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RESEARCH ARTICLE

Borealization of nearshore fishes on an interior Arctic shelf over multiple decades

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Abstract

Borealization is a type of community reorganization where Arctic specialists are replaced by species with more boreal distributions in response to climatic warming. The process of borealization is often exemplified by the northward range expansions and subsequent proliferation of boreal species on the Pacific and Atlantic inflow Arctic shelves (i.e., Bering/Chukchi and Barents seas, respectively). But the circumpolar nearshore distribution of Arctic-boreal fishes that predates recent warming suggests borealization is possible beyond inflow shelves. To examine this question, we revisited two nearshore lagoons in the eastern Alaska Beaufort Sea (Kaktovik and Jago lagoons, Arctic National Wildlife Refuge, Alaska, USA), a High Arctic interior shelf. We compared summer fish species assemblage, catch rate, and size distribution among three periods that spanned a 30-year record (baseline conditions, 1988–1991; moderate sea ice decline, 2003–2005; rapid sea ice decline, 2017–2019). Fish assemblages differed among periods in both lagoons, consistent with borealization. Among Arctic specialists, a clear decline in fourhorn sculpin (*Myoxocephalus quadricornis*, Kanayuq in Iñupiaq) occurred in both lagoons with 86%–90% lower catch rates compared with the baseline period. Among the Arctic-boreal species, a dramatic 18- to 19-fold increase in saffron cod (*Eleginus gracilis*, Uugaq) occurred in both lagoons. Fish size (length) distributions demonstrated increases in the proportion of larger fish for most species examined, consistent with increasing survival and addition of age-classes. These field data illustrate borealization of an Arctic nearshore fish community during a period of rapid warming. Our results agree with predictions that Arctic-boreal fishes (e.g., saffron cod) are well positioned to exploit the changing Arctic ecosystem. Another Arctic-boreal species, Dolly Varden (*Salvelinus malma*, Iqalukpik), appear to have already responded to warming by shifting from Arctic nearshore to shelf waters. More broadly, our findings suggest that areas of borealization could be widespread in the circumpolar nearshore.

KEYWORDS
Alaska, Arctic, Beaufort Sea, borealization, community reorganization, Dolly Varden, fourhorn sculpin, saffron cod, warming climate

1 | INTRODUCTION

In Arctic and boreal (i.e., subarctic) marine systems, community reorganizations have been associated with simultaneous shifts in climate and northward range expansions of boreal species over the Arctic's two gateway inflow shelves, the Bering-Chukchi seas in the Pacific Arctic and the Barents Sea in the Atlantic Arctic (Fossheim et al., 2015; Huntington et al., 2020; Mueter et al., 2021; Mueter & Litzow, 2008; Polyakov et al., 2020; Wassmann et al., 2011). Replacement of Arctic species in favor of boreal species reflects "borealization" of the community (Fossheim et al., 2015). The relationship between warming and range expansion is described in the Arctic Marine Pulses (AMP) model framework as a long-term increase in the seasonally pulsed transport of water and heat concurrent with the movement of lower trophic prey fields and their upper trophic predators (Moore et al., 2018), similar to the atlantification and pacification described by Polyakov et al. (2020). We seek to understand borealization in circumpolar nearshore waters where boreal species have existed across the Arctic for decades (Alabia et al., 2020; Underwood et al., 1995). Because these fish species are not strictly boreal, they are termed "Arctic-boreal" species and contrast the "Arctic" and "predominantly Arctic" species. An increase in Arctic-boreal species and/or a decrease in (predominantly) Arctic species would be consistent with borealization. In this study, we focus on the nearshore and examine the evidence for borealization beyond the two inflow Arctic shelves.

Our example comes from lagoons in the eastern Beaufort Sea (~70°N), near Kaktovik, Alaska, because they offer a glimpse of Arctic fish communities in a warmer future (typical summer temperatures 5–15°C; Harris et al., 2017), while also serving as important fisheries for local subsistence users (NPFMC, 2009). The area surrounding Kaktovik is an Iñupiaq fishing area with the traditional name Qaaktuġvik which translates to "seining place," highlighting the importance of the area for fisheries (Jacobson & Wentworth, 1982). Recognition of the area's importance continues today as the lagoons and lands extending south through the Brooks Range lie within the Arctic National Wildlife Refuge (ANWR). In ANWR and most other public lands in Alaska, the U.S. Federal government aims to provide the opportunity for subsistence and maintain healthy fish and wildlife populations per the Alaska National Interest Lands Conservation Act of 1980, 16 U.S.C. § 3101–3233. Studies supporting the development and decision-making for Outer Continental Shelf oil and gas activities have focused on subsistence species as well (e.g., BOEM, 2018). Baseline biological studies in the 1970s and 1980s, prior to dramatic warming and sea ice loss, revealed wide seasonal variation in nearshore water temperatures (−2 to 15°C) with fish communities comprised of marine resident and diadromous fishes (Craig, 1984; Underwood et al., 1995).

Successive studies of two adjacent lagoons, Kaktovik Lagoon and Jago Lagoon (Figure 1), provide a data time series needed to assess borealization. Fishes in the lagoons were sampled from 1988–1991 for baseline studies of assemblage, catch rates, and length distribution during a time period when persistent summer sea ice was common on the Beaufort Sea shelf and sea ice regularly entered lagoons during summer (Figure 2a; Underwood et al., 1995). The study sites were revisited in two later periods when sea ice concentration was moderately (2003–2005) and greatly (2017–2019) reduced (Figure 2b) (Garcia-Soto et al., 2021). This multidecade data set compares favorably with other time series of Arctic biological indicators that often begin in the 2000s (Fossheim et al., 2015; Huntington et al., 2020). Our most recent study period in the Beaufort Sea focuses on the same years (2017–2019) as Huntington et al. (2020), who document a distinct transformation of the Pacific boreal to Arctic transition zone (i.e., inflow shelves of Bring and Chukchi seas) characterized by low sea ice extent, warmer water, and changes is biological indicators from primary producers to predators. Our 30-year timespan has been a period of rapid change in the Beaufort Sea and adjacent Arctic Coastal Plain, which is experiencing accelerating rates of air temperature warming, erosion, permafrost degradation, glacier mass loss, and vegetation change (Bhatt et al., 2010; Garcia-Soto et al., 2021; Jones et al., 2018; Jorgenson et al., 2006; Nolan et al., 2011; Onarheim et al., 2018; Post et al., 2019).

Our objective was to assess potential climate-related shifts in the fish community by comparing fish assemblages, catch rates, and length distributions of common fish species in two eastern Beaufort Sea lagoons across the three time periods. We present evidence of community reorganization consistent with borealization of the nearshore fish community, including a decline in a species with a more Arctic distribution and an increase in a species with Arctic-boreal distribution. We anticipated an increase in the proportion of saffron cod (*Eleginus gracilis*, Uugaq in Iñupiaq) based on their Arctic-boreal distribution and evidence from laboratory experiments that demonstrated their eurythermic tolerance and positive growth responses to water temperatures as warm as 20°C (Laurel et al., 2016). We also expect that for many species, the length of juvenile fishes will shift toward larger individuals in response to increasing growth rates associated with warming (Laurel et al., 2016; Reist et al., 2006; von Biela et al., 2011).

2 | MATERIALS AND METHODS

2.1 | Fish community setting

Eight species are commonly encountered across the two lagoons and include species with five different biogeographic distribution categories after Thorsteinson and Love (2016): Arctic, predominantly

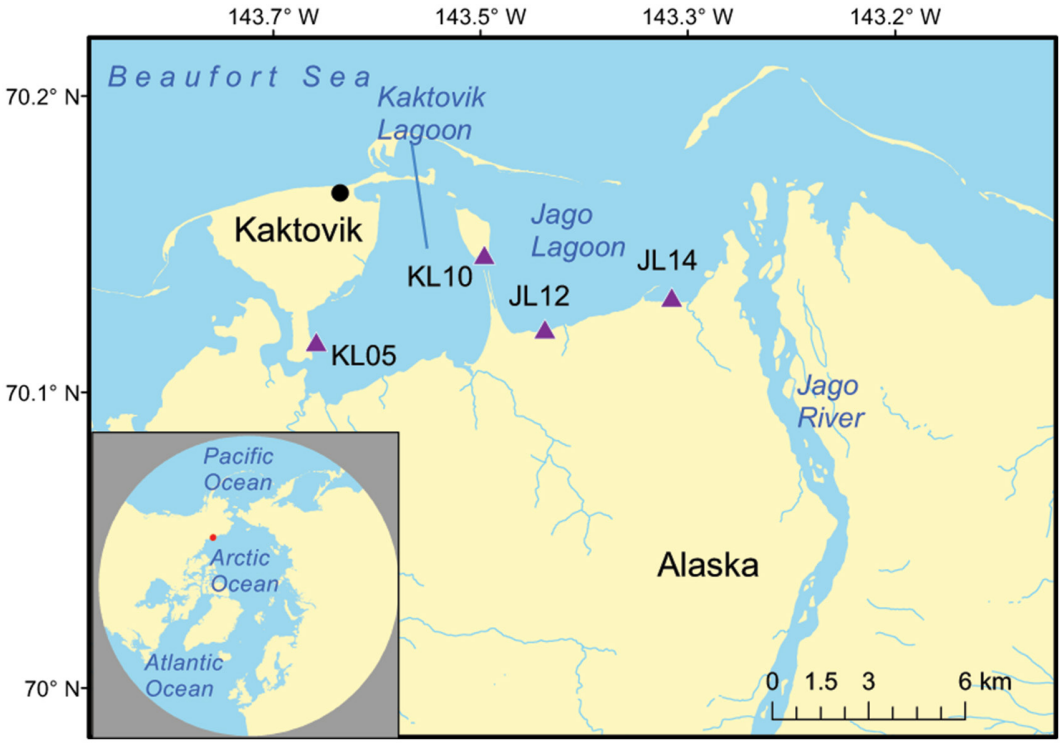

FIGURE 1 Study area along the Beaufort Sea coast of Alaska, USA. Fyke net stations are identified by purple triangles. Inset shows the location of the study area (red circle) with respect to the circumpolar Arctic.

Arctic, Arctic-boreal Pacific, Arctic-boreal, and predominantly boreal (Table 1). For this paper, we combine Arctic and predominantly Arctic as "Arctic specialists" and the remaining categories as "Arctic-boreal." The Arctic specialists are Arctic cod (*Boreogadus saida*, Iqaluġaq, sometimes also called polar cod), Arctic cisco (*Coregonus autumnalis*, Qaaktaq), fourhorn sculpin (*Myoxocephalus quadricornis*, Kanayuq), and Arctic flounder (*Liopsetta glacialis*, Nataaġnaq). Arctic-boreal species are saffron cod, Dolly Varden (*Salvelinus malma*, Iqalukpik, which is often identified as Arctic char in literature prior to the 1990s), Pacific capelin (*Mallotus catervarius* per Mecklenburg and Steinke (2015) and often also referred to as *M. villosus*, Paŋmaksraq), and ninespine stickleback (*Pungitius pungitius*, Kakalisauraq). These fishes use the lagoon habitat for summer feeding and growth (Jarvela & Thorsteinson, 1999) with a tendency for benthic foraging, particularly for fourhorn sculpin and Arctic flounder which are morphologically specialized for benthic living. Small epibenthic crustaceans like mysids, amphipods, and isopods are common to the diet of all nearshore Beaufort Sea fishes with some species also consuming small fishes (Craig, 1984).

Strong research interest in four of these fishes has resulted in a better understanding of their life histories. Arctic cisco and Dolly Varden support subsistence fisheries (Harcharek et al., 2018). Like other diadromous salmonids, they reproduce in freshwater and use marine waters for feeding, but unlike Pacific salmon (*Oncorhynchus* spp.) that remain at sea, they overwinter in brackish or freshwater habitats to avoid subzero marine water temperatures in the Arctic winter (Brown et al., 2019; Carey et al., 2021). Arctic cod and saffron cod are co-occurring Arctic gadids that play an important intermediate trophic role in Arctic marine food webs connecting primary consumers and predators (Harwood et al., 2015) and have been focal species in the Arctic Fishery Management Plan due to their potential as future commercial fisheries (NPFMC, 2009). Stenothermic Arctic cod are part of the cryopelagic ecosystem where they are a key forage fish on the Arctic's continental shelves and basin or in exposed, cold nearshore waters (Moulton & Tarbox, 1987; Underwood et al., 1995). Eurythermic saffron cod dominate in warmer waters (Copeman et al., 2020; Laurel et al., 2016; Vestfals et al., 2019). High variability in the daily and annual catch rates of Arctic cod and Arctic cisco will likely make the detection of decadal shifts difficult (Underwood et al., 1995). Arctic cod presence in warmer, protected lagoons is episodic, and the abundance of Arctic cisco in the Alaskan Beaufort Sea is dictated by interannual variability in wind-driven recruitment of age-0 individuals from spawning grounds in Canada (Fechhelm & Griffiths, 1990; Zimmerman et al., 2013).

2.2 | Study area

Kaktovik and Jago lagoons are adjacent to Kaktovik, Alaska, USA, in the eastern Beaufort Sea within the Arctic National Wildlife Refuge and are relatively well studied (Figure 1) (Dunton et al., 2006, 2012; Hale, 1990; Harris et al., 2017, 2018; Underwood et al., 1995). Both lagoons are shallow with mean depths of 3–4 m, soft-bottomed and exhibit large variability in water temperature (−2 to 14°C) and salinity (0 to >45) across seasons and years (Harris et al., 2017). The average summer water temperatures in the lagoons have likely

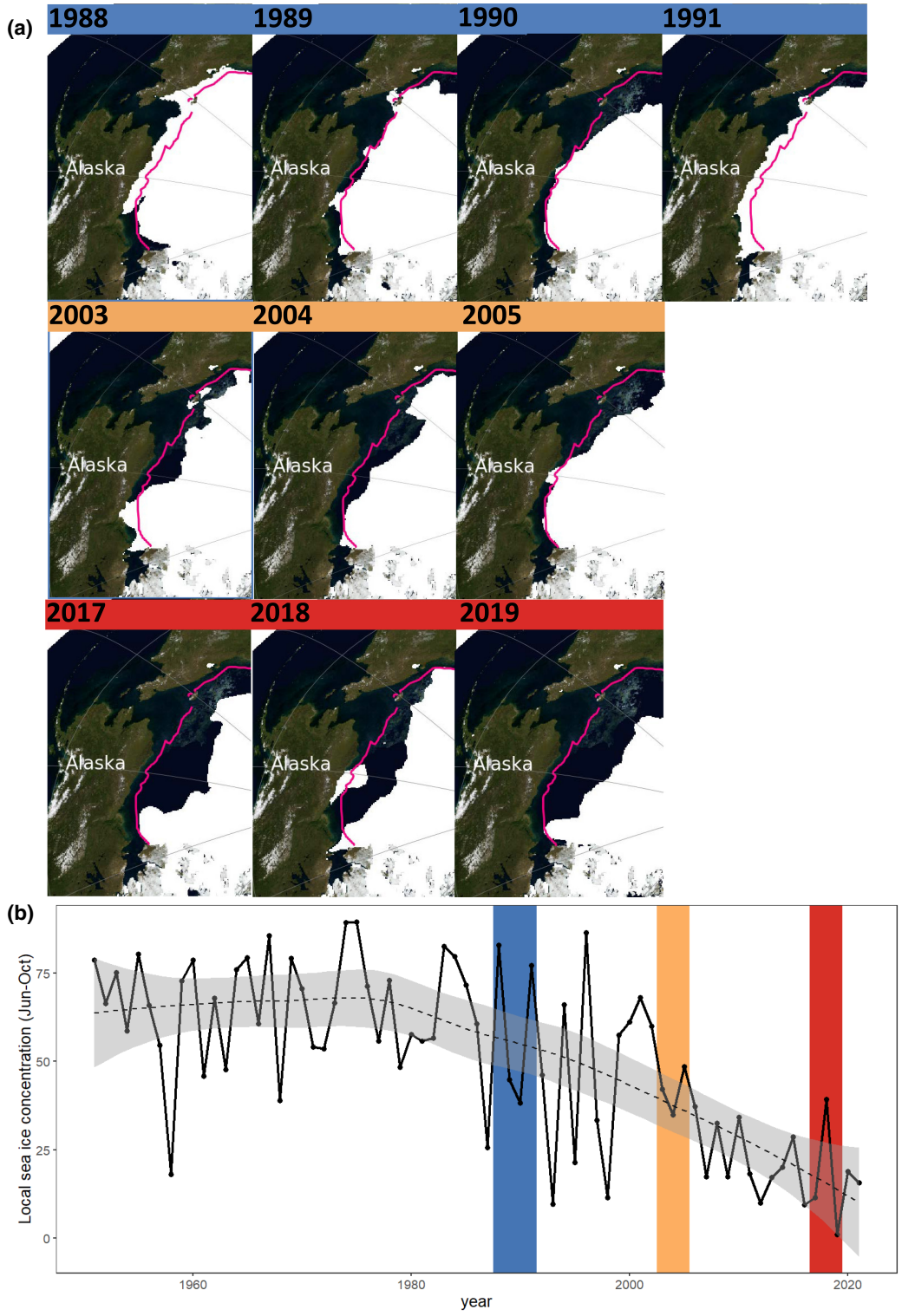

FIGURE 2 (a) Sea ice extent (white) image for each study year and (b) local sea ice concentration decline. Sea ice extent images show 15 August of each study year in the Pacific Arctic where the solid line (pink) is the median ice edge for 1981–2010 from the National Snow and Ice Data Center/NASA Earth Observatory (https://nsidc.org/data/seaice_index). Local sea ice concentration for Kaktovik, Alaska, calculated as the mean of monthly values for June to October in each year (1950–2021) from the Historical Sea Ice Atlas (https://www.snap.uaf.edu/tools/sea-ice-atlas).

increased in response to warming air temperatures, reduced ice, and resultant higher surface water temperatures in the Arctic (Bonsell & Dunton, 2018; Huntington et al., 2020; Priest et al., 2022). Few records exist, however, to directly assess long-term temperature increases in the nearshore marine Beaufort Sea or freshwaters of the Arctic Coastal Plain. For example, water temperature and salinity

TABLE 1 Fish species common to Kaktovik and Jago lagoons in the eastern Beaufort Sea, Alaska, USA. Species are listed with common English names, scientific names, Iñupiaq names (Harcharek et al., 2018), and their biogeographic distribution patterns (Thorsteinson & Love, 2016). Each species comprised >1% of the numeric catch rate in at least one of the three sampling periods in both lagoons (1988–1991, 2003–2005, or 2017–2019) except Pacific capelin which was only common in Jago lagoon

Common western name	Scientific name	Iñupiaq name	Life history	Distribution pattern
Arctic cod	*Boreogadus saida*	Iqaluġaq	Marine	Arctic
Arctic cisco	*Coregonus autumnalis*	Qaaktaq	Diadromous	Arctic
Fourhorn sculpin	*Myoxocephalus quadricornis*	Kanayuq	Marine	Predominantly Arctic
Arctic flounder	*Liopsetta glacialis*	Nataaġnaq	Marine	Predominantly Arctic
Saffron cod	*Eleginus gracilis*	Uugaq	Marine	Arctic-boreal Pacific
Dolly Varden	*Salvelinus malma*	Iqalukpik	Diadromous	Arctic-boreal Pacific
Pacific capelin	*Mallotus catervarius*	Paŋmaksraq	Marine	Arctic-boreal
Ninespine stickleback	*Pungitius pungitius*	Kakalisauraq	Marine	Predominantly boreal

data associated with the fish community data used here were not archived in a readable format for current software programs from the 1988–1991 study period and environmental monitoring was discontinued from 2003 to 2005 (Brown, 2008; Underwood et al., 1995).

In the absence of any novel environmental time series data, we present a time-series of sea ice concentration changes for the Kaktovik region (Figure 2b) and highlight available water temperature and salinity data from the nearshore Beaufort Sea. The sea ice time-series agrees with the interannual and long-term trends as experienced by the fisheries field crews including colder summers with heavier ice cover in 1988 and 1991 compared with 1989 and 1990 (Underwood et al., 1995), more ice in 2018 than in 2017 or 2019, and a long-term decline in summer sea ice. Nearshore water temperatures and salinities (2001–2018) near Prudhoe Bay, Alaska, in the central Beaufort Sea provide evidence of a 1.4°C increase in average summer water temperature and no long-term change in salinity (Priest et al., 2022).

Kaktovik and Jago lagoons differ in their connections to freshwater and marine habitats. Kaktovik Lagoon is a pulsing lagoon (Hale, 1990) that is relatively isolated from meteorological events, has no direct connection to the Beaufort Sea, and receives freshwater input from only small tundra streams. Kaktovik Lagoon has a shallow connection to Jago Lagoon, which has a shallow but direct connection to Beaufort Sea marine waters. Jago Lagoon is a limited exchange lagoon (Hale, 1990) and more responsive to meteorological events with a relatively strong connection to both freshwater and marine habitats including direct freshwater input from the Jago River and smaller tundra streams, and two wide shallow (<3 m) channels open to the Beaufort Sea. Fish data collected between the two lagoons are not strictly independent as the fish can move between lagoons. Tagging studies from 1988 to 1991 indicate that movement among lagoons is common for diadromous Dolly Varden and Arctic cisco along wide swaths of the Beaufort Sea coastline, but the movement is far more limited among lagoons for marine resident species (e.g., fourhorn sculpin and Arctic flounder; Underwood et al., 1995).

In summer, Arctic lagoons can be well mixed or stratified with cool, saline waters near the bottom and warmer, fresher waters at the surface (Hale, 1990; Harris et al., 2017). There is little evidence of vertical stratification in Jago Lagoon during the open water season in past or recent study periods (Hale, 1990; Harris et al., 2017). In Kaktovik Lagoon, the oceanographic research associated with the initial study period indicated periods of stratification (Hale, 1990), but more recent sampling demonstrates that the lagoon is well-mixed (Harris et al., 2017). Recent mixing in Kaktovik Lagoon may result from concurrent reductions in ice-cover and increases in storm intensity (Hinzman et al., 2005). If stratification has diminished over time, it would also confer a particularly dramatic temperature and salinity shift along the benthos and the loss of cold (<2°C), saline (>28) habitat in protected lagoons.

2.3 | Sampling

All fish were captured using fyke nets. Fyke nets consisted of a lead net extending perpendicular from the shoreline connected to the middle of a metal framed trap. A set of net wings extended from the side of the metal frame, angled toward the shoreline. Fish swimming along the shoreline encounter the lead net and are funneled toward the trap and collected in the cod-end. Fyke nets have been used extensively to study fishes in the Beaufort Sea as they are less-size selective, less-lethal, and are less-destructive to habitat than nearly any alternative (e.g., gillnet, beam trawl) and can be fished unattended for ~24 h. In addition, fyke nets are effective at catching fish because many species travel parallel to the shoreline of lagoons in between forays to other locations in the central part of the lagoons and other coastal areas (Craig, 1984). Fyke net specifications were similar among the sampling periods with a 61 m lead net and 15 m net wings constructed of 2.54 cm stretch mesh and the fyke net trap with an opening of 1.5 m wide and 1.2 m height made from 1.27 cm stretch mesh. The fyke net trap was set away from the shoreline at a water depth of ~1 m and no more than 60 m distance from shore. Two sites in each lagoon were established during the initial sampling in 1988–1991 (Figure 1). In Kaktovik Lagoon, one site was located on the west side of the lagoon on the southeast corner of Barter Island (KL05), and a second site was in a small cove on the east side of the lagoon (KL10) on the spit separating Kaktovik Lagoon and

Jago Lagoon. In Jago Lagoon, both sites were on the mainland coast and separated by approximately 5 km (JL12 and JL14 in Underwood et al., 1995).

All captured individuals were identified to species or lowest taxonomic level and counted. Occasionally catch rates of Arctic cod or age-0 Arctic cisco were too large for counting and volumetric estimates of abundance were used (Brown, 2008; Underwood et al., 1995). Length measurements from a subsample of 50 randomly selected individuals from each daily fyke net catch and each common species were obtained to the nearest mm. Fork length was measured for species with forked tails and total length was measured for all other species. All data used in this study are available in Stanek et al. (2022).

2.4 | Statistical analysis

Analyses considered data collected during a common temporal period in the first half of August (August 1–15). Only species that contributed >1% of the catch in at least one period and lagoon were included in the analyses. During the 1988–1991 and 2003–2005 periods, fyke net data were available for the entire open water season, and the reports associated with those data sets did describe the changes within seasons and across those years (Brown, 2008; Underwood et al., 1995).

All catch data were converted to daily (i.e., 24 h) catch per unit effort (CPUE) for each fyke net station. Nearshore fish assemblages were compared among periods within each lagoon using multivariate statistical techniques in R statistical software package vegan (Oksanen et al., 2020). Non-metric multidimensional scaling (NMDS) ordinations were used to visually assess the dissimilarity of fish assemblages in each of the three periods using the metaMDS function. Daily CPUE values were standardized by scaling to the species maximum and normalized using a square root transformation and then evaluated using Bray–Curtis dissimilarities on $k = 3$ dimensions to reduce stress. A permutational multivariate analysis of variance (PERMANOVA) was used to test if the centroids and dispersion of points representing the fish communities differed among collection periods using the adonis function with the default 999 permutations within stations as strata to control for variation among stations in the lagoons. Influential species, based on their contribution to community variation, were identified with similarity percentage analyses (SIMPER), and permutations tests ($n = 1000$) were used to discover for which species the difference in catch between periods was an important component of their contribution to dissimilarities between time periods. Differences in the catch rates among periods were examined for the combined total catch of the common species and individual species by comparing the mean catch rates with a one-way analysis of variance ($\alpha = .05$) and Tukey's HSD post-hoc test. Length distribution data are presented in histograms without accompanying statistics because at least some species and size classes of fish school and violate the assumption of independence for the typical distribution test (Kolmogorov–Smirnov test). We have no way to disentangle the degree of pseudoreplication in the length data set that would allow for an appropriate statistical test of distribution. Pacific capelin and ninespine stickleback length distributions were not examined because length data were not collected for Pacific capelin in the first two periods and fyke-nets capture only the largest ninespine stickleback such that length data for this species does not provide a true representation of most individuals.

Our data set did not provide an opportunity to consider environmental conditions as predictors for the statistical analysis. This nearshore study uses just four shoreline fyke net stations that were not designed to identify spatial distribution changes. Other borealization studies have explicitly considered environmental conditions in their data analyses by relying on data sets that combine temporal and spatial differences in environment and fish response (Fossheim et al., 2015; Mueter & Litzow, 2008). Dozens of sampling stations have unique environmental records, and the fish response combines temporal changes in population dynamics and spatial shifts in distribution in these examples.

3 | RESULTS

3.1 | Kaktovik Lagoon

Fyke net catch data were available for 167 net-days in Kaktovik Lagoon with 95 net-days from 1988 to 1991, 56 net-days from 2003 to 2005, and 16 days from 2017 to 2019. A total of 45,900 fish were captured across this effort with 67% captured in 1988–1991, 26% captured in 2003–2005, and 7% in 2017–2019. Seven frequently captured species accounted for 99% of all fish captured in Kaktovik Lagoon across all data considered in this analysis: Arctic cisco (44%), fourhorn sculpin (16%), saffron cod (16%), Arctic flounder (14%), Dolly Varden (4%), Arctic cod (4%), and ninespine stickleback (2%).

Fish communities are separated between periods in ordination space (stress = 0.13). On the first and second axes, a clear separation of communities occurred between 1988 and 1991 and 2017 and 2019 (Figure 3a). In the middle period, 2003–2005, the dispersion of points was greater, and the fish communities were not dissimilar to either the early or later period (Figure 3a,c,e). The PERMANOVA supported the visual differences in the NMDS ordination, and differences in the centroids or dispersion of the fish community differed among the time periods ($F = 19.0$, $p = .001$, n iterations = 999, Table 2). Similarity percentages between periods revealed three contributing species: fourhorn sculpin, saffron cod, and Arctic flounder (Figure 4a). About 35% of the variation can be attributed to fourhorn sculpin when differentiating the 1988–1991 period from both the 2003–2005 period and the 2017–2019 period. Saffron cod also contributed an additional 14% to the variation when contrasting the 1989–1991 period and the 2003–2005 period. When comparing the communities in the 2003–2005 period to those in the 2017–2019 period, Arctic flounder contributed 28% of the variation, and saffron cod contributed 26% of the variation.

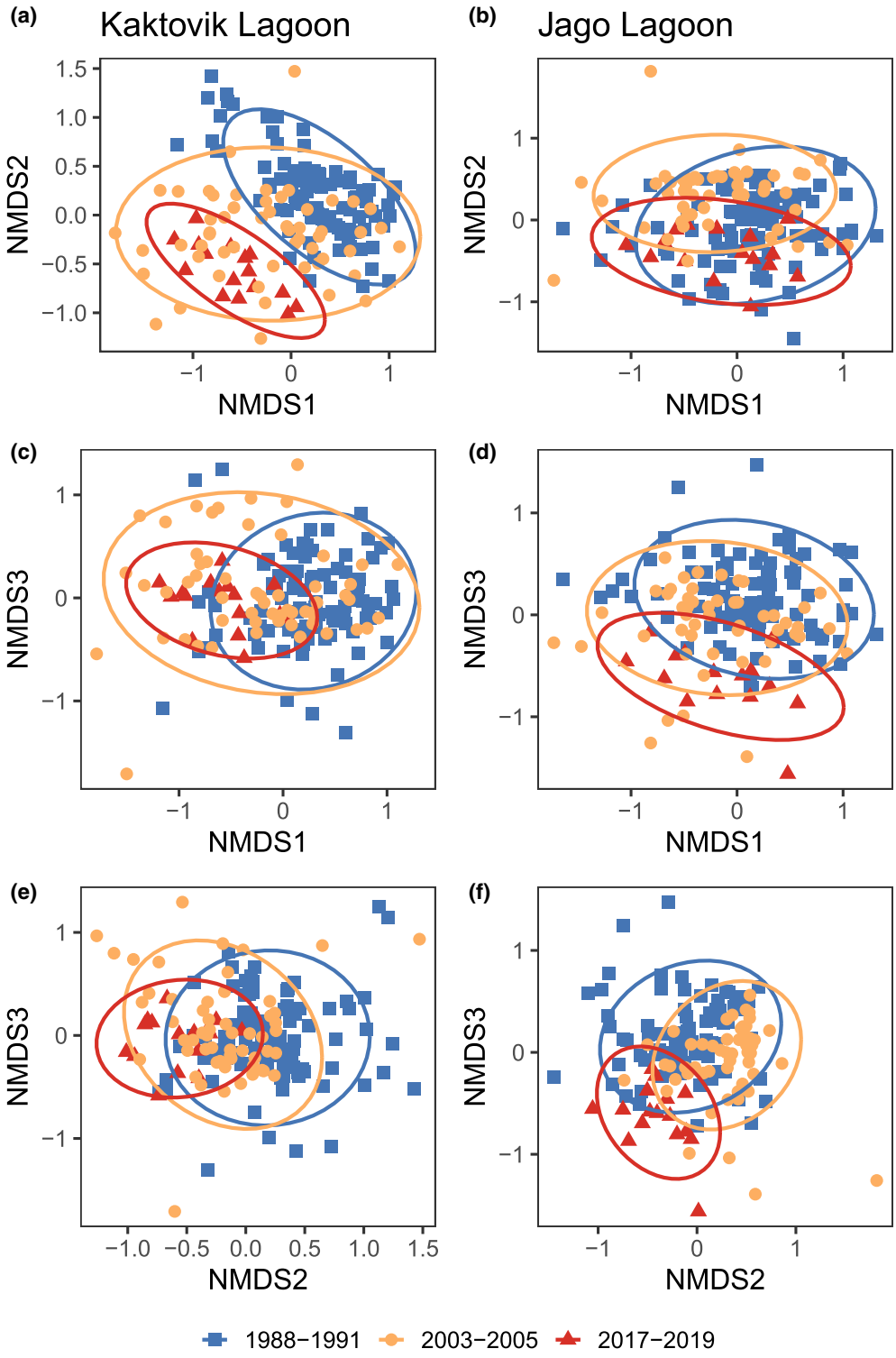

FIGURE 3 Community ordinations of nearshore fish assemblages by time period from Beaufort Sea, Alaska, USA. Each point represents the fish community captured at a station during a 24 h net-day during early August in Kaktovik Lagoon (left: (a), (c), and (e)) and Jago Lagoon (right: (b), (d), and (f)) where blue squares denote 1988–1991, orange circles denote 2003–2005, and red triangles denote 2017–2019. Communities for each lagoon are represented on three dimensions, NMDS1 and NMDS2 (a, b), NMDS1 and NMDS3 (c, d), and NMDS2 and NMDS3 (e, f). Stress value for Kaktovik Lagoon = 0.13 and Jago Lagoon = 0.12. Ellipses depict 95% confidence limits.

The total catch rate, fish per day, of common species was similar among periods ($F = 0.52$, $p = .59$, df = 164) in Kaktovik Lagoon. Mean catch rates differed in three species in Kaktovik Lagoon (Table 3). Fourhorn sculpin catch rates declined by 38% from 1988–1991 to 2003–2005 and 90% from 1988–1991 to 2017–2019 (Figure 5c). Compared with 1988–1991, Dolly Varden catch rates declined by 66% by 2003–2005 and 93% by 2017–2019 (Figure 5f). Saffron cod catch rates peaked in 2003–2005 at 105 fish/day, a 35-fold increase

	df	SS	R^2	F	p
Kaktovik Lagoon					
Time period	2	3.68	0.188	19.0	.001
Residual	164	15.9	0.811		
Total	166	19.5	1.00		
Jago Lagoon					
Time period	2	2.69	0.155	14.5	.001
Residual	158	14.6	0.845		
Total	160	17.3	1.00		

TABLE 2 Results from a permutational multivariate analysis of variance (PERMANOVA) test to determine if the fish communities differed among periods in each lagoon. Column headings are degrees of freedom (df), sum of squares (SS), partial *r*-squared (R^2), pseudo *F* statistic (*F*), and the *p*-value associated with the *F* statistic (*p*)

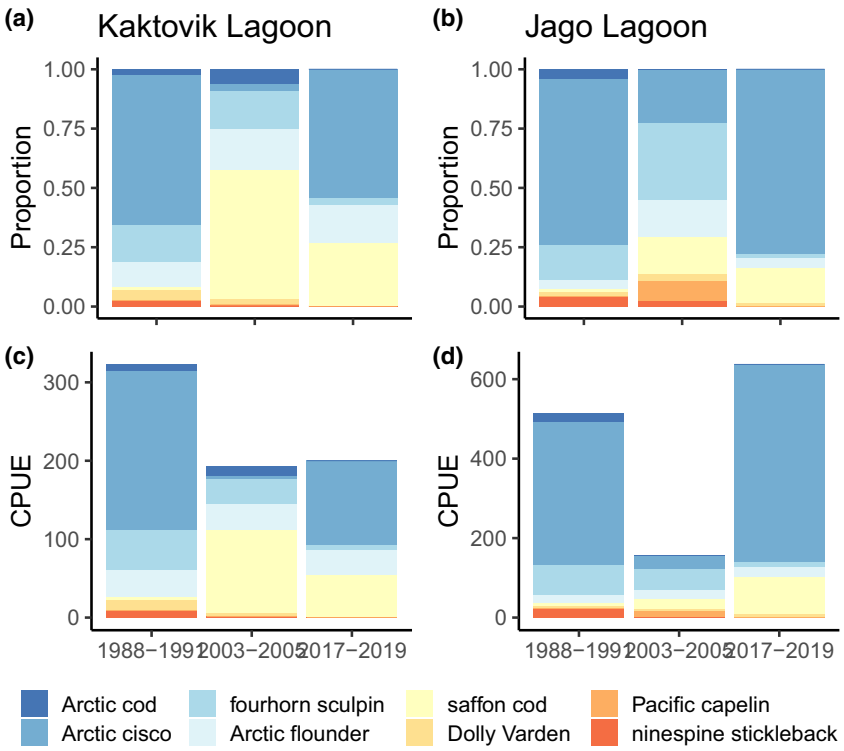

FIGURE 4 Fish community composition as numeric proportion and catch rate from Beaufort Sea, Alaska, USA. (a) Numeric proportion of each common fish species in Kaktovik Lagoon. (b) Numeric proportion of each common fish species in Jago Lagoon. (c) Catch per unit effort (CPUE, catch per station in 24 h) of each common fish species in Kaktovik lagoon. (d) Catch per unit effort (CPUE, catch per station in 24 h) of each common fish species in Jago Lagoon. All data from early August. Fill color indicates species ordered from more Arctic (blue colors) to more boreal (yellow and orange colors).

compared with 1988–1991 and reached an intermediate catch rate in 2017–2019 that was an 18-fold increase compared with 1988–1991 (Table 3, Figure 5f). The length distribution of many species shifted over time based on visual inspection (sample sizes used for distribution plots are provided in Table 4). There was a general pattern of fewer fish in the smaller size classes and more fish in the larger size classes across all species except Arctic cod (Figure 6). Some shifts in the position of the juvenile peaks were also apparent. For Arctic flounder, the size of juveniles was smaller in 2003–2005 and then disappeared by 2017–2019. For saffron cod, the size of juveniles was largest during 2003–2005. For Dolly Varden juveniles appear to be slightly larger in recent years.

3.2 | Jago Lagoon

Fyke net catch data were available for 163 net-days in the first half of August with 94 net-days in 1988–1991, 53 net-days in 2003–2005, and 16 net-days in 2017–2019. A total of 66,023 fish were captured across this effort with 70% captured in 1988–1991 and ~15% in each of the remaining two periods. The commonly captured species in Jago Lagoon across all periods were as follows: Arctic cisco (63%), fourhorn sculpin (15%), Arctic flounder (6%), saffron cod (5%), ninespine stickleback (3%), Arctic cod (3%), Dolly Varden (2%), and Pacific capelin (2%). These eight species accounted for >98% of the fish captured.

Fish communities in Jago Lagoon are separated between periods in ordination space (stress = 0.12). Community dissimilarities were most prominent on the second and third NMDS axes (Figure 3f). The 2017–2019 period separated most strongly from the other periods on the second axis. The 1988–1991 period separated from the other two on the third axis. The PERMANOVA indicated a difference in the centroids or dispersion of communities among periods ($F = 14.5$, $p = .001$, n iterations = 999, Table 2). Similarity percentages between periods revealed three contributing species: saffron cod, Dolly Varden, and Arctic flounder.

TABLE 3 Mean ± SD proportion of the numeric catch and catch rate, per unit effort (CPUE, 24 h net-day) for each species and period in Kaktovik Lagoon and Jago Lagoon, eastern Beaufort Sea, Alaska, USA. Species in bold were influential in fish assemblage differences among periods by SIMPER analysis following a significant effect of period on fish assemblage by PERMANOVA. Proportions with a value of 0.00 indicate that the species was present but captured at a rate <0.005 individuals per 24 h net-day, while "none" indicates that the species was not present in the lagoon and period. Catch rates were compared for each species among periods with a one-way ANOVA and the *F*-value and *p*-values from that analysis are provided. In the event than the ANOVA detected a significant difference in CPUE among periods, a Tukey HSD post-hoc test was used to assess pairwise differences indicated by letter superscripts

		Catch proportion			Catch rate				
Lagoon	Common name	1988–1991	2003–2005	2017–2019	1988–1991	2003–2005	2017–2019	*F*-value	*p*-value
Kaktovik	Arctic cod	0.07 ± 0.20	0.03 ± 0.13	None	8 ± 22	12 ± 80	0 ± 0	0.394	.675
	Arctic cisco	0.09 ± 0.22	0.06 ± 0.12	0.34 ± 0.32	171 ± 950	5 ± 12	108 ± 206	0.919	.401
	Fourhorn sculpin	**0.40 ± 0.26**	**0.21 ± 0.20**	**0.04 ± 0.04**	**50 ± 40^{a}**	**31 ± 38^{b}**	**5 ± 3^{c}**	**12.064**	**<.001**
	Arctic flounder	**0.22 ± 0.19**	**0.27 ± 0.20**	**0.22 ± 0.18**	35 ± 39	34 ± 42	32 ± 25	0.029	.972
	Saffron cod	**0.02 ± 0.05**	**0.37 ± 0.32**	**0.36 ± 0.30**	**3 ± 10^{a}**	**105 ± 214^{b}**	**53 ± 53^{a,b}**	**11.528**	**<.001**
	Dolly Varden	0.12 ± 0.15	0.04 ± 0.08	0.01 ± 0.01	15 ± 22^{a}	5 ± 10^{b}	1 ± 1^{b}	7.472	<.001
	Pacific capelin	0.00 ± 0.00	None	None	0 ± 0	None	None	0.760	.469
	Ninespine stickleback	0.03 ± 0.09	0.01 ± 0.03	0.001 ± 0.00	9 ± 28	1 ± 4	0 ± 1	2.391	.095
Jago	Arctic cod	0.09 ± 0.22	0.01 ± 0.05	None	21 ± 74	1 ± 1	0 ± 0	2.600	.077
	Arctic cisco	0.17 ± 0.32	0.15 ± 0.23	0.49 ± 0.31	317 ± 967	35 ± 87	497 ± 1008	2.956	.055
	Fourhorn sculpin	0.42 ± 0.27	0.40 ± 0.23	0.04 ± 0.05	74 ± 64^{a}	50 ± 45^{b}	10 ± 8^{c}	10.453	<.001
	Arctic flounder	**0.09 ± 0.09**	**0.17 ± 0.13**	**0.10 ± 0.11**	21 ± 39	25 ± 27	27 ± 22	0.370	.691
	Saffron cod	**0.03 ± 0.05**	**0.14 ± 0.18**	**0.19 ± 0.18**	**5 ± 8^{a}**	**24 ± 43^{a}**	**93 ± 181^{b}**	**14.383**	**<.001**
	Dolly Varden	**0.07 ± 0.11**	**0.03 ± 0.06**	**0.03 ± 0.04**	**9 ± 11^{a}**	**5 ± 12^{b}**	**8 ± 6^{a,b}**	**3.132**	**.046**
	Pacific capelin	0.00 ± 0.00	0.03 ± 0.15	0.00 ± 0.00	0 ± 0	13 ± 73	0 ± 1	1.638	.198
	Ninespine stickleback	0.08 ± 0.15	0.03 ± 0.08	0.00 ± 0.01	22 ± 62	4 ± 13	1 ± 1	3.002	.052

Saffron cod contributed 15% of the variation when differentiating the 1988–1991 period from the 2017–2019 period and contributed 19% of the variation when differentiating the 2003–2005 period from the 2017–2019 period (Figure 4b). Arctic flounder contributed an additional 16% of the variation between the 2003–2005 period to the 2017–2019 period. Dolly Varden contributed 26% of the variation when contrasting the 1988–1991 period and the 2003–2005 period. By at least 2017–2019, the proportions of fourhorn sculpin and Arctic flounder decreased, while the proportion of saffron cod increased (Figure 4b).

The total catch rate of the eight common species varied among periods in Jago Lagoon ($F = 3.5$, $p = .03$, df = 158) with lower total catch in the middle period, 2003–2005. Mean catch rates of three of the eight species examined differed among periods with declines in fourhorn sculpin and Dolly Varden and increases in saffron cod (Table 3). Fourhorn sculpin catch rates declined by 32% by 2003–2005 and 86% by 2017–2019 compared with 1988–1991 (Figure 5c). Dolly Varden catch rates declined by 44% from 1988–1991 to 2003–2005 before reaching an intermediate level in 2017–2019 (Figure 5f). Saffron cod catch rates were statistically similar between 1988–1991 and 2003–2005 before rising sharply by 2017–2019 (Figure 5e). The increase in saffron cod catch rates was 19-fold compared with 1988–1991 and fourfold compared with 2003–2005. Length distribution shifts were similar to those noted for Kaktovik Lagoon. The length distribution histograms demonstrate an increase in the proportion of longer individuals and a decrease in the proportion of shorter individuals in later periods (Figure 6). Some shifts in the position of the juvenile peaks were also apparent and followed the patterns noted for Kaktovik Lagoon. In addition, an extra juvenile size class for saffron cod in Jago Lagoon was apparent near ~50 mm in 2017–2019 (Figure 6e).

4 | DISCUSSION

Repeated sampling campaigns between 1988 and 2019 provided evidence of fish community reorganization in Arctic nearshore waters concurrent with a dramatic loss of summer sea ice through this period (Bonsell & Dunton, 2018) (Figure 7). The shift in fish communities demonstrated here is consistent with borealization because the catch rate and proportion of species spanning boreal and Arctic habitats (i.e., Arctic-boreal distribution) increased over 30 years, while the catch rate and proportion of Arctic specialists declined. This borealization shift is novel because it did not

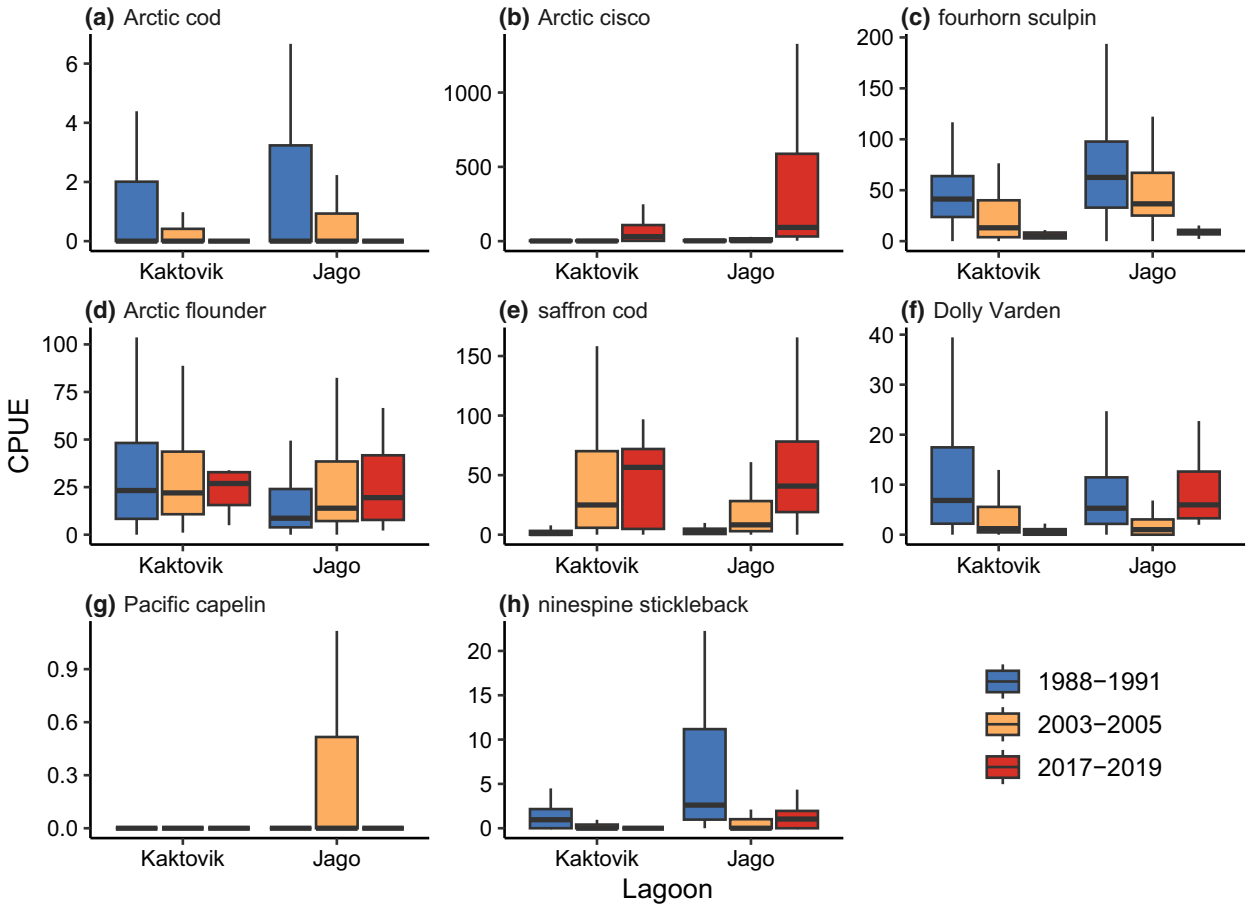

FIGURE 5 Catch rate of eight common nearshore fishes among three time periods shown as boxplots. Catch rate (CPUE) is the number of fish captured per fyke-net station in 24 h. Boxplot color denotes time period (blue, 1988–1991; orange, 2003–2005; red, 2017–2019). All data from early August and two adjacent lagoons (Kaktovik Lagoon and Jago Lagoon) in the eastern Beaufort Sea, Arctic National Wildlife Refuge, Alaska, USA. In each boxplot, horizontal lines are the median value of CPUE, the rectangle denotes the first and third quartiles, and the whiskers extend to observations within 1.5× the inter-quartile range. Outliers are not denoted. Catch rates vary significantly among periods for saffron cod (e) and fourhorn sculpin (c) in both lagoons and Dolly Varden (f) in Kaktovik Lagoon. Catch rates were similar among periods for Arctic cod (a), Arctic cisco (b), and Arctic flounder (d).

occur on an Arctic inflow shelf and was not connected to recent climate-driven northward range expansions across the Arctic inflow shelves (Fossheim et al., 2015; Mueter et al., 2021; Mueter & Litzow, 2008; Wassmann et al., 2011). Similar increases in boreal species with a pre-existing presence in the Arctic and declines in endemic Arctic species have been identified for fish (Fossheim et al., 2015; Mueter & Litzow, 2008) and seabirds (Descamps & Strøm, 2021). The strongest shifts in both the catch rate and the proportion of the fish community were related to two marine resident species, saffron cod, and fourhorn sculpin. These observations agreed with the expectations of borealization: Arctic-boreal saffron cod increased and Arctic fourhorn sculpin decreased in proportion and catch. Priest et al. (2022) documented similar long-term increases in saffron cod catch rates and declines in fourhorn sculpin catch rates in the central Beaufort Sea near Prudhoe Bay and concluded that eurythermal and/or euryhaline "generalist" species were benefiting from climate change without using the "borealization" label. While our statistical analysis did not include environmental variables, reduction in sea ice and warming conditions have been well-documented in our study area and provided a consensus of environmental change that informed our interpretation (Bhatt et al., 2010; Bonsell & Dunton, 2018; Garcia-Soto et al., 2021; Jones et al., 2018; Jorgenson et al., 2006; Nolan et al., 2011; Onarheim et al., 2018; Post et al., 2019; Priest et al., 2022).

This reorganization is incomplete in that the block of remaining Arctic specialists (Arctic cisco, fourhorn sculpin, Arctic flounder) still make up >50% of the fishes captured (Figure 4). The continued dominance of the Arctic species hinges on the Arctic cisco, a diadromous species that overwinter in freshwater and does not appear to be a typical Arctic species with cold-stenothermic physiology (Carey et al., 2021). Not all Arctic-boreal species were increasing in proportion or catