# Introduction

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 inclement weather and inaccessibility. The shallow, broad coastal shelves in the Arctic comprise a much higher proportion of the coast compared to other oceans (Eakins and Sharman 2010), and are not accessible by deep-drafted, ocean-research vessels, causing nearshore ecotypes in Arctic regions to be under-studied. The nearshore regions of the Arctic support a robust fish community comprised of marine, freshwater, and diadromous species of all life stages that subsist in the seasonally estuarine conditions. There are approximately 211 circumpolar marine fish species in 39 families (Mecklenburg et al. 2011), as well as approximately 99 freshwater or diadromous fish species in 17 families (Reist et al. 2006) that inhabit Arctic waters, many of them found in the coastal Beaufort Sea along the northern Alaskan coast. Despite this diversity, there are few aquatic long-term studies in the Arctic (Kortsch et al. 2012), with most research focusing on either permafrost and resulting greenhouse gas emissions from thawing or high trophic-level organisms (Fritz et al. 2017).

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. For example, mean annual temperatures are predicted to outpace global averages rising 3–10°C over the next 80 years (IPCC 2014). Expected changes are much broader than just temperature; observed mean annual sea-ice spatial extent has been decreasing 3.5–4.1% per decade and precipitation is expected to increase 30–50% (IPCC 2014). A reduced duration of shore-fast sea ice coverage also means that winter storms will likely erode shores more quickly, with coastlines in many locations along the Beaufort Sea expected to increase in erosion rates two m/year and up to 25 m/year in many locations, while barrier islands may erode completely (Jones et al. 2009; Lantuit et al. 2012; Gibbs and Richmond 2015). The loss of sea ice coverage was predicted to increase benthic light budgets (Clark et al. 2013), increasing primary productivity in polar regions. However, the reduction in sea ice in the Beaufort Sea has increased suspended sediment load due to an increase in coastal erosion rates, decreasing benthic and water column primary production (Bonsell and Dunton 2018). Such changes in environmental conditions of Arctic nearshore regions hold implications for the ecological responses of local fish species.

Fishes are affected by fluctuations in surrounding environmental conditions such as water temperature, salinity, and light availability. 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). As a result, fish exhibit behaviors to seek environmental conditions that optimize growth and survival (Cushing 1990; Monaghan 2008). Such parameters may vary by life stage, especially for diadromous fishes (Werner and Gilliam 1984). 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 is another important environmental variable that may fluctuate, and subsequent osmoregulation can incur a significant 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). Unique to the Arctic Ocean is the persistent presence of sea ice and its effect upon the local ecosystem. Many ice-associated taxa (e.g., calanoid copepods and amphipods) exist at the sea ice edges (Bradstreet and Cross 1982), supporting fishes such as Arctic Cod *Boreogadus saida* that prey upon such species (Gradinger and Bluhm 2004). The dynamic nature of the Arctic means that resources are highly variable and patchy at both spatial and temporal scales (Power 1997). These conditions cause several Arctic fishes to adopt migratory life-history strategies to utilize multiple habitats, leading to a higher chance of encountering favorable conditions (Craig 1984; Roux et al. 2016). Thus, the intensity, duration, and variability of environmental factors play a large role in determining fish species presence and abundance in a region, especially in the nearshore Arctic.

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). There are a variety of habitat types within nearshore habitats, which comprise a gradient of temperatures and salinities, that influence fish species that prefer a specific niche. These environmental conditions can be reflected by the presence/absence 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). For example, the distribution of juveniles in estuarine conditions can be a function of turbidity (Blaber and Blaber 1980). The variability of ecological community composition is thought to be indicative of stressors acting upon the populations (Warwick and Clarke 1993). 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).

Due to the dynamic nature of resources and conditions in the Arctic, some Arctic fishes adopt migratory life history strategies to increase chances of encountering habitats with favorable conditions (Craig 1984; Power 1997; Roux et al. 2016). Arctic whitefishes species like Broad Whitefish *Coregonus nasus*, Arctic Cisco *Coregonus autumnalis*, Least Cisco *Coregonus sardinella*, and Humpback Whitefish *Coregonus pidschian* are amphidromous and tolerant of moderate levels of salinity (Bond and Erickson 1985; de March 1989; Fechhelm et al. 1993). For example, Arctic Cisco in Alaskan waters are from the Mackenzie River, Northwest Territories, Canada, and are transported east as juveniles via easterly winds pushing surface currents where they spend six to eight years rearing in Alaskan estuaries and rivers before returning westward to spawn in their natal waters within the Mackenzie River (von Biela et al. 2013; Zimmerman et al. 2013). Conversely, Least Cisco, Broad Whitefish, and Humpback Whitefish spawning populations occur in many rivers across northern Alaska (Craig 1984, 1989; Fechhelm et al. 1994). The juveniles of all four of these whitefish species 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).

