



Effects of environmental variables on a nearshore arctic fish community, 2001–2018

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Abstract

Nearshore fish communities comprise a fundamental component of Arctic marine ecosystems and serve as an important subsistence resource. As changing climate conditions affect Arctic waters, nearshore fish communities may also shift; however, how these communities will respond to climate change is not well understood. This study summarizes trends from a long-term (2001–2018) nearshore fish sampling program near Prudhoe Bay, Alaska, in the central Beaufort Sea. Abundance data ($n = 1.78$ million fish) from daily sampling (July–August) at four fixed sampling locations showed distinct shifts in fish community metrics. Since 2001, annual species richness has significantly increased by approximately one species per decade ($p = 0.0167$) while water temperature has warmed by approximately 1.4 °C. Results from non-metric multidimensional scaling (nMDS) and Permutational Analysis of Variance (PERMANOVA) models indicated that species composition based on biweekly catch data has significantly changed across years with distinct variations among sample locations and throughout the season. Salinity and water temperature were significantly related to multivariate species composition; specifically, the abundances of five species changed significantly over time. The species that increased in response to observed changes in the aquatic environment appear to be eurythermic and/or euryhaline generalist species such as Broad Whitefish *Coregonus nasus* and Saffron Cod *Eleginus gracilis*. Such patterns of altered species compositions demonstrate that continued long-term changes in environmental conditions will likely favor generalist species, potentially causing substantial shifts within the Arctic nearshore ecosystem with impacts on important subsistence resources.

Keywords Arctic fishes · Climate change effects · Beaufort sea · Nearshore · Long-term monitoring · Broad whitefish · *Coregonus nasus*

Introduction

Climate models predict that the effects of environmental change will be felt most acutely in the Arctic, with far-reaching and cascading ecological consequences. Shifts in climate conditions include a predicted increase in sea surface temperatures, while Arctic mean annual temperatures

will outpace global averages and rise 3–10 °C over the next 80 years (IPCC 2014). Effects of climate change are much broader than just temperature; precipitation is predicted to increase 30–50% and the mean annual sea ice spatial extent is expected to continue the observed decrease of 3.5–4.1% per decade (IPCC 2014). The persistent presence of sea ice and its effects on local ecosystems are unique in the Arctic Ocean. The reduction of Arctic sea ice has increased coastal erosion rates, which has increased nearshore suspended sediment load and reduced benthic and water column primary production in the central Beaufort Sea (Gibbs and Richmond 2015; Bonsell and Dunton 2018). Reductions in primary productivity and increases in temperature have direct implications on the ecological responses of many cold-adapted taxa (e.g., calanoid copepods and amphipods) and fishes such as Polar Cod *Boreogadus saida*, with further indirect responses resulting from predator–prey interactions (Bradstreet and Cross 1982; Gradinger and Bluhm 2004; Majewski et al.

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2016). As a result of such dependence, changes in Arctic environmental conditions are expected to impact regional fish assemblages.

Fish abundance is affected by environmental conditions such as water temperature and salinity because individual fish exhibit behaviors to optimize growth and survival (Cushing 1990; Monaghan 2008). Requirements for water temperature and salinity conditions 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 affects their rate-dynamic parameters (e.g., metabolic rate; Pauly 1980). Conditions outside of their optimal thermal ranges can be lethal, but it is often difficult to determine sub-lethal effects (Coutant 1987). Within estuarine areas, salinity can fluctuate widely on a daily basis, 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 increases in mortality (Arnesen et al. 1993; Dutil et al. 1997). Therefore, environmental conditions are reflected in the presence or abundance of individual fishes and in fish community composition (Jackson et al. 2001; Collie et al. 2008). Ever-fluctuating weather and water conditions can cause Arctic fishes to adopt migratory life-history strategies to utilize multiple habitats, leading to a higher probability of encountering favorable conditions (Craig 1984; Power 1997; Roux et al. 2016).

Despite the variable polar environment, nearshore Arctic waters are host to a variety of fishes. Whitefishes, such as Arctic Cisco *Coregonus autumnalis*, Broad Whitefish *C. nasus*, Least Cisco *C. sardinella*, and Humpback Whitefish *C. pidschian*, are amphidromous, tolerant of moderate levels of salinity, and capable of far-ranging migrations (Bond and Erickson 1985; de March 1989; Fechhelm et al. 1993). Arctic Cisco in Alaska waters originate in the Mackenzie River, Northwest Territories, Canada, and are transported > 500 km east as juveniles via easterly winds pushing surface currents (Fechhelm and Fissel 1988; Fechhelm and Griffiths 1990; von Biela et al. 2013; Zimmerman et al. 2013). In contrast, Broad Whitefish, Least Cisco, and Humpback Whitefish spawn in various 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, freshwater pools or areas of upwelling in local rivers (Craig et al. 1985; Fechhelm et al. 1999; Seigle and Gottschalk 2013). Arctic gadids, predominantly Polar Cod, are also ecologically important and support the Arctic marine ecosystem with their numerical prevalence and high energetic content (Elliott and Gaston 2008; Harter et al. 2013; Thorsteinson and Love 2016). This species displays migratory

behaviors, ostensibly to encounter habitats with favorable conditions, helping it to be 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; Divoky et al. 2021). Pacific salmon *Oncorhynchus* spp. have also been documented in the Arctic, with a natal population in the Mackenzie River in Canada (Irvine et al. 2009). Arctic diadromous species undergo movements to find suitable conditions in this dynamic region, and subsequently make up a disproportionately high percentage of the fish community in nearshore waters of the Alaska Arctic.

In addition to playing a key ecological role in coastal marine ecosystems, nearshore fishes also provide important subsistence food for local indigenous communities (Fechhelm et al. 2007; Thorsteinson and Love 2016). While there are no commercial fisheries in Arctic federal waters, subsistence fisheries in the nearshore Alaska Arctic are important social and nutritional contributions to local Inupiaq communities (Fechhelm et al. 2007; NPFMC 2009). Although these fisheries have limited economic impact, ecological changes to Arctic fish communities would have substantial social ramifications for human communities because of the cultural importance of some fish species (Moerlein and Carothers 2012).

Previous studies in Prudhoe Bay and the Alaska Arctic have often focused on single species or lacked long-term monitoring (Fechhelm et al. 1993, 1999; Thedinga et al. 2013). Assessing long-term trends and spatial patterns of species composition is imperative for understanding how fish communities respond to changes in environmental variables over time, especially in nearshore populations (Neves et al. 2016). Further, examining species composition in a multivariate framework provides a more comprehensive understanding of changes occurring to the fish community as a whole, rather than to one or two species individually (Fechhelm et al. 1995).

In this study, we assessed long-term changes in the Arctic fish community in response to shifts in environmental conditions within a nearshore semi-estuarine ecosystem in and around Prudhoe Bay, Alaska. We hypothesized that ongoing shifts in Arctic environmental conditions would result in measurable changes in fish populations over the past two decades (2001–2018). To quantify changes in fish communities, we assessed: (1) effects of environmental variables on species composition; (2) seasonal and interannual trends in species composition, abundance, and variability; and (3) temporal patterns in species richness and rare species presence. Given the importance of nearshore Arctic fishes to marine ecosystems and to local subsistence users, it is critical to understand how fishes respond to dynamic changes in environmental conditions.

Methods

Study area

This study was conducted in the Arctic Ocean along the coast near and in Prudhoe Bay, Alaska, 2001–2018 (Fig. 1). Prudhoe Bay is a semi-estuarine bay of the Beaufort Sea formed near the mouth of the Sagavanirktok River delta. The Sagavanirktok River is a braided river with an annual discharge of $1.5 \text{ km}^3 \text{ year}^{-1}$ (USGS 2018). For much of the year, landfast sea ice is prevalent and freezing temperatures reduce river discharge, influencing patterns of temperature and salinity in the nearshore area (Ross 1988). The immediate surrounding coastal waters are shallow, with the 6-m depth contour less than 5 km from most parts of natural, unaltered shore. Several barrier islands are also 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 and natural gas, with many permanent structures inland from the coast. Several oil extraction and processing facilities have been constructed on man-made islands that are connected to shore with gravel causeways and bridge breaches (Ross 1988).

Fish sampling

Fish monitoring in nearshore locations close to Prudhoe Bay has occurred since 1981 with standardized protocols and unchanged locations since 2001 (Fechhelm et al. 2002). Four stations spaced approximately 27 km apart along the coast were established for daily fish monitoring (Fig. 1). From west to east, these sites are identified as Site 220 (“West Dock” causeway), Site 218 (“West Beach” drilling pad), Site

214 (“Niakuk” drilling pad), and Site 230 (eastern “Endicott” causeway). Sites 230 and 214 are located near the Sagavanirktok River delta (Fig. 1). Fish monitoring occurred at each of the four sampling locations using side-by-side fyke nets, each with an opening of 1.8 m by 1.7 m, opening toward the coastline, with a 60-m block net leading to shore. A 15-m blocker wing was attached to the outer edge of each net cod end. Using this bi-directional sampling method, fyke nets intercepted and caught fish moving along the shoreline in either direction. All block nets and wings were constructed from 2.5-cm stretch mesh, while the fyke net mesh consisted of 1.27-cm stretch mesh. Three consecutive throats were located behind each 1.7-m frame opening, with the outermost throat having a functional width of 11.4 cm. Net specifications were consistently used during the study, with a modification in 2009 to add a vertical metal bar to the fyke net funnel to prevent entry by marine mammals.

