. 2016). There are no commercial fisheries in Arctic federal waters, but subsistence fisheries in the nearshore Alaska Arctic contribute to local Inupiaq communities (Fechhelm et al. 2007; NPFMC 2009). While changes to such fisheries are unlikely to have substantial economic impact, the ecological and social ramifications for biological and human communities could be substantial (Moerlein and Carothers 2012).

## Unexamined Variables

One variable that was not 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.

Some of the environmental variables are correlated, making significant changes in one variable difficult to distinguish from another variable with no significant change. 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. We found a significant change in easterly winds but did not find a significant change in salinity. 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.

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 may 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 pooling samples to a biweekly sampling period 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, the samples 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 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.

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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. Estimates of regression coefficients and significance 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.

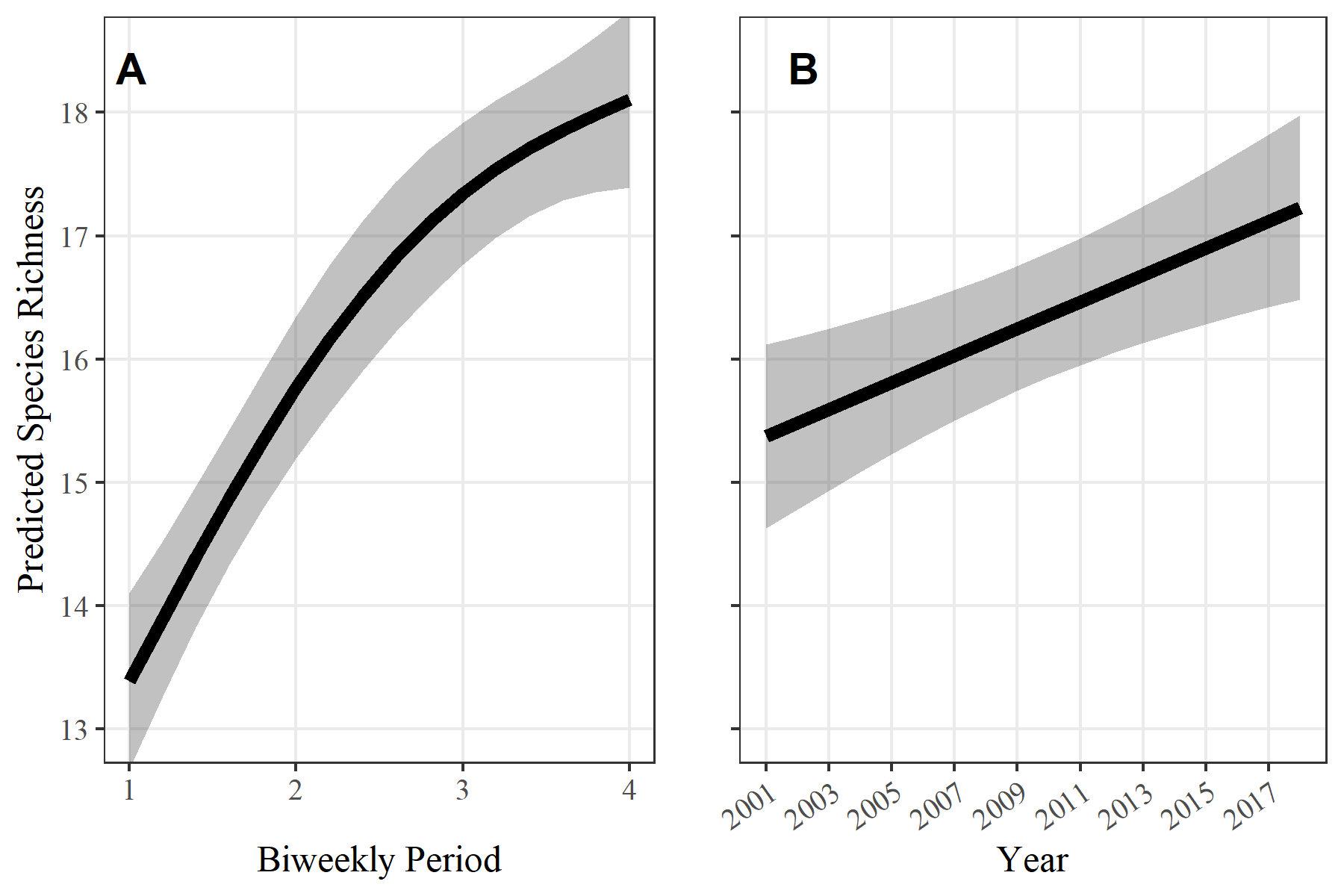


Figure 2. Predicted species richness by biweekly period (A) and year (B) for Prudhoe Bay, Alaska, 2001–2018. Modeled results from a Generalized Additive Model showed a predicted increase in species richness across years and biweekly periods.