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. 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. These analyses demonstrate how the nearshore Alaskan Arctic fish community is changing in response to shifts in climate and environmental conditions.

# 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). Daily fish monitoring was performed 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, with the exception of a modification in 2009 to add a vertical metal bar to the fyke net funnel to prevent incidental seal catches.

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 select species. Fish were released away and offshore 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 (°C) and salinity (ppt) 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 (m3/s) were collected by a United States Geological Survey (USGS) gaging station upriver from the river mouth, near Pump Station 3. Meteorological data was collected hourly by the National Weather Service (NWS) at the nearby Deadhorse Airport data collecting site (PASC), located 12 km inland from Prudhoe Bay. Wind speed was measured in km/h; 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:

## Species Richness and Rare Species Presence / Absence

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. 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 responsive to non-linear response curves commonly found in ecological response scenarios (Guisan et al. 2002). 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).

Total number of species was defined using all sites combined. Top fitting model fits 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 presence/absence of “rare” species (defined as species ≤ 100 individuals caught in all years combined; *n*=15 species), each rare species was assessed using binomial Generalized Linear Models (GLMs) of presence / absence:

where is the mean value of species *j*, and is the effect for each Station *s*. is the biweekly sampling period (1–4).

## Effects of Environmental Variables Upon Species Composition

Multivariate analyses were conducted using the “vegan” package in R (Oksanen et al. 2018). This package allows for the multivariate analysis of quantitative environmental variables upon the responding species assemblages. To prevent rare species from dominating multivariate analyses (CITE XXXXX), we restricted analysis to the species whose abundance was greater than 100 fish, all years combined (*n*=17 species). 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. A dissimilarity matrix of the multivariate catch data was created using Bray-Curtis distances. The Bray-Curtis dissimilarity matrix was then reduced to three dimensions using non-metric multidimensional scaling (nMDS) using k=3.

To determine the effects of environmental variables upon species assemblage structure, we used a Mantel test (vegan command: bioenv()) on the Bray-Curtis distances with a Euclidean distance metric and Spearman correlation method, resulting in the optimal subset of environmental variables. Significance testing of environmental variables was performed 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 between groups (Oksanen ; Clark 1993). This performs pairwise comparisons between each sample year, station, and biweekly period.

The most parsimonious model of environmental variables upon the species CPUE dissimilarity matrix was determined by Permutational Analysis of Variance (PERMANOVA) using environmental variables (for each variable and all combined variables). PERMANOVA models were run for both annual and biweekly aggregations; biweekly periods that had gaps in data coverage in environmental monitoring were excluded from analysis. All environmental variables were assessed in a correlation matrix. Results of a correlation matrix showed no variables were highly correlated (>0.5). Environmental variables were square root transformed for PERMANOVA modeling. 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()). The full model for PERMANOVA was:

where are the Bray-Curtis dissimilarity matrix of transformed and standardized CPUE for all non-rare species, is the East-West wind vector (-1 = 270° West wind; 1 = 90° East wind).

## Species Composition Changes Over Time

Modeling of the nMDS time series data compared a nested linear effects models (station effects by year) 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).

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).

# Results

## Fish Sampling

From 2001 to 2018, a total of 1,784,593 fish were collected 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, XXXXXX, were present in all biweekly station samples.

## Species Richness and Rare Species Presence / Absence

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 = 0.0011) and over the season (GAM, k=3: F = 62.85, edf = 1.83, p < 0.00001). The rate of increase of species richness was not constant among biweekly periods, with a larger 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.

In total, there were 14 rare species captured (<100 fish, total catch all years). Results from the binomial presence/absence GLM of rare species over 2001–2018 showed a significant increase for Slimy Sculpin *Cottus cognatus* (estimate = 0.484, SE = 0.2202, p = 0.028) and Burbot *Lota lota* (estimate = 0.234, SE = 0.0793, p = 0.003) and a significant decrease for Bering Cisco *Coregonus laurettae* (estimate = -0.101, SE = 0.043, p = 0.019; Figure 3). Two additional species showed a significant trend in binomial presence/absence over the course of the season: Chum Salmon *Oncorhynchus keta* and *Liparis* spp. both increased in abundance during a season (estimate = 0.716, SE = 0.222, p = 0.001, and estimate = 2.995, SE = 0.9903, p = 0.002, respectively).