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

Environmental data sources

Environmental variables examined were water temperature ($^{\circ}\text{C}$), salinity (psu), discharge for the Sagavanirktok River ($\text{m}^3 \text{ s}^{-1}$), and wind speed and directionality (km h^{-1} ; east or 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, and temperature meter (YSI Inc., Yellow Springs, Ohio) at the bottom, mid-point, and just below the surface of the water column. For data analyses, measurements taken near the top of the water column were used as measurements at other depths were not always taken. Daily Sagavanirktok River discharge data were collected by a US Geological Survey (USGS) gaging station approximately 170 km upriver from the river mouth near Pump Station 3. Wind data were collected hourly by the National Weather Service at the Deadhorse Airport meteorological data collecting site (PASC) located 12 km inland from Prudhoe Bay. Wind direction was recorded hourly as cardinal direction (0–360) and averaged for each biweekly period using the circular mean, then converted from polar to Cartesian coordinates to get the East–West unit vectors using:

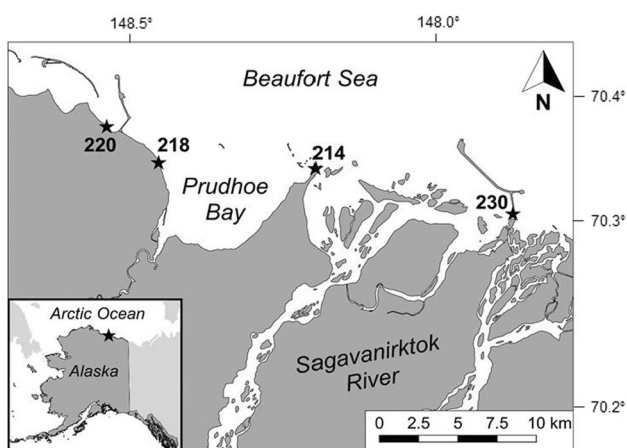


Fig. 1 Map of study sample locations around Prudhoe Bay, Alaska. Projection is in Alaska Albers, NAD83

East/West Wind Vector = $\sin(\text{polar degrees} \times \pi/180) \times r$,

where r was the absolute wind speed in km hr^{-1} , which resulted in positive values for easterly winds and negative values for westerly winds. East/west winds were used in the analysis rather than absolute wind speeds because of their effects on alongshore flow and upwelling/downwelling dynamics (Nikolopoulos et al. 2009; Pickart et al. 2009). Biweekly periods were consistent among years (e.g., biweekly period 1 was always 1–15 July).

Data analyses

Abundance data were recorded by net site and each net side for each species; however, both net sides were aggregated for analyses. All years (2001–2018) were included for analyses; while fish catches from 2014 were known to be influenced by local seismic testing, catches were predominately within previously observed ranges (Streever et al. 2016). Fish abundance data were pooled and standardized by the combined sampling effort as biweekly catch per unit effort (CPUE) by species and station in a 17 species by 280 biweekly samples matrix. Relationships among environmental variables were assessed using pairwise correlations and showed no pairs that were highly correlated (> 0.5). Response variables for multivariate analyses were CPUE values for each species which were fourth-root transformed, while explanatory environmental variables were square-root transformed. The CPUE values for each species were first transformed to mitigate the influence of large catches and then standardized to species maximums (percent of the maximum transformed catch) so that each species had the same weight in the analysis, regardless of the abundance. All significance testing was done at the $\alpha = 0.05$ level, and data were imported and analyzed using the statistical program R Version 3.6.1 (R Core Team 2019).

Effects of environmental variables on species composition

To determine the effects of environmental variables on species assemblage structure (Objective 1), we first computed pairwise Bray–Curtis distances among biweekly samples based on the fourth-root transformed and standardized CPUE data. The Bray–Curtis dissimilarity matrix was then used to visualize differences among samples using an ordination, relate differences in species composition to environmental variables using Mantel correlations and model multivariate dispersion using permutation-based ANOVAs.

To visualize differences in species composition among samples, we reduced the matrix of species abundances

to three dimensions using non-metric multidimensional scaling (nMDS) to achieve a stress value of less than 20% (Kruskal 1964). To prevent rare species from dominating multivariate analyses, we restricted analyses to those species with an abundance greater than 100 fish, all catches combined (Poos and Jackson 2012). Multivariate analyses were conducted using the “vegan” package in R (Oksanen et al. 2019). A multivariate Mantel-type test (BIOENV; Clarke and Ainsworth 1993) was conducted by computing Spearman rank correlations between the biweekly Bray–Curtis distances computed from CPUE data and the corresponding Euclidean distances computed from different subsets of environmental data. The subset of environmental variables that resulted in the largest Mantel correlation was tested for significance using a randomization test and this subset, along with the spatial–temporal variables *Year* and *Station*, was used in subsequent analyses (Legendre and Legendre 2012). Similarity percentages (SIMPER) were calculated to determine which species contributed most to the average Bray–Curtis dissimilarities between the eastern stations (Stations 230 and 214) and the western stations (Stations 218 and 220; Clarke 1993; Oksanen et al. 2019).

The optimal model of partitioning variability in species composition (as quantified by Bray–Curtis distances) based on environmental variables 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 explanatory variables for the full PERMANOVA model were *Year*, *Station*, *Biweek Period*, *Temperature*, *Salinity*, *Discharge*, and *East/West Wind Vector*. The response variable *Catch* was the Bray–Curtis dissimilarity matrix of transformed and standardized CPUE for all non-rare species, *Biweek Period* was one of four sample periods (i.e., period 1 = start date–15 July, period 2 = 16–31 July, period 3 = 1–15 August, and period 4 = 16 August–end date), *Temperature* and *Salinity* were from surface water measurements, and *East/West Wind Vector* was the East–West wind vector. The best-fitting PERMANOVA model was determined using backward-stepwise model selection based on the marginal reduction in residual R^2 associated with a given variable (Anderson 2001).

Species composition changes over time

To assess how species composition may have changed over time (Objective 2), we used indices of species composition from the nMDS (nMDS axes scores) as response variables in several alternative model formulations. First, to test for trends over time, we modeled the nMDS time series for all three axes as either a single time trend or

separate trends by station (Year nested in station). Linear models were compared to Generalized Additive Models (GAMs) that allowed for non-linear trends over time, as implemented in the package “mgcv” in R (Wood 2011, 2017). The full model was as follows:

$$MDS_j = \beta_0 + f_s(Year_t) + Station_s + BiweekPeriod_i + \varepsilon,$$

where MDS_j was each of the three multidimensional scaling axes ($j = 1, 2, 3$) and variables $Year_t$, $Station_s$, and $BiweekPeriod_i$ were the same as defined for previous models. The smooth time trend $f_s(Year_t)$ for each station s was compared to a linear trend ($\beta_s * Year_t$) and to a model with a single smooth temporal trend across all stations $f(Year_t)$; the top model was selected by AIC. In addition, we fit piecewise linear regressions over time that allowed for structural changes (breakpoints) in the time series to test for abrupt changes in species composition. The optimal number of breakpoints in the time series was tested using the Chow Test for structural breaks using package “strucchange” (Zeileis et al. 2002, 2003; Bai and Perron 2003).

Given that we found significant trends in species composition over time and as a function of environmental variables, we tested for whether catches or variability in catches of individual species have changed over time or in response to water temperature and salinity (Objective 2). Trends in species catches were investigated using linear regressions:

$$CPUE_k = \beta_0 + \beta_1 Year_t + Station_s + BiweekPeriod_i + \beta_2 Temperature_{t,s,i} + \beta_3 Salinity_{t,s,i} + \varepsilon,$$

where $CPUE_k$ was the biweekly CPUE of species k . As the magnitude of variability in community samples can be indicative of increased environmental stressors, we tested if the coefficient of variation (CV) in CPUE changed over time (Warwick and Clarke 1993). To quantify these temporal trends in the variability of catches for different species, we used a simple linear regression:

$$CV_k = \beta_0 + Year_t + \varepsilon,$$

where CV_k was the annual coefficient of variation of CPUE across four biweekly periods at and four stations for each species k , regressed on $Year$. p values were not adjusted for multiple tests.

Trends in species richness and rare species presence

To investigate interannual and seasonal trends in species richness (Objective 3), we modeled species richness as a function of year and biweekly sampling period using Generalized Additive Models. We used GAMs to allow for possible non-linear trends commonly found in ecological

modeling (Guisan et al. 2002). Species richness was modeled as:

$$Species\ Richness_{ii} = \alpha + a_t + f_1(Year_t) + f_2(Biweek\ Period_i) + f_2(Effort_{ii}) + \varepsilon_{ii},$$

where $Species\ Richness_{ii}$ was the number of unique species across all sites combined for each biweekly period i in year t , $Effort_{ii}$ was the proportion (0–1) of total time that the four stations were sampling, α was the overall model intercept, a_t was the year-specific deviation from the overall mean for year t , which was modeled as a random effect, and the f_i are smooth functions of the predictor variables. The random effects a_t are assumed to follow a Normal distribution with mean 0 and variance σ_a^2 . The full model was compared to models without effort, without random year effects, and to the null model (intercept only); the best-fitting model was determined using Akaike’s Information Criterion (AIC). Smoothing functions were restricted to 3 degrees of freedom to guard against overfitting.

To determine whether there were changes in the 15 “rare” species (≤ 100 individuals caught in all samples combined) that were excluded from the multivariate analysis of species composition, the probability of occurrence of each rare species was modeled using Generalized Linear Models (GLMs) with a binomial distribution (logistic regression) and a logit link. The expected probability of occurrence (μ) of a given species in year t and biweekly period i at station s was modeled as:

$$\log\left(\frac{\mu}{1-\mu}\right) = \beta_0 + \beta_1 Year_t + Station_s + \beta_2 Biweek\ Period_i.$$

For each rare species, the most parsimonious reduced model was determined using AIC.