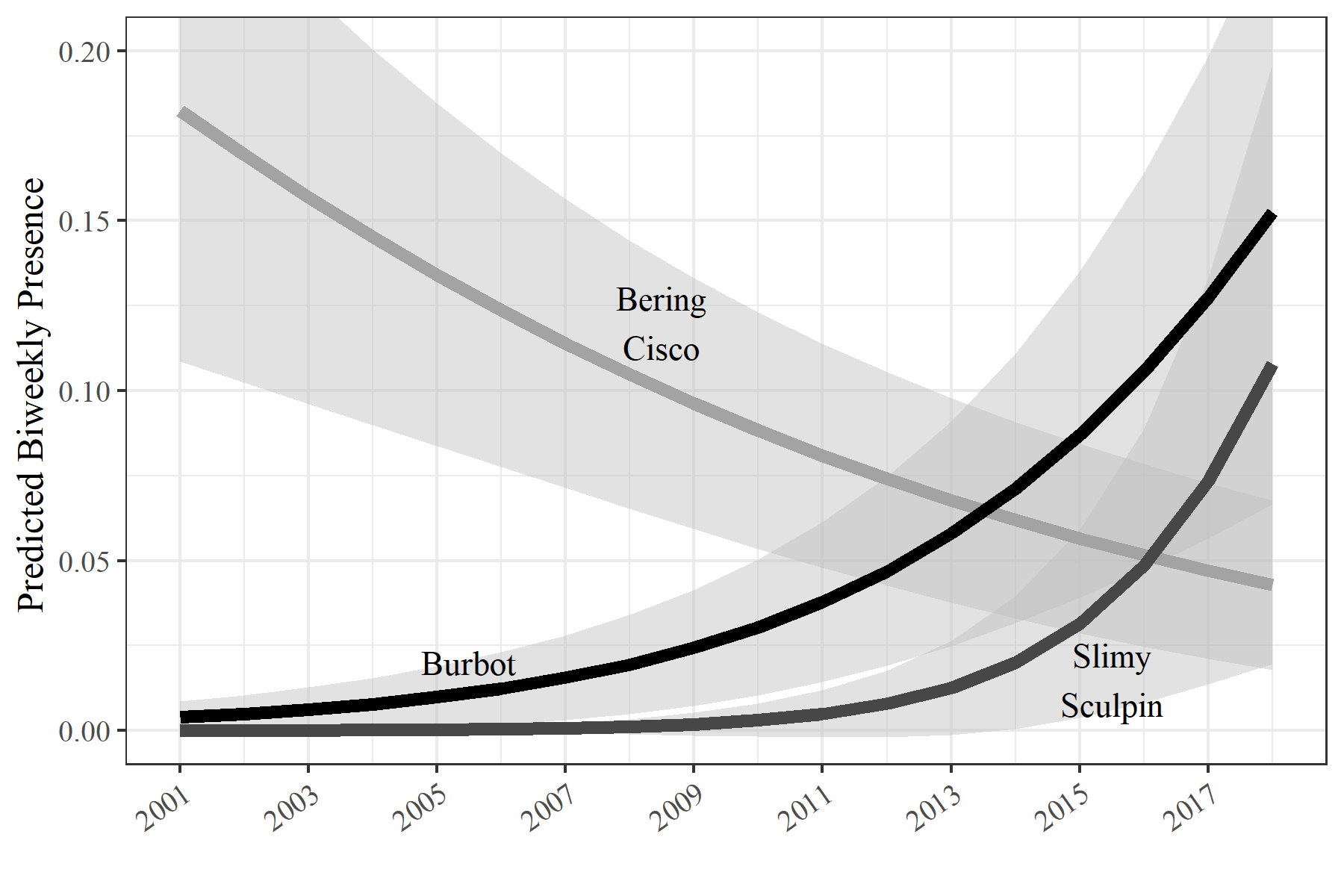


Figure 3. Predicted proportion of presence in a biweekly sample from a binomial Generalized Linear Model, Prudhoe Bay, Alaska, 2001–2018, all stations are combined. Only the three significant species are displayed. Standard error bars are shown as shaded.