## Effects of Environmental Variables Upon Species Composition

For 2001–2018, water conditions at the sampling stations varied greatly on a biweekly basis. For example, water temperature ranged from 2.1 to 12.7° C (mean = 8.1° C) and salinity ranged from 0.14 to 28.7 ppt (mean = 11.4 ppt). Mean wind speed was 17.1 kph (range 10.5 – 36.1 kph), with a mean direction of 42.9° (i.e., Northeast). The discharge from the Sagavanirktok River ranged from 39.3 m3/s to 327.7 m3/s, with an average of 135.1 m3/s. Water conditions varied by station: salinity was highest at station 220 and lowest at station 230, while water temperature fluctuated substantially but was highest at station 230 and lowest at station 220 (Figure 4). Linear regression did not show significant changes for annual salinity (estimate = 0.06, SE = 0.096, p = 0.53) and wind speed (estimate = 0.046, SE = 0.028, p = 0.109). East-West wind directionality (-1 to 1) significantly shifted to become more easterly over time (estimate = 0.020, SE = 0.0083, p = 0.015), and there was also a significant increase in annual water temperature (estimate = 0.079, SE = 0.021, p = 0.001) and Sagavanirktok River discharge (estimate = 65.17, SE = 31.83, p = 0.045).

To determine the effects of these of environmental variables upon the species composition, we first performed a multivariate Mantel-type test upon the biweekly catch matrix. The optimal subset of parameters describing species composition were biweekly period, water salinity, and water temperature (correlation 0.391). Multivariate models after this included only these parameters and the spatial-temporal variables year and station. To prevent rare species from overwhelming multivariate analyses, the catch dataset removed all rare species. These five variables were the subset modeled in nMDS assessment as well as PERMANOVA.

The marginal PERMANOVA model containing year, station, biweekly period, water temperature, and salinity explained 46.8% of the sample variation. There was significant association between the species composition and year (marginal R2 = 0.029, pseudo-F = 13.62, p = 0.001), station (marginal R2 = 0.087, pseudo-F = 13.81, p = 0.001), biweekly period (marginal R2 = 0.110, pseudo-F = 17.56, p = 0.001), water temperature (marginal R2 =0.012, pseudo-F = 5.68, p = 0.001), and salinity (marginal R2 =0.020, pseudo-F = 9.47, p = 0.001). The sequential (Type I) sums of squares PERMANOVA model (Station + biweekly + Year + water temperature + salinity) shows some effects of water temperature (R2 =0.017) and salinity (R2 =0.020) upon species composition once spatio-temporal variables have been isolated.

Fish species composition (nMDS) had significant temporal associations on a yearly (R2 = 0.048, p = 0.003) and biweekly basis (R2 = 0.442, p < 0.001). 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). Analysis of the nMDS factors revealed 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). Thus, while there was significant overlap in species composition between locations, 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). Top species presented in Figure 5 were based upon the correlation between species and the first two nMDS axes using the sum of the absolute value of both correlations.

## Species Composition Changes Over Time

To investigate changes in the species community over time, we modeled nMDS axes by Year, Station, and biweekly period. 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 were no significant changes over years for any station. To test whether there were structural breakpoints in the time series, we tested the F-statistic (Chow test statistic) of the optimal number of breakpoints in the nMDS regression relationships. 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 timeseries of the nMDS axes showed no structural change.