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 ($n = 76$), as hybrids ($n = 22$), or those that 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,

Table 1 Total catch by species, mean catch, range per biweekly period, and frequency of occurrence in biweekly catch per station

Species	Latin name	Total catch	Biweekly mean catch	Biweekly catch range	Percent present in biweekly station catch (%)
Arctic char†	<i>Salvelinus alpinus</i>	1	0	0–1	0.4
Arctic cisco	<i>Coregonus autumnalis</i>	251,131	897	15–10,760	100.0
Arctic flounder	<i>Liopsetta glacialis</i>	182,323	651	10–3,297	100.0
Arctic grayling	<i>Thymallus arcticus</i>	845	3	0–141	46.4
Bering cisco†	<i>Coregonus laurettae</i>	53	0	0–10	10.0
Bering wolffish†	<i>Anarhichas orientalis</i>	3	0	0–1	1.1
Broad whitefish	<i>Coregonus nasus</i>	172,310	615	5–5,858	100.0
Burbot†	<i>Lota lota</i>	19	0	0–3	4.6
Capelin	<i>Mallotus villosus</i>	950	3	0–262	31.1
Chum salmon†	<i>Oncorhynchus keta</i>	32	0	0–3	9.3
Dolly varden	<i>Salvelinus malma</i>	32,055	114	0–1,068	98.9
Fourhorn sculpin	<i>Myoxocephalus quadricornis</i>	139,952	500	10–2,482	100.0
Humpback whitefish	<i>Coregonus pidschian</i>	32,575	116	0–865	97.9
Kelp greenling†	<i>Hexagrammos decagrammus</i>	2	0	0–2	0.4
Kelp snailfish†	<i>Liparis tunicatus</i>	4	0	0–2	0.7
Least cisco	<i>Coregonus sardinella</i>	231,000	825	12–4,327	100.0
Longnose sucker†	<i>Catostomus catostomus</i>	1	0	0–1	0.4
Ninespine stickleback	<i>Pungitius pungitius</i>	8,983	32	0–909	75.4
Pacific herring	<i>Clupea pallasii</i>	487	2	0–40	34.6
Pink salmon	<i>Oncorhynchus gorbuscha</i>	530	2	0–72	36.1
Polar cod	<i>Boreogadus saida</i>	595,271	2126	0–180,483	89.6
Rainbow smelt	<i>Osmerus mordax</i>	77,433	277	4–2,335	100.0
Rock greenling†	<i>Hexagrammos lagocephalus</i>	9	0	0–4	1.8
Round whitefish	<i>Prosopium cylindraceum</i>	7,318	26	0–380	68.6
Saffron cod	<i>Eleginus gracilis</i>	50,716	181	0–2,866	96.8
Shorthorn sculpin†	<i>Myoxocephalus scorpius</i>	2	0	0–1	0.7
Slender eelblenny†	<i>Lumpenus fabricii</i>	2	0	0–1	0.7
Slimy sculpin†	<i>Cottus cognatus</i>	6	0	0–2	1.8
Sockeye salmon†	<i>Oncorhynchus nerka</i>	1	0	0–1	0.4
Threespine stickleback	<i>Gasterosteus aculeatus</i>	577	2	0–48	36.1
Whitespotted greenling†	<i>Hexagrammos stelleri</i>	2	0	0–2	0.4

Species that are only included in rare species analysis (< 100 total catch) are marked with †

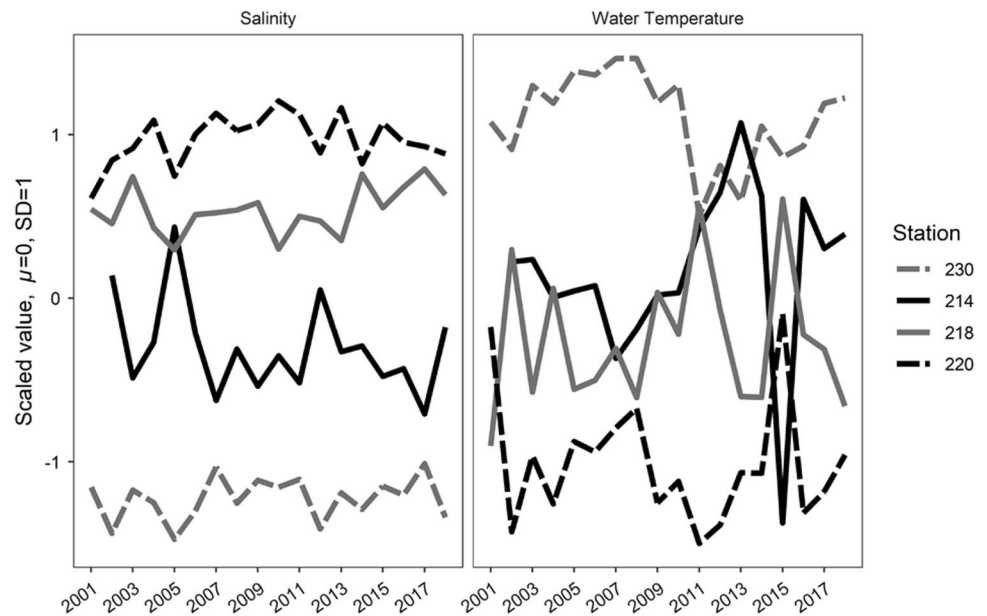
with the most numerous species (Polar Cod) accounting for 33% of the total catch. Six species (Arctic Cisco, Arctic Flounder *Liopsetta glacialis*, Broad Whitefish, Fourhorn Sculpin *Myoxocephalus quadricornis*, Least Cisco, and Rainbow Smelt *Osmerus mordax*) were present in all biweekly station samples.

Effects of environmental variables on species composition

From 2001 to 2018, environmental conditions at the four sampling stations varied both temporally and spatially. Water temperature ranged from 2.1 to 12.7 °C (mean = 8.1 °C, SD = 1.98), and salinity ranged from 0.14

to 28.7 (mean = 11.4, SD = 7.40). Mean summer water temperature increased significantly from 2001 to 2018 by 1.4 °C (linear regression, slope = 0.08, SE = 0.023, $p = 0.0005$), but there was no significant trend in salinity over time (linear regression, slope = 0.02, SE = 0.089, $p = 0.8030$). Among stations, water temperature fluctuated substantially but was highest on average at station 230 and lowest at station 220, while salinity was highest on average at station 220 and lowest at station 230 (Fig. 2). For each biweek period, mean daily discharge from the Sagavanirktok River ranged from 39.3 to 327.7 m³ s⁻¹ (mean = 135.1 m³ s⁻¹, SD = 54.1), with a significant increase in mean annual discharge from 2001 to 2018 (linear regression, slope = 1.85, SE = 0.90, $p = 0.0445$). Wind speed ranged from 10.5 to 36.1 kph (mean = 17.1 kph,

Fig. 2 Annual variability in salinity and water temperature by station near Prudhoe Bay, Alaska, 2001–2018, scaled to $\mu=0$ and $\sigma=1$



SD = 3.84), with a mean direction of 42.9° (i.e., from the northeast). There were no significant changes in annual wind speed (linear regression, slope = 0.05, SE = 0.028, $p=0.1086$), while the annual East–West wind directionality shifted to become more easterly over time (slope = 0.02, SE = 0.008, $p=0.0153$). Correlations among environmental variables were generally low with the largest correlation occurring between salinity and Sagavanirktok River discharge ($r=-0.28$).

The subset of environmental variables most strongly correlated with variability in species composition was *Biweekly Period*, *Salinity*, and *Water Temperature* ($r=0.288$, Mantel test, $p<0.0001$). Only these three variables and the spatial–temporal variables *Year* and *Station* were used in the subsequent nMDS analyses and PERMANOVA models. The nMDS was fit in three dimensions with a convergent stress of 0.156. Species composition was significantly related to biweekly periods and years ($R^2=0.442$, $p<0.0001$; $R^2=0.048$, $p=0.0030$, respectively). Species composition was associated with water salinity ($R^2=0.571$, $p<0.0001$), while water temperature was marginally significant ($R^2=0.021$, $p=0.0580$). We also found that species composition was significantly different among stations ($R^2=0.306$, $p<0.0001$).

While there was substantial overlap in species composition among all stations, there was a clear divide between eastern (214 and 230) and western (218 and 220) sampling sites. The nMDS centroids for stations 214 and 230 were outside the 95% CI ellipses for stations 218 and 220, and the centroids for stations 218 and 220 were outside the 95% CI ellipses for stations 214 and 230 (Fig. 3). The top five species accounting for the difference between eastern vs. western sites were Round Whitefish *Prosopium cylindraceum*

(found more in the eastern sites), Threespine Stickleback *Gasterosteus aculeatus* (found more in the western sites), Pacific Herring *Clupea pallasii* (found more in the western sites), Ninespine Stickleback *Pungitius pungitius* (found more in the eastern sites), and Arctic Grayling *Thymallus arcticus* (found more in the eastern sites), which contributed 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 PERMANOVA model that contained *Year*, *Station*, *Biweekly Period*, *Water Temperature*, and *Salinity* explained 47.5% of the sample variation. There were significant associations between the species composition and each of the five variables: *Year* (marginal $R^2=0.029$, $pseudo-F=13.9$, $p<0.0001$), *Station* (marginal $R^2=0.087$, $pseudo-F=14.0$, $p<0.0001$), *Biweekly Period* (marginal $R^2=0.110$, $pseudo-F=17.6$, $p<0.0001$), *Water Temperature* (marginal $R^2=0.012$, $pseudo-F=5.6$, $p<0.0001$), and *Salinity* (marginal $R^2=0.026$, $pseudo-F=12.8$, $p<0.0001$). Marginal R^2 values were low because water characteristics with confounded with spatial, seasonal and interannual patterns. The maximum proportion of variability in species composition that could be explained by each variable individually (i.e., the PERMANOVA model without any other variables) suggest weak interannual variability (*Year*: $R^2=0.038$; $p<0.0001$) and moderate spatial (*Station*: $R^2=0.203$; $p<0.0001$) and seasonal patterns (*Biweekly Period*: $R^2=0.194$; $p<0.0001$) that