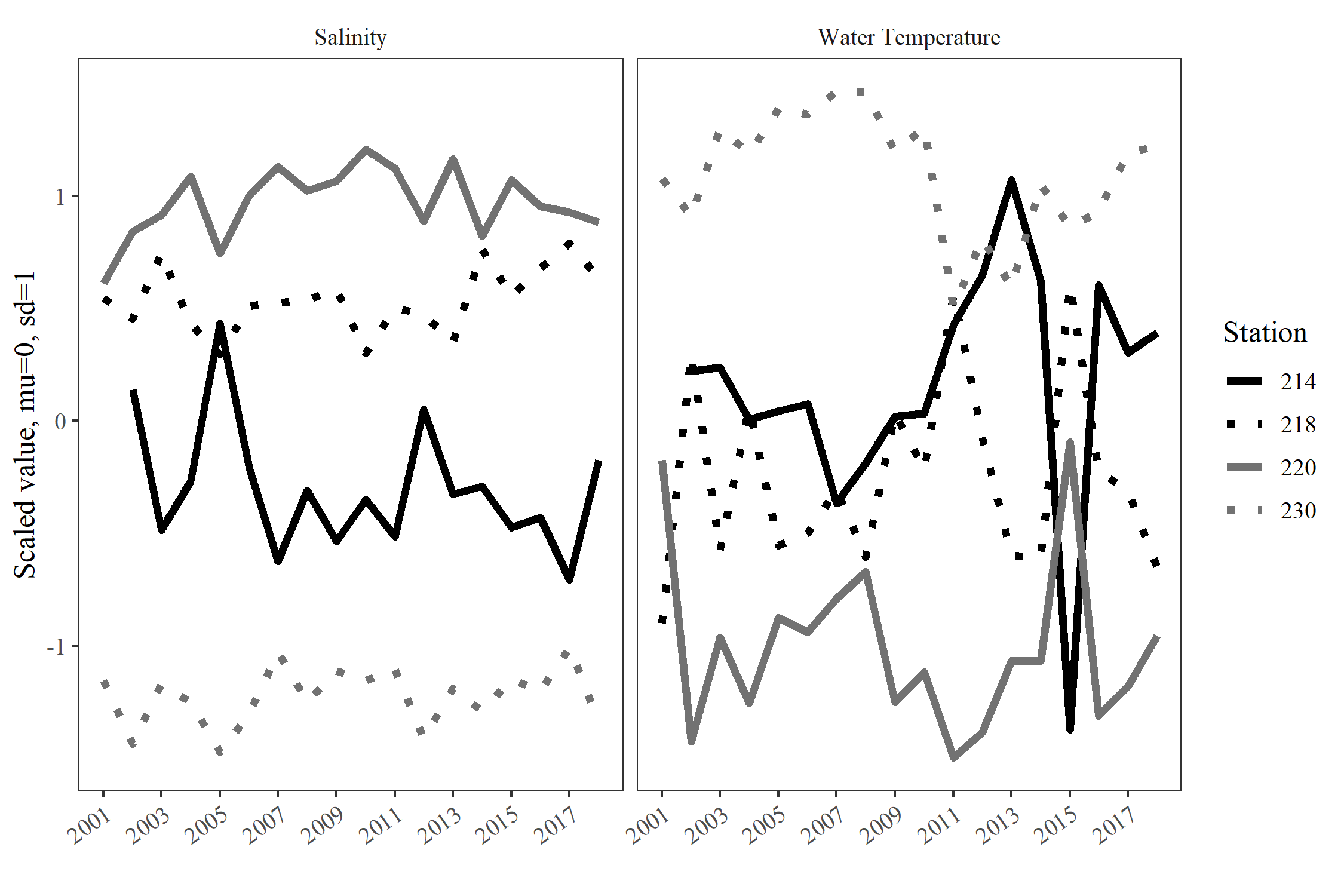


Figure 4. Annual trends of salinity and water temperature by station, Prudhoe Bay, Alaska, 2001–2018, scaled to µ=0 and σ=1.