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# Tables

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

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# Figures

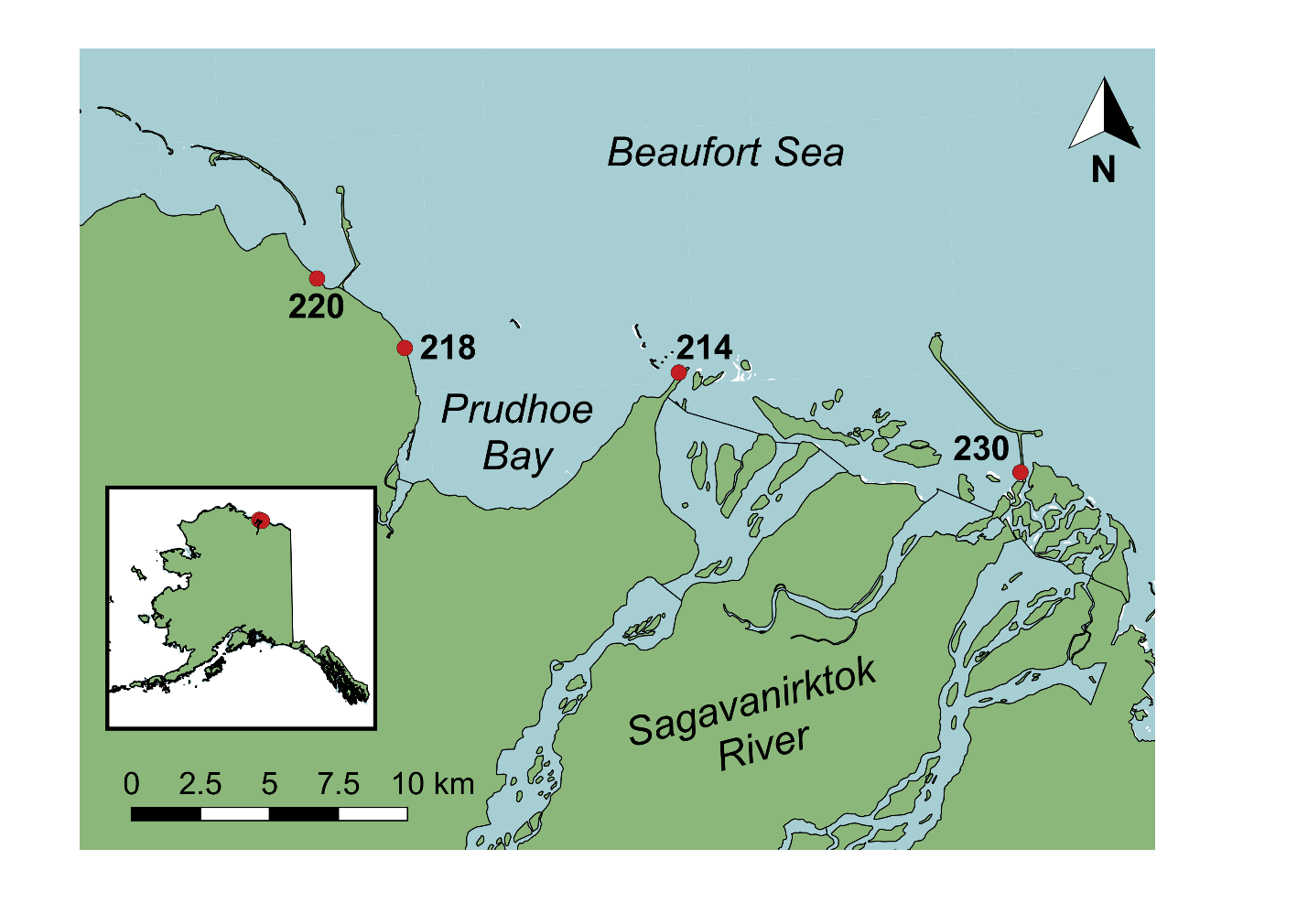


Figure 1. Map of study sample locations, Prudhoe Bay, Alaska.