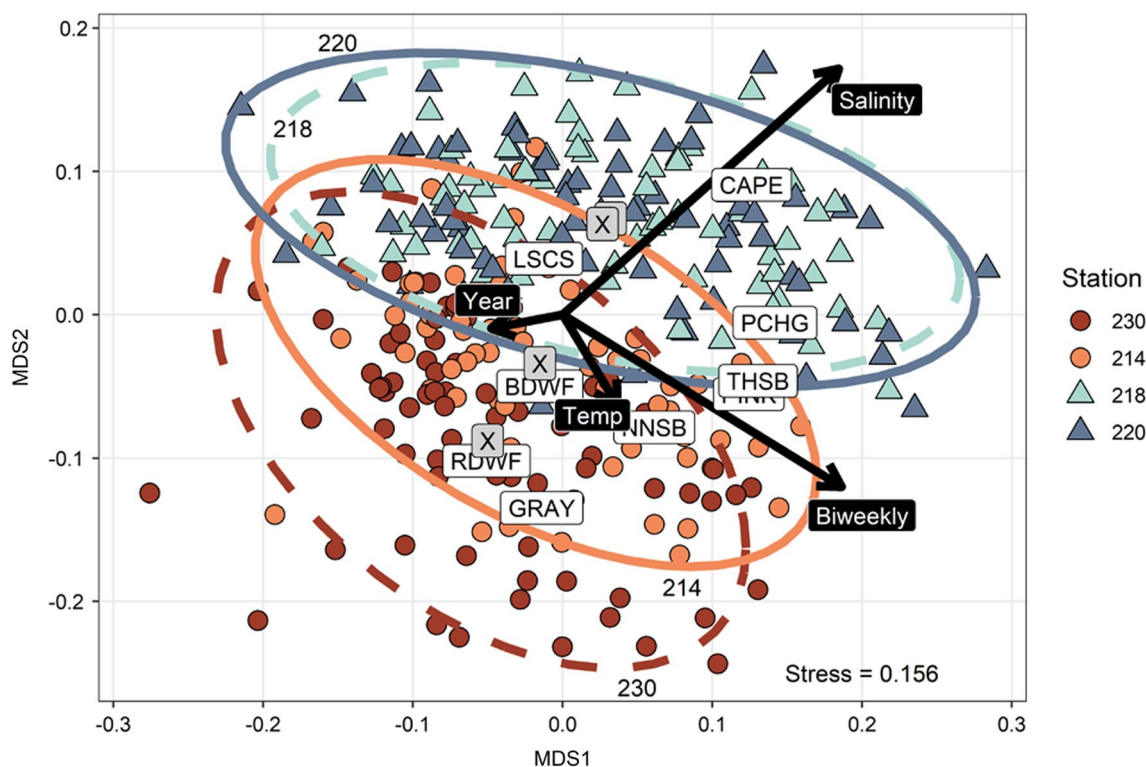


Fig. 3 Non-metric multidimensional scaling (nMDS) ordination of fish species composition near Prudhoe Bay, Alaska, 2001–2018. For each station, 95% confidence ellipses and centroids (“X”) are indicated. Environmental vectors for salinity, water temperature, biweekly period, and year are orthogonal to the gradient contours, pointing toward the direction of maximum association with the ordination axes. Weighted species scores are shown for the nine species that

were most strongly associated with nMDS axes 1 and 2: *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*

were at least in part related to variations in *Water temperature* ($R^2=0.042$; $p<0.0001$) and *Salinity* ($R^2=0.160$; $p<0.0001$).

Species composition and abundance changes

The two primary axes of species composition, nMDS axes 1 and 2, showed a significantly increasing and significantly decreasing non-linear time trend from 2001 to 2018, respectively (GAM, $p<0.0001$, not shown), with the same temporal trend across all stations. The third nMDS axis did not have a significant annual time trend. Across the four stations and three nMDS axes (12 station/axis combinations), only three showed weak support of a single structural break based on the Chow test statistic and a marginally lower Bayesian Information Criterion (axis 2, Station 220; axis 2, Station 214; and axis 2, Station 218). The three estimated break-points occurred between 2013 and 2016. Based on these results, it was concluded that the composition of the fish community around Prudhoe Bay, as indexed by three nMDS axes showed no structural change but displayed a gradual trend in species composition over time.

The CPUE of six individual species showed significant linear trends in abundance from 2001 to 2018: Broad Whitefish and Saffron Cod *Eleginus gracilis* increased in abundance, while Polar Cod, Fourhorn Sculpin, Humpback Whitefish, and Least Cisco decreased in abundance (Table 2). The abundances of Arctic Flounder, Broad Whitefish, Fourhorn Sculpin, and Saffron Cod were significantly and positively associated with water temperatures. Only the abundance of Dolly Varden *Salvelinus malma* decreased with increasing temperatures. Salinity was significantly and positively associated with the abundance of Arctic Cisco, Capelin *Mallotus villosus*, Pacific Herring, and Saffron Cod; the abundance of Dolly Varden, Humpback Whitefish, and Least Cisco each decreased with increasing salinity. The annual variability in catches increased over time for Dolly Varden and decreased for Saffron Cod.

Species richness and rare species presence

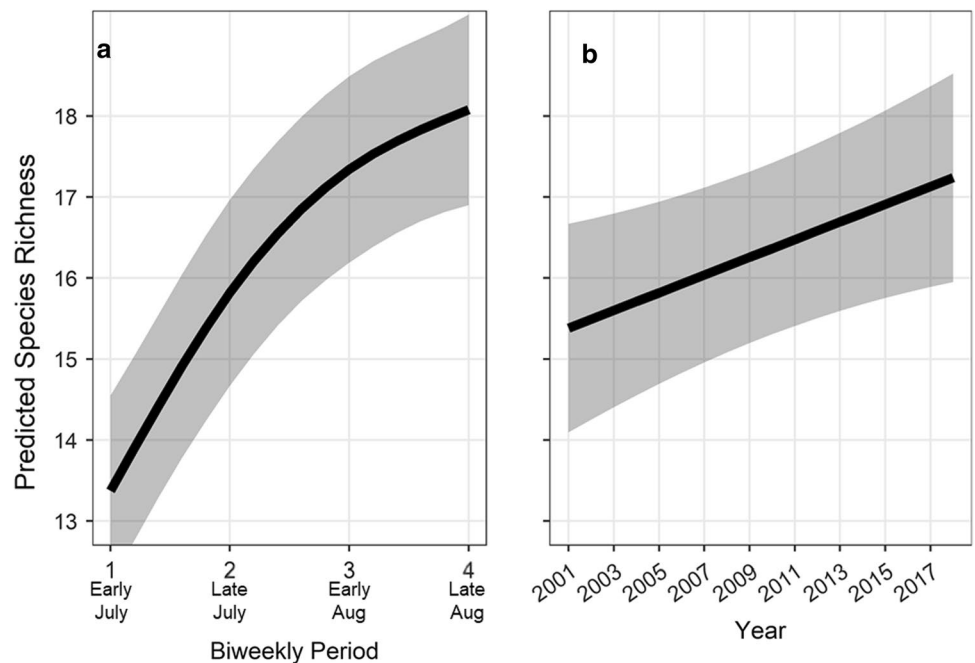
Species richness in the aggregated samples (year by biweekly period by station) ranged from 9 to 21 species,

Table 2 Regression coefficients and significance levels for continuous variables in multiple linear regressions of annual mean catch per unit effort on station (categorical; not shown), biweekly period (categorical; not shown), year, water temperature, and salinity, as well as a simple linear regression of the annual coefficient of variation (CV) in catch per unit effort on year for each species, Prudhoe Bay, Alaska, 2001–2018

Species	Year		Water temperature		Salinity		CV	
	Slope	<i>p</i> value	Slope	<i>p</i> value	Slope	<i>p</i> value	Slope	<i>p</i> value
Arctic cisco	-16.3	0.578	24.7	0.789	161.9	<0.001	0.00	0.962
Arctic flounder	15.5	0.086	128.7	<0.001	-8.3	0.368	0.02	0.059
Arctic grayling	0.0	0.880	-0.1	0.802	-0.3	0.105	-0.01	0.718
Broad whitefish	44.3	<0.001	148.8	<0.001	-23.8	0.066	0.01	0.347
Capelin	0.0	0.996	-0.5	0.643	1.0	0.003	-0.06	0.126
Dolly varden	-0.9	0.764	-45.9	<0.001	-7.9	0.013	0.03	0.035
Fourhorn sculpin	-18.1	0.005	43.5	0.033	-1.2	0.858	0.00	0.548
Humpback whitefish	-3.9	0.018	-0.8	0.875	-5.4	0.002	-0.01	0.252
Least cisco	-90.3	<0.001	29.5	0.402	-61.0	<0.001	0.01	0.108
Ninespine stickleback	0.8	0.515	2.7	0.469	0.3	0.794	0.00	0.786
Pacific herring	-0.1	0.230	-0.2	0.568	0.4	<0.001	-0.05	0.082
Pink salmon	0.0	0.704	-0.3	0.432	0.1	0.189	0.04	0.338
Polar cod	-813.7	0.041	-1,592.9	0.204	-538.6	0.189	0.03	0.326
Rainbow smelt	-1.4	0.791	14.2	0.407	-1.4	0.805	0.02	0.227
Round whitefish	0.6	0.496	0.5	0.855	-1.6	0.064	-0.04	0.155
Saffron cod	13.6	0.014	50.4	0.004	17.6	0.002	-0.04	0.029
Threespine stickleback	0.2	0.071	-0.1	0.821	0.1	0.207	-0.06	0.159

Significant effects ($\alpha < 0.05$) are in bold

Fig. 4 Predicted increases in species richness by season (biweekly period; **a**) and year (**b**), for the Prudhoe Bay area, Alaska, 2001–2018, based on a Generalized Additive Model and visualized for year 2018 and biweekly period 3. Shaded areas are the 95% confidence intervals



with a mean of 13.6 species present (SD = 2.10). Species richness was not significantly influenced by sampling effort, suggesting that the full community was sampled at all levels of sampling effort. Species richness showed a significant linear increase from 2001 to 2018 (GAM regression; slope = 0.11, SE = 0.044, $p = 0.0167$) and a significant non-linear trend over the season (GAM; $p = 0.008$); Fig. 4). Although the rate of species richness

trends varied among stations, the increasing trends in species richness over years and during the season occurred at all four stations.