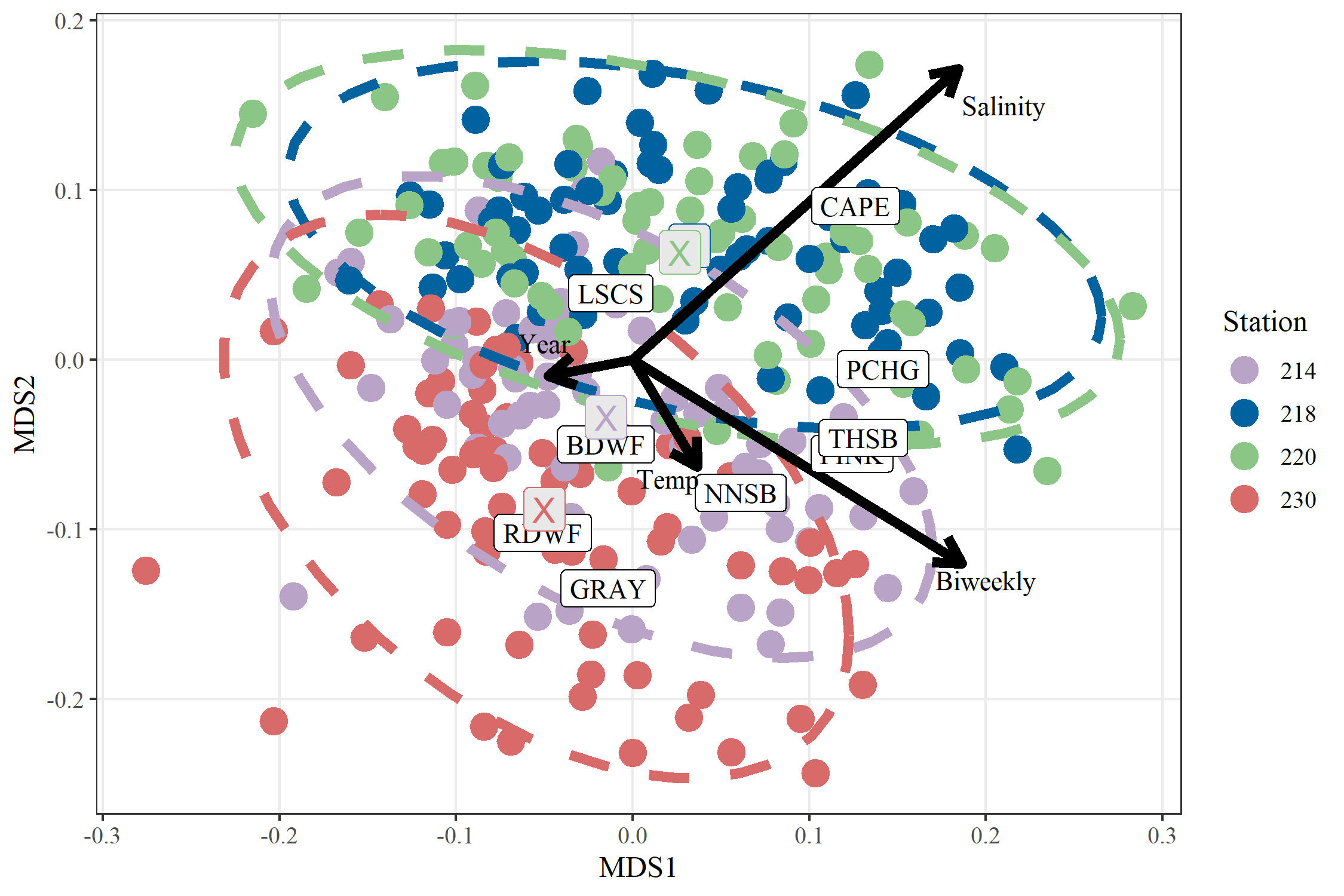


Figure 5. Non-metric multidimensional scaling (nMDS) ordination of fish species composition from Prudhoe Bay, Alaska, 2001–2018. Dashed ellipses are 95% confidence intervals; “X” labels mark centroids for each station. Environmental vectors of salinity, water temperature, biweekly period, and year are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