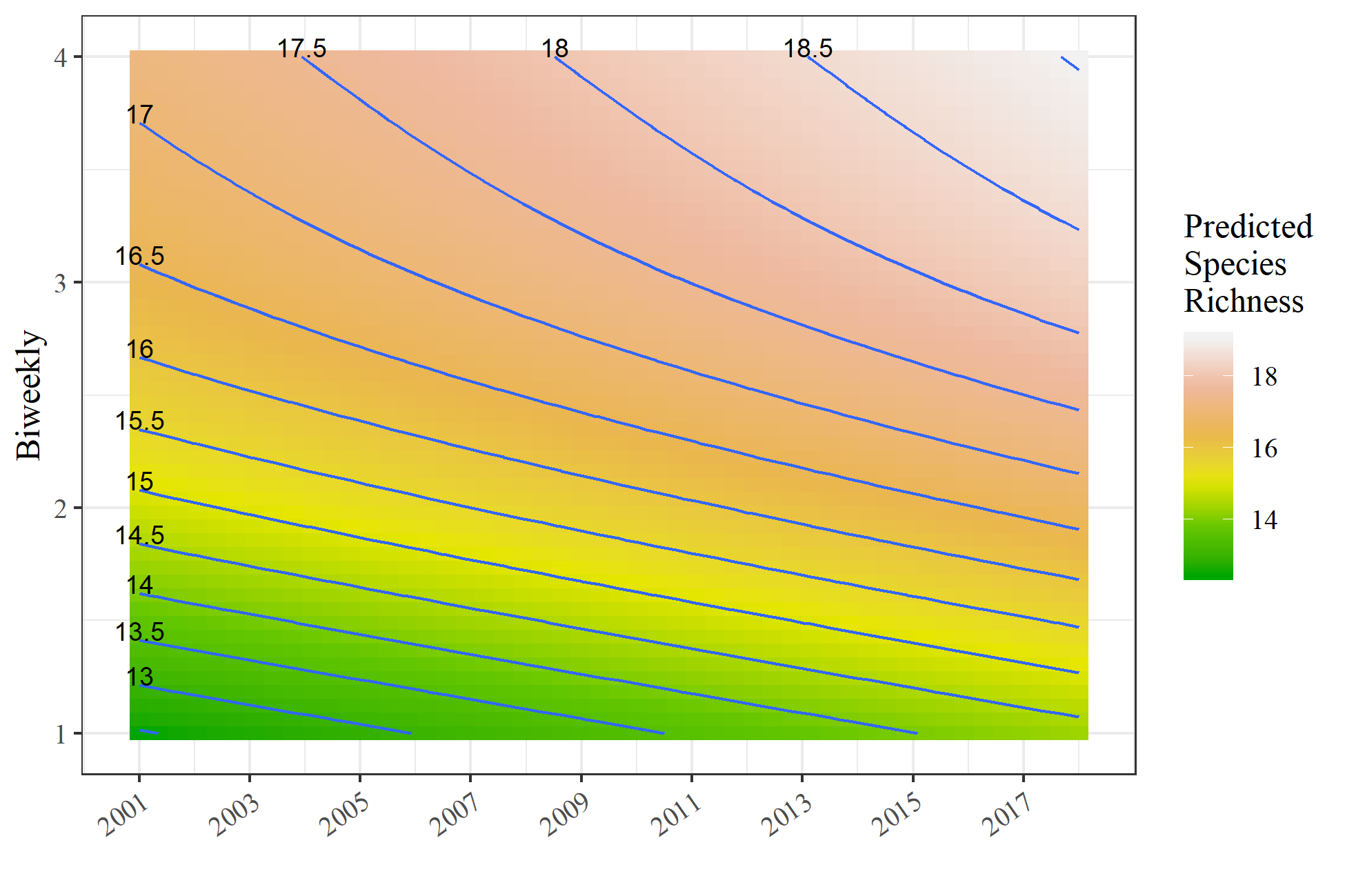


Figure 2. Predicted species richness by biweekly period and year, 2001–2018. Modeled results from a Generalized Additive Model showed a predicted increase in species richness across years and biweekly periods.

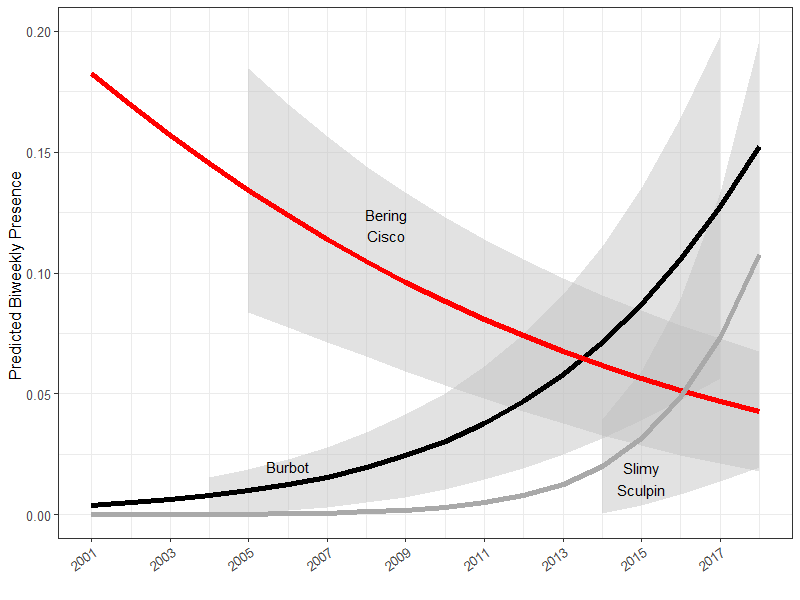


Figure 3. Predicted proportion of presence in a biweekly sample from a binomial Generalized Linear Model, 2001–2018. Only the three significant species are displayed. Standard error bars are shown as shaded.

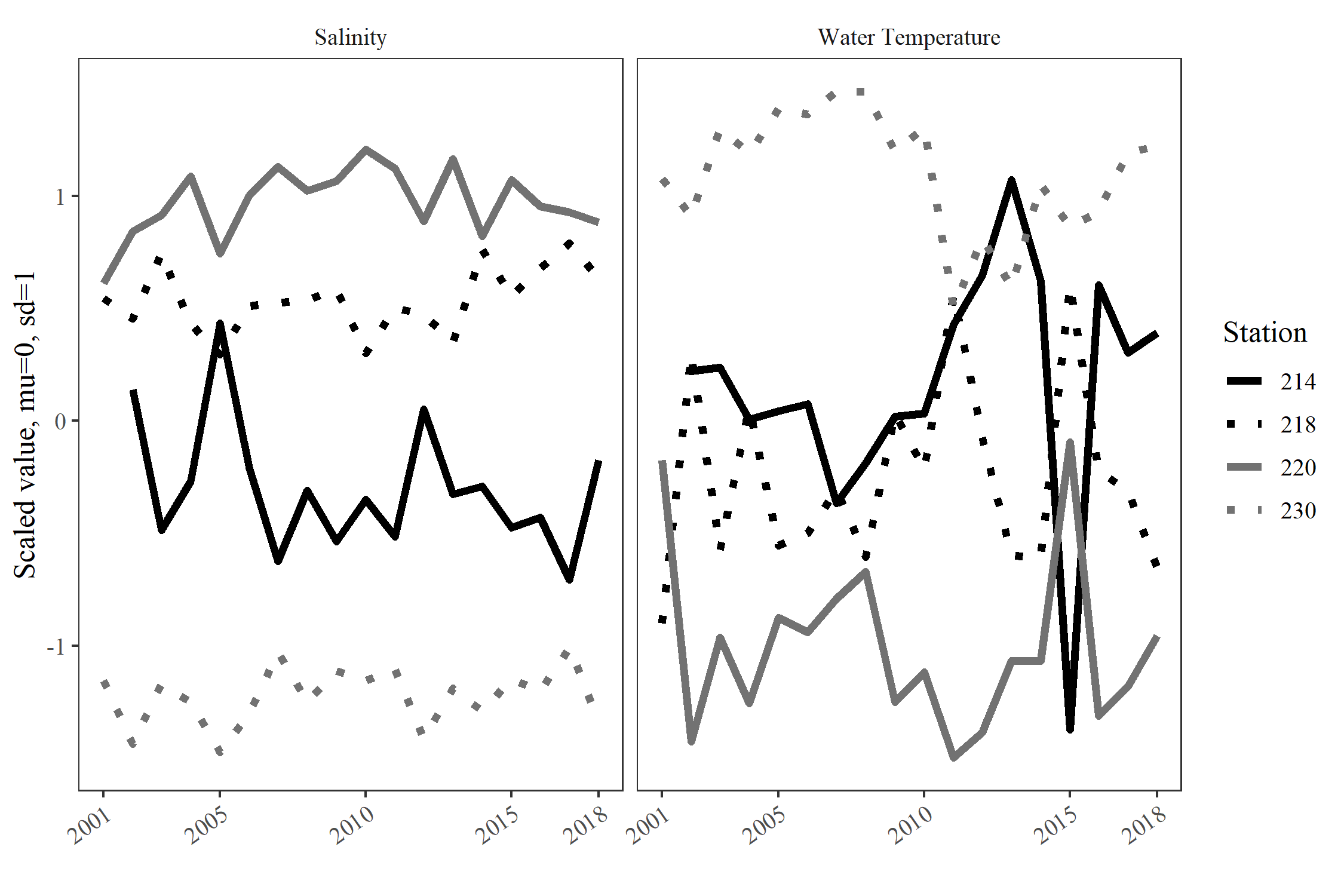


Figure 4. Annual trends of salinity and water temperature by station, 2001–2018, scaled to µ=0 and σ=1.

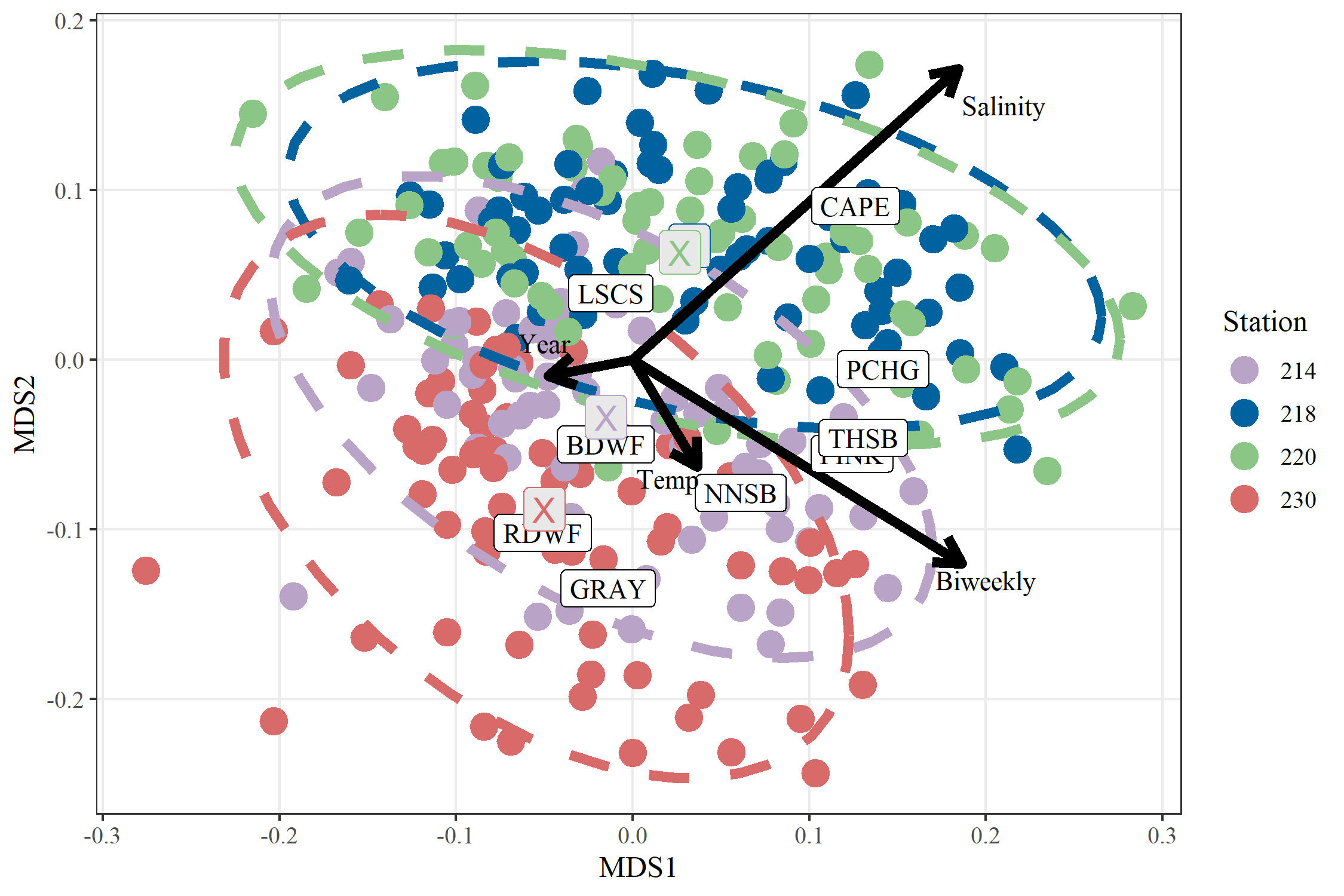


Figure 5. Non-metric multidimensional scaling (nMDS) ordination of fish species composition for each of the four stations from Prudhoe Bay, 2001–2018. Dashed ellipses are 95% confidence intervals; “X” labels mark centroids for each station. Environmental vectors of salinity, water temperature, biweekly period, and year are orthogonal to the gradient contours, pointing towards the direction of maximum association with the ordination. The top nine species that were associated with axes 1 and 2 are displayed, positioned according to their ordination score.