The probability of occurrence of rare species ($n = 14$) increased significantly from 2001 to 2018 for Slimy Sculpin *Cottus cognatus* (slope = 0.48, SE = 0.220, $p = 0.0278$) and Burbot *Lota lota* (slope = 0.23, SE = 0.079, $p = 0.0032$) and declined significantly for Bering Cisco *Coregonus laurettae*

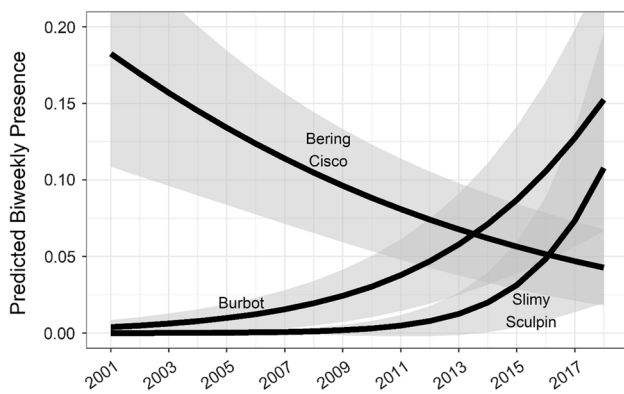


Fig. 5 Predicted probability of occurrence in a biweekly sample from a binomial Generalized Linear Model, visualized for Station 218 and biweekly period 2 near Prudhoe Bay, Alaska, 2001–2018. Only the three significant species are displayed. Standard error bands (± 1 SE) are shown as shaded areas

(slope = -0.10 , SE = 0.043 , $p = 0.0189$; Fig. 5). Two additional species showed a significant increase in probability of occurrence over the course of the season but not over years 2001–2018: Chum Salmon *Oncorhynchus keta* and unidentified snailfish *Liparis* spp. (biweekly periods 1–4; slope = 0.72 , SE = 0.222 , $p = 0.0013$, and slope = 3.00 , SE = 0.990 , $p = 0.0025$, respectively).

Discussion

We found several changes in metrics of fish species composition as well as significant associations between environmental conditions and the fish populations around Prudhoe Bay, Alaska, providing insight into a region undergoing substantial climatic changes (IPCC 2014). Local and regional shifts in some environmental drivers (e.g., increased water temperature, river discharge, eastern winds) were associated with changes in species abundances and relative proportions. Continued increases in water temperature, river discharge, and eastern winds may create competitive advantages for a fish community that is more reflective of estuarine conditions and more anadromous in composition. With competition for limited resources, we would expect increases in abundances of species that are better suited for these new conditions, such as Broad Whitefish and Saffron Cod, and declines in abundance of species that are stenohaline and/or stenothermal, such as Polar Cod (Fechhelm et al. 1992, 1993, 1995; Laurel et al. 2016; Dahlke et al. 2018; Vestfals et al. 2019). Generalist species (e.g., Fourhorn Sculpin, Broad Whitefish, etc.) may have a competitive advantage in a wide range of conditions (including new and old conditions) and therefore may proliferate as conditions change (Wilson et al. 2008; Fossheim et al. 2015; Kortsch et al.

2015). Overall, this study found changes in fish species composition were associated with changes in environmental conditions in Prudhoe Bay and favored species that were more generalist in physiological tolerance.

We identified 31 unique species in this study, representing 10% of the approximately 310 fish species known to inhabit the Arctic Ocean (Mecklenburg et al. 2011; Reist et al. 2006). Our study found that species richness increased significantly from 2001 to 2018 around Prudhoe Bay, Alaska, at a rate of approximately one additional species per decade. Species richness increased nonlinearly throughout the sampling season, tapering off at the end of the season when species richness was highest and ice coverage was lowest (Priest, unpubl. data). This was likely due to the typical seasonal wind patterns (increased upwelling) and reduced ice cover (increasing fetch) during mid- to late-August, which caused nearshore increases in salinity and in the catches of marine fishes. Ecosystem transitions such as shifts in fish populations and expansion of their geographic ranges northward with warming marine water temperatures may lead to increases in fish species richness (Grebmeier et al. 2006; Hiddink and ter Hofstede 2008; Bluhm et al. 2011; Stevenson and Lauth 2019). Previous studies have documented northward shifts in Arctic and sub-Arctic species distribution; for example, several Pacific species of crabs and bivalves were documented in large numbers in the Chukchi Sea for the first time in 2004 (Sirenko and Gagaev 2007). Additionally, fish and invertebrates captured in bottom trawl surveys in the southeastern Bering Sea demonstrated community-wide northward shifts, while northward expansions have been documented for the Pacific gray whale *Eschrichtius robustus* in the Chukchi and Beaufort seas and for killer whales *Orcinus orca* in the Canadian Arctic (Moore 2008; Mueter and Litzow 2008; Higdon and Ferguson 2009). Although no major changes in species composition are likely due to increased rare species abundances, the two rare species that increased in abundance (Slimy Sculpin and Burbot) are freshwater species, which demonstrates either a potential shift in acceptable nearshore environmental conditions or possibly an expansion in the freshwater populations as individuals search for more suitable habitat. Spatial range expansion by freshwater fishes into the marginal estuarine habitat could be reflective of favorable recruitment conditions in local rivers, or the increased river discharge could be displacing and transporting freshwater fishes into the Saganavirktok River delta.

In addition to increasing species richness, the species composition of Prudhoe Bay showed strong evidence for being influenced by spatio-temporal and environmental variables. Prevailing theories of life-history responses to environmental alterations posit that changes to water conditions will result in observable shifts in fish populations (Lehodey et al. 2006). While several environmental

variables significantly changed over the course of the study (e.g., increased river discharge and easterly winds), it is notable that annual water temperature increased by 1.4 °C. These changes in water temperature were associated with changes in relative species composition. At the individual species level, water temperature positively affects growth of whitefishes and parabolically influences the growth of cold-water adapted Polar Cod, a species that maximizes growth around 5 °C (Fechhelm et al. 1992, 1993; Laurel et al. 2016). Our results suggest that long-term abundance trends in several species may be the result of warming water temperatures: Broad Whitefish, Fourhorn Sculpin, and Saffron Cod abundances were positively associated with water temperature, consistent with previous studies, suggesting benefits to their recruitment or survival from warmer conditions (Fechhelm et al. 1992; Vestfals et al. 2019). In contrast, Humpback Whitefish were negatively associated with water temperature. Although several species were positively associated with water temperature, continued warming could push fish past optimal metabolic conditions or cause species interactions such as increased trophic competition for limited resources (Reist et al. 2006).

Increases in water temperature could also be linked to changes in river discharge. The annual freshwater discharge from the Sagavanirktok River significantly increased 25.4 m³ s⁻¹ over the course of the study. While river discharge appeared only to have minor influence on models of species composition, the volume of freshwater input to nearshore areas strongly affected salinity and temperature, which made it difficult to separate the effects of these variables due to multicollinearity. River discharge affects estuarine species composition and contributes to nearshore productivity by way of terrestrial carbon transfer, increasing habitat extents, and providing sediment transport to create barrier islands (Loneragan and Bunn 1999; Costa et al. 2007). Such contributions suggest that the significant changes in Sagavanirktok River discharge have the potential to disrupt fish community composition in nearshore areas.

We found a significant increase in easterly winds over the study period and associations between wind direction and species composition. The change to more easterly winds increases the occurrence of marine upwelling events, which lowers local water levels and brings nutrient-rich, high-saline waters toward nearshore regions (Ross 1988). Easterly winds also facilitated the transport of juvenile Arctic Cisco from the Mackenzie River, while hindering movements of fish from the Colville River (Fechhelm and Fissel 1988). Under such wind regimes in Prudhoe Bay, Arctic Cisco abundance increases, while Least Cisco abundance declines (Fechhelm et al. 1994). Wind direction in Prudhoe Bay also strongly affects both nearshore water depth and local salinity by causing upwelling or intrusions of marine waters to either

retreat or advance shoreward, affecting species composition by drawing marine species to the study area (Ross 1988).

While salinity did not change significantly from 2001 to 2018, it had strong effects on species composition, with marine species being associated with higher salinity. The significant increase in river discharge likely influenced the distribution of salinity gradients around Prudhoe Bay by extending or retracting freshwater plumes, which affects osmoregulation and feeding rates (de March 1989; Arnesen et al. 1993; Bœuf and Payan 2001). Salinity may be partially responsible for distinct spatial patterns in species composition in Prudhoe Bay. Each sampling station had a unique salinity profile; as a result, differences in species composition among stations were distinct in the nMDS ordination, caused mainly by species with different salinity tolerances. For example, the wide-ranging but generally lower salinities at the eastern stations meant that amphidromous species able to tolerate the fluctuations in salinity were more prolific at these locations. There does not appear to be a shift toward more predominantly marine or freshwater species, as species that drove the observed long-term changes in species composition were euryhaline and eurythermal, but rather a selection toward species that are more generalist in nature. Anadromous fishes are tolerant of a wide range of conditions and would be expected to be better adapted to greater environmental variability (Fechhelm et al. 1993; Bisson et al. 2009; IPCC 2014). Several species significantly changed in abundance and also were influenced by salinity, including Humpback Whitefish and Least Cisco that were negatively associated with salinity and Saffron Cod that were positively associated with salinity. Local salinity conditions were also highly dependent on other variables such as wind direction and river discharge. Because salinity was important to many models influencing species assemblage structure, we posit that any potential future changes to wind patterns and regional precipitation will affect the nearshore fish assemblage by altering local salinity (Fechhelm et al. 1993).

One variable that was not explicitly considered in this study was sea ice extent and duration, due to the lack of available fine-scale sea ice data. Sea ice influences the distribution of Arctic fish species such as Polar Cod, and is known to affect nearshore turbidity by mitigating nearshore erosional rates (Bradstreet and Cross 1982; Gradinger and Bluhm 2004; Bonsell and Dunton 2018; Dahlke et al. 2018). Researchers are currently processing high-resolution shorefast ice imagery that will include the Prudhoe Bay area (A. Mahoney, University of Alaska Fairbanks Geophysical Institute, personal communication). Preliminary modeling efforts of coarse-scale ice coverage from the National Snow and Ice Data Center did not show a relationship between species composition and regional sea ice indices (Priest, unpubl. data). Future research should examine whether declines in

sea ice and the duration of open water period influence patterns in nearshore species assemblage, as ice cover can affect ecosystem productivity and influence prey availability for planktivorous fishes by altering the growth and timing of the spring bloom as found in open ocean conditions (Hunt et al. 2002).

We used a combination of univariate and multivariate approaches to relate environmental conditions to changes in species abundances and composition. Results need to be interpreted with caution due to multicollinearity among explanatory variables. These concerns were addressed by excluding variables that were strongly confounded with others in univariate analyses and by quantifying the marginal effects of each variable in the PERMANOVA. In spite of including all explanatory variables in the PERMANOVA, approximately 50% of the variability in overall species composition remains unexplained, which is not unusual for PERMANOVA models especially given the large environmental variability (e.g., solar insolation and temperature swings) that can affect Arctic marine ecosystems (Anderson 2001).

While this study did not address ages or age structures of fish species, many of the fishes captured were juveniles because the nearshore environment around Prudhoe Bay serves as an important nursery area for many early life stages (Craig 1984; von Biela et al. 2013). Nearshore areas are important habitats that provide a wide diversity of trophic contributions, increased nursery production of juvenile fishes, and ontogenetic migration corridors (Beck et al. 2001; Sheaves et al. 2014). The variety of environmental conditions within the Prudhoe Bay nearshore area, comprised of strong gradients in water temperatures, salinities, and turbidities, ideally allow juvenile fishes to have access to a range of conditions that optimize their growth (Cyrus and Blaber 1987; Marchand 1991; Thorpe 1994). Changes to environmental conditions or to the community structure of populations may have a detrimental effect on the recruitment of juveniles of many species (Bailey 2000; Vinagre et al. 2009). Future studies are recommended to assess the impacts of changing climate conditions on juvenile recruitment.

The observed variability in catches was assumed to represent changes in local abundance and not a function of changing sampling efficiency. For example, changes in assemblage structure under different wind conditions were thought to reflect fish movement patterns in response to wind and not due to changes in sampling selectivity or efficacy (Bergström et al. 2013). To counter changes in spatio-temporal sampling efficiency, we pooled samples to a biweekly sampling period (to account for short-term fluctuations and minor gaps in sampling) and grouped eastern and western sampling sites. The geographic spread of sample sites attempted to mitigate effects from any potential inshore/offshore or east/west species distribution

by virtue of sampling locations that varied in proximity to river deltas and along isthmuses that extended into the Arctic Ocean. By having four sample sites and biweekly sample periods across broad spatial and temporal sampling units, fish catches were assumed to be representative of the entire Prudhoe Bay fish species composition.

Resilience of ecological communities to changes in their environment is a characteristic of healthy communities with high biological diversity and wide response diversity (Peterson et al. 1998; Elmqvist et al. 2003). Despite shifts in environmental conditions, the observed changes in species composition in this study demonstrate a fish community able to respond to increased stressors. However, as the pace of environmental change increases, and with it variability in the nearshore fish community, it is less clear whether the Arctic fish community can maintain its resilience (Karr 1981; Pimm 1984; Warwick and Clarke 1993). Increased population variability could indicate imminent sudden changes in community organization or collapses in abundances but suitable reference points that could serve as early warning signs have not been established for fish communities (Scheffer et al. 2001; Carpenter et al. 2011). Therefore, the continued monitoring of nearshore fish populations in the Beaufort Sea is critical to assessing how future species communities might organize and respond to perturbations in their natural environment with changing climate conditions.

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Author contributions JTP and TMS conceived and designed the overall research objectives. JTP performed data collection and fieldwork. FJM and SWR contributed oversight and feedback regarding data analysis. JTP conducted the data analysis and wrote the manuscript. TMS, FJM, and SWR provided manuscript edits. All authors read and approved the manuscript.

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Data availability All code is publicly available on the author's repository at https://github.com/justinpriest/envvar_effects_arctic_fish_comm or by request. The data are available on reasonable request.

Declarations

Conflict of interest All authors declare that they have no conflict of interest.

Ethical approval This work was conducted as part of an M.Sc. research project at the University of Alaska Fairbanks (Priest et al. 2020). All fish sampling was conducted under authority from annual permits issued by the Alaska Department of Fish and Game and followed protocols approved by the University of Alaska Fairbanks Institutional Animal Care and Use Committee (IACUC Permit Number 1054743).

References

- Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecol* 26:32–46
- Arnesen AM, Jørgensen EH, Jobling M (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. [https://doi.org/10.1016/0044-8486\(93\)90307-K](https://doi.org/10.1016/0044-8486(93)90307-K)
- Bai J, Perron P (2003) Computation and analysis of multiple structural change models. *J Appl Econ* 18:1–22. <https://doi.org/10.1002/jae.659>
- Bailey KM (2000) Shifting control of recruitment of walleye pollock *Theragra chalcogramma* after a major climatic and ecosystem change. *Mar Ecol Prog Ser* 198:215–224
- Beck MW, Heck KL, Able KW et al (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* 51:633–641. [https://doi.org/10.1641/0006-3568\(2001\)051\[0633:TICAMO\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0633:TICAMO]2.0.CO;2)
- Bergström L, Karlsson M, Pihl L (2013) Comparison of gill nets and fyke nets for the status assessment of coastal fish communities. WATERS Report 2013:7. Havsmiljöinstitutet / Swedish Institute for the Marine Environment, Göteborg, Sweden
- Bisson PA, Dunham JB, Reeves GH (2009) Freshwater ecosystems and resilience of Pacific salmon: habitat management based on natural variability. *Ecol Soc* 14:45. <https://doi.org/10.5751/ES-02784-140145>
- Bluhm BA, Gebruk A, Gradinger RR et al (2011) Arctic marine biodiversity: an update of species richness and examples of biodiversity change. *Oceanography* 24:232–248. <https://doi.org/10.5670/oceanog.2011.75>
- Bœuf G, Payan P (2001) How should salinity influence fish growth? *Comp Biochem Physiol - Part C Toxicol Pharmacol* 130:411–423. [https://doi.org/10.1016/S1532-0456\(01\)00268-X](https://doi.org/10.1016/S1532-0456(01)00268-X)
- Bond WA, Erickson RN (1985) Life history studies of anadromous coregonid fishes in two freshwater lake systems on the Tuktoyaktuk Peninsula, Northwest Territories. *Can Tech Rep Fish Aquat Sci* 1336:1–61
- Bonsell C, Dunton KH (2018) Long-term patterns of benthic irradiance and kelp production in the central Beaufort Sea reveal implications of warming for Arctic inner shelves. *Prog Oceanogr* 162:160–170. <https://doi.org/10.1016/j.pocean.2018.02.016>
- Bradstreet MSW, Cross WE (1982) Trophic relationships at high Arctic ice edges. *Arctic* 35:1–12. [https://doi.org/10.1016/0266-9838\(93\)90013-8](https://doi.org/10.1016/0266-9838(93)90013-8)
- Carpenter SR, Cole JJ, Pace ML et al (2011) Early warnings of regime shifts: a whole-ecosystem experiment. *Science* 332:1079–1082. <https://doi.org/10.1126/science.1203672>
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Austral Ecol* 18:117–143
- Clarke KR, Ainsworth M (1993) A method of linking multivariate community structure to environmental variables. *Mar Ecol Prog Ser* 92:205–219. <https://doi.org/10.3354/meps092205>
- Collie JS, Wood AD, Jeffries HP (2008) Long-term shifts in the species composition of a coastal fish community. *Can J Fish Aquat Sci* 65:1352–1365. <https://doi.org/10.1139/F08-048>
- Costa MJ, Vasconcelos R, Costa JL, Cabral HN (2007) River flow influence on the fish community of the Tagus estuary (Portugal). *Hydrobiologia* 587:113–123. <https://doi.org/10.1007/s10750-007-0690-x>
- Coutant CC (1987) Thermal preference: when does an asset become a liability? *Environ Biol Fishes* 18:161–172. <https://doi.org/10.1007/BF00000356>
- Craig PC (1984) Fish use of coastal waters of the Alaska Beaufort Sea: a review. *Trans Am Fish Soc* 113:265–282. [https://doi.org/10.1577/1548-8659\(1984\)113%3c265:FUOCWO%3e2.0.CO;2](https://doi.org/10.1577/1548-8659(1984)113%3c265:FUOCWO%3e2.0.CO;2)
- Craig PC (1989) An introduction to anadromous fishes in the Alaskan Arctic. *Biol Pap Univ Alaska* 24:27–54
- Craig PC, Griffiths WB, Haldorson L, McElderry H (1985) Distributional patterns of fishes in an Alaskan Arctic lagoon. *Polar Biol* 4:9–18
- Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Adv Mar Biol* 26:249–293. [https://doi.org/10.1016/S0065-2881\(08\)60202-3](https://doi.org/10.1016/S0065-2881(08)60202-3)
- Cyrus DP, Blaber SJM (1987) The influence of turbidity on juvenile marine fishes in estuaries. Part 1. Field studies at Lake St. Lucia on the southeastern coast of Africa. *J Exp Mar Bio Ecol* 109:53–70. [https://doi.org/10.1016/0022-0981\(87\)90185-7](https://doi.org/10.1016/0022-0981(87)90185-7)
- Dahlke FT, Butzin M, Nahrgang J et al (2018) Northern cod species face spawning habitat losses if global warming exceeds 1.5°C. *Sci Adv* 4:1–11. <https://doi.org/10.1126/sciadv.aas8821>
- de March BGE (1989) Salinity tolerance of larval and juvenile Broad Whitefish (*Coregonus nasus*). *Can J Zool* 67:2392–2397
- Divoky GJ, Brown E, Elliott KH (2021) Reduced seasonal sea ice and increased sea surface temperature change prey and foraging behaviour in an ice-obligate Arctic seabird, Mandt's black guillemot (*Cephus grylle mandtii*). *Polar Biol* 44:701–715. <https://doi.org/10.1007/s00300-021-02826-3>
- Dutil J-D, Lambert Y, Boucher E (1997) Does higher growth rate in Atlantic cod (*Gadus morhua*) at low salinity result from lower standard metabolic rate or increased protein digestibility? *Can J Fish Aquat Sci* 54:99–103. <https://doi.org/10.1139/f96-148>
- Elliott KH, Gaston AJ (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. *Mar Ornithol* 36:25–34
- Elmqvist T, Folke C, Nystrom M et al (2003) Response diversity, ecosystem change, and resilience. *Front Ecol Environ* 1:488–494. <https://doi.org/10.2307/3868116>
- Fechhelm RG, Bryan JD, Griffiths WB et al (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. *Can J Fish Aquat Sci* 51:890–899. <https://doi.org/10.1139/f94-088>
- Fechhelm RG, Dillinger RE Jr, Gallaway BJ, Griffiths WB (1992) Modeling of in situ temperature and growth relationships for yearling Broad Whitefish in Prudhoe Bay, Alaska. *Trans Am Fish Soc* 121:1–12. [https://doi.org/10.1577/1548-8659\(1992\)121%3c0001:MOISTA%3e2.3.CO;2](https://doi.org/10.1577/1548-8659(1992)121%3c0001:MOISTA%3e2.3.CO;2)
- Fechhelm RG, Fissel DB (1988) Recruitment of Canadian Arctic cisco (*Coregonus autumnalis*) into Alaskan waters. *Can J Fish Aquat Sci* 45:906–910. <https://doi.org/10.1139/f88-110>
- Fechhelm RG, Fitzgerald PS, Bryan JD, Gallaway BJ (1993) Effect of salinity and temperature on the growth of yearling Arctic Cisco (*Coregonus autumnalis*) of the Alaskan Beaufort Sea. *J Fish Biol* 43:463–474. <https://doi.org/10.1111/j.1095-8649.1993.tb00581.x>
- Fechhelm RG, Griffiths WB (1990) Effect of wind on the recruitment of Canadian Arctic Cisco (*Coregonus autumnalis*) into the central Alaskan Beaufort Sea. *Can J Fish Aquat Sci* 47:2164–2171. <https://doi.org/10.1139/f90-241>

- Fechhelm RG, Griffiths WB, Bryan JD et al (1995) Application of an in situ growth model: Inferred instance of interspecific trophic competition between anadromous fishes of Prudhoe Bay, Alaska. *Trans Am Fish Soc* 124:55–69. [https://doi.org/10.1577/1548-8659\(1995\)124%3c0055:AOAISG%3e2.3.CO;2](https://doi.org/10.1577/1548-8659(1995)124%3c0055:AOAISG%3e2.3.CO;2)
- Fechhelm RG, Haskell SP, Wilson WJ, Griffiths WB (2002) Nearshore Beaufort Sea fish monitoring in the Prudhoe Bay region, 2001. Report for BP Exploration (Alaska) Inc. by LGL Alaska Research Associates, Inc., Anchorage, Alaska
- Fechhelm RG, Martin LR, Gallaway BJ et al (1999) Prudhoe Bay causeways and the summer coastal movements of Arctic Cisco and Least Cisco. *Arctic* 52:139–151
- Fechhelm RG, Streever B, Gallaway BJ (2007) The Arctic Cisco (*Coregonus autumnalis*) subsistence and commercial fisheries, Colville River, Alaska: a conceptual model. *Arctic* 60:421–429
- Fossheim M, Primicerio R, Johannesen E et al (2015) Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nat Clim Chang* 5:673–677. <https://doi.org/10.1038/nclimate2647>
- George C, Moulton LL, Johnson M (2009) A field guide to the common fishes of the North Slope of Alaska. North Slope Borough, Department of Wildlife Management, Barrow, Alaska
- Gibbs AE, Richmond BM (2015) National assessment of shoreline change—historical shoreline change along the North coast of Alaska, U.S.-Canadian border to Icy Cape. U.S. Geological Survey Open File Report 2015–1048. <https://doi.org/10.3133/ofr20151048>
- Gradinger RR, Bluhm BA (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 Biol* 27:595–603. <https://doi.org/10.1007/s00300-004-0630-4>
- Grebmeier JM, Overland JE, Moore SE et al (2006) A major ecosystem shift in the northern Bering Sea. *Science* 311:1461–1464. <https://doi.org/10.1126/science.1121365>
- Green DG, Priest JT, Gatt KP, Sutton TM (2018) Beaufort Sea nearshore fish monitoring study: 2018 annual report. Fairbanks, Alaska
- Guisan A, Edwards TC, Hastie T (2002) Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecol Modell* 157:89–100. [https://doi.org/10.1016/S0304-3800\(02\)00204-1](https://doi.org/10.1016/S0304-3800(02)00204-1)
- Harter BB, Elliott KH, Divoky GJ, Davoren GK (2013) Arctic Cod (*Boreogadus saida*) as prey: fish length-energetics relationships in the Beaufort Sea and Hudson Bay. *Arctic* 66:191–196
- Hiddink JG, ter Hofstede R (2008) Climate induced increases in species richness of marine fishes. *Glob Chang Biol* 14:453–460. <https://doi.org/10.1111/j.1365-2486.2007.01518.x>
- Higdon JW, Ferguson SH (2009) Loss of Arctic sea ice causing punctuated change in sightings of killer whales (*Orcinus orca*) over the past century. *Ecol Appl* 19:1365–1375
- Hunt GL, Stabeno P, Walters G et al (2002) Climate change and control of the southeastern Bering Sea pelagic ecosystem. *Deep Res Part II Top Stud Oceanogr* 49:5821–5853. [https://doi.org/10.1016/S0967-0645\(02\)00321-1](https://doi.org/10.1016/S0967-0645(02)00321-1)
- 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. In: Team CW, Pachauri RK, Meyer L (eds) IPCC. Switzerland, Geneva, pp 1–151
- Irvine JR, Macdonald RW, Brown RJ et al (2009) Salmon in the Arctic and how they avoid lethal low temperatures. *North Pacific Anadromous Fish Comm Bull* 5:39–50
- Jackson DA, Peres-Neto PR, Olden JD (2001) What controls who is where in freshwater fish communities: the roles of biotic, abiotic, and spatial factors. *Can J Fish Aquat Sci* 58:157–170. <https://doi.org/10.1139/cjfas-58-1-157>
- Karr JR (1981) Assessment of biotic integrity using fish communities. *Fisheries* 6:21–27. [https://doi.org/10.1577/1548-8446\(1981\)006%3c0021:aobiuf%3e2.0.co;2](https://doi.org/10.1577/1548-8446(1981)006%3c0021:aobiuf%3e2.0.co;2)
- Kortsch S, Primicerio R, Fossheim M et al (2015) Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. *Proc R Soc B Biol Sci* 282:20151546. <https://doi.org/10.1098/rspb.2015.1546>
- Kruskal JB (1964) Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* 29:1–27. <https://doi.org/10.1007/bf02289565>
- Laurel BJ, Spencer M, Iseri P, Copeman LA (2016) Temperature-dependent growth and behavior of juvenile Arctic cod (*Boreogadus saida*) and co-occurring North Pacific gadids. *Polar Biol* 39:1127–1135. <https://doi.org/10.1007/s00300-015-1761-5>
- Legendre P, Legendre L (2012) Numerical ecology, 3rd edn. Elsevier
- Lehodey P, Alheit J, Barange M et al (2006) Climate variability, fish, and fisheries. *J Clim* 19:5009–5030. <https://doi.org/10.1175/jcli3898.1>
- Loneragan NR, Bunn SE (1999) River flows and estuarine ecosystems: implications for coastal fisheries from a review and a case study of the Logan River, southeast Queensland. *Aust J Ecol* 24:431–440. <https://doi.org/10.1046/j.1442-9993.1999.00975.x>
- Majewski AR, Walkusz W, Lynn BR et al (2016) Distribution and diet of demersal Arctic Cod, *Boreogadus saida*, in relation to habitat characteristics in the Canadian Beaufort Sea. *Polar Biol* 39:1087–1098. <https://doi.org/10.1007/s00300-015-1857-y>
- Marchand J (1991) The influence of environmental conditions on settlement, distribution and growth of 0-group sole (*Solea solea* (L.)) in a macrotidal estuary (Vilaine France). *Netherlands J Sea Res* 27:307–316
- Mecklenburg CW, Mecklenburg TA, Thorsteinson LK (2002) Fishes of Alaska. American Fisheries Society, Bethesda, Maryland
- Mecklenburg CW, Møller PR, Steinke D (2011) Biodiversity of arctic marine fishes: taxonomy and zoogeography. *Mar Biodiv* 41:109–140
- Moerlein KJ, Carothers C (2012) Total environment of change: Impacts of climate change and social transitions on subsistence fisheries in Northwest Alaska. *Ecol Soc* 17:10. <https://doi.org/10.5751/ES-04543-170110>
- Monaghan P (2008) Early growth conditions, phenotypic development and environmental change. *Philos Trans R Soc B Biol Sci* 363:1635–1645. <https://doi.org/10.1098/rstb.2007.0011>
- Moore SE (2008) Marine mammals as ecosystem sentinels. *J Mammal* 89:534–540. <https://doi.org/10.1644/07-mamm-s-312r1.1>
- Mueter FJ, Litzow MA (2008) Sea ice retreat alters the biogeography of the Bering Sea. *Ecol Appl* 18:309–320
- Neves LM, Teixeira-Neves TP, Pereira-Filho GH, Araújo FG (2016) The farther the better: effects of multiple environmental variables on reef fish assemblages along a distance gradient from river influences. *PLoS ONE* 11:1–23. <https://doi.org/10.1371/journal.pone.0166679>
- Nikolopoulos A, Pickart RS, Fratantoni PS et al (2009) The western Arctic boundary current at 152°W: structure, variability, and transport. *Deep Res Part II Top Stud Oceanogr* 56:1164–1181. <https://doi.org/10.1016/j.dsr2.2008.10.014>
- NPFMC (2009) Fishery management plan for fish resources of the Arctic management area. North Pacific Fishery Management Council, Anchorage, Alaska
- Oksanen J, Blanchet FG, Friendly M, et al (2019) vegan: community ecology Package. R package version 2.5–5. <https://CRAN.R-project.org/package=vegan>
- Pauly D (1980) On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175

- fish stocks. *ICES J Mar Sci* 39:175–192. <https://doi.org/10.1093/icesjms/39.2.175>
- Peterson G, Allen CR, Holling CS (1998) Ecological resilience, biodiversity, and scale. *Ecosystems* 1:6–18. <https://doi.org/10.1007/s100219900002>
- Pickart RS, Moore GWK, Torres DJ et al (2009) Upwelling on the continental slope of the Alaskan Beaufort Sea: storms, ice, and oceanographic response. *J Geophys Res* 114:1–17. <https://doi.org/10.1029/2008JC005009>
- Pimm SL (1984) The complexity and stability of ecosystems. *Nature* 307:321–326
- Poos MS, Jackson DA (2012) Addressing the removal of rare species in multivariate bioassessments: the impact of methodological choices. *Ecol Indic* 18:82–90. <https://doi.org/10.1016/j.ecolind.2011.10.008>
- Power G (1997) A review of fish ecology in Arctic North America. In: Reynolds JB (ed) *Fish Ecology in Arctic North America*. American Fisheries Society, Bethesda, Maryland, pp 13–39
- Priest JT, Green DG, Fletcher BM, Sutton TM (2018) Beaufort Sea nearshore fish monitoring study: 2017 annual report. Fairbanks, Alaska
- Priest, JT, Mueter FJ, Raborn SW, T. M. Sutton (2020) Long-term shifts in community structure, growth, and relative abundance of nearshore Arctic fishes: a response to changing environmental conditions. M.Sc. thesis, College of Fisheries and Ocean Sciences, University of Alaska Fairbanks
- R Core Team (2019) R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. <https://www.R-project.org/>
- Reist JD, Wrona FJ, Prowse TD et al (2006) General effects of climate change on Arctic fishes and fish populations. *Ambio* 35:370–380. [https://doi.org/10.1579/0044-7447\(2006\)35](https://doi.org/10.1579/0044-7447(2006)35)
- Ross BD (1988) Causeways in the Alaskan Beaufort Sea. United States Environmental Protection Agency, Anchorage, Alaska
- Roux MJ, Harwood LA, Zhu X, Sparling P (2016) Early summer nearshore fish assemblage and environmental correlates in an Arctic estuary. *J Great Lakes Res* 42:256–266. <https://doi.org/10.1016/j.jglr.2015.04.005>
- Scheffer M, Carpenter SR, Foley JA et al (2001) Catastrophic shifts in ecosystems. *Nature* 413:591–596
- Seigle JC, Gottschalk JM (2013) Fall 2012 subsistence fishery monitoring on the Colville River. ABR, Inc. – Environmental Research & Services, Fairbanks, Alaska
- Sheaves M, Baker R, Nagelkerken I, Connolly RM (2014) True value of estuarine and coastal nurseries for fish: incorporating complexity and dynamics. *Estuaries Coasts* 38:401–414. <https://doi.org/10.1007/s12237-014-9846-x>
- Sirenko BI, Gagaev SY (2007) Unusual abundance of macrobenthos and biological invasions in the Chukchi Sea. *Russ J Mar Biol* 33:355–364. <https://doi.org/10.1134/S1063074007060016>
- Stevenson DE, Lauth RR (2019) Bottom trawl surveys in the northern Bering Sea indicate recent shifts in the distribution of marine species. *Polar Biol* 42:407–421. <https://doi.org/10.1007/s00300-018-2431-1>
- Streever B, Raborn SW, Kim KH et al (2016) Changes in fish catch rates in the presence of air gun sounds in Prudhoe Bay, Alaska. *Arctic* 69:346–358. <https://doi.org/10.14430/arctic4596>
- Thedinga JF, Johnson SW, Neff AD et al (2013) Nearshore fish assemblages of the Northeastern Chukchi Sea, Alaska. *Arctic* 66:257–268
- Thorpe JE (1994) Salmonid fishes and the estuarine environment. *Estuaries* 17:76–93
- Thorsteinson LK, Love MS (2016) Alaska Arctic marine fish ecology catalog. U.S. Geological Survey Scientific Investigations Report 2016–5038 (OCS Study, BOEM 2016–048)
- USGS (2018) USGS National Water Information System—Sagavanirktok River near Pump Station 3, Alaska. https://waterdata.usgs.gov/ak/nwis/uv?site_no=15908000. Accessed 2 Apr 2018
- Vestfals CD, Mueter FJ, Duffy-Anderson JT et al (2019) Spatio-temporal distribution of Polar Cod (*Boreogadus saida*) and Saffron Cod (*Eleginus gracilis*) early life stages in the Pacific Arctic. *Polar Biol* 42:969–990. <https://doi.org/10.1007/s00300-019-02494-4>
- Vinagre C, Santos FD, Cabral HN, Costa MJ (2009) Impact of climate and hydrology on juvenile fish recruitment towards estuarine nursery grounds in the context of climate change. *Estuar Coast Shelf Sci* 85:479–486. <https://doi.org/10.1016/j.ecss.2009.09.013>
- von Biela VR, Zimmerman CE, Cohn BR, Welker JM (2013) Terrestrial and marine trophic pathways support young-of-year growth in a nearshore Arctic fish. *Polar Biol* 36:137–146. <https://doi.org/10.1007/s00300-012-1244-x>
- Warwick RM, Clarke KR (1993) Increased variability as a symptom of stress in marine communities. *J Exp Mar Bio Ecol* 172:215–226. [https://doi.org/10.1016/0022-0981\(93\)90098-9](https://doi.org/10.1016/0022-0981(93)90098-9)
- Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. *Annu Rev Ecol Syst* 15:393–425
- Wilson SK, Burgess SC, Cheal AJ et al (2008) Habitat utilization by coral reef fish: implications for specialists vs. generalists in a changing environment. *J Anim Ecol* 77:220–228. <https://doi.org/10.1111/j.1365-2656.2007.01341.x>
- Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J R Stat Soc* 73:3–36
- Wood SN (2017) *Generalized Additive Models: an introduction with R* (2nd edition). Chapman and Hall/CRC
- Zeileis A, Kleiber C, Walter K, Hornik K (2003) Testing and dating of structural changes in practice. *Comput Stat Data Anal* 44:109–123. [https://doi.org/10.1016/S0167-9473\(03\)00030-6](https://doi.org/10.1016/S0167-9473(03)00030-6)
- Zeileis A, Leisch F, Hornik K, Kleiber C (2002) strucchange: an R package for testing for structural change in linear regression models. *J Stat Softw* 7:1–38
- Zimmerman CE, Ramey AM, Turner SM et al (2013) Genetics, recruitment, and migration patterns of Arctic Cisco (*Coregonus autumnalis*) in the Colville River, Alaska, and Mackenzie River, Canada. *Polar Biol* 36:1543–1555. <https://doi.org/10.1007/s00300-013-1372-y>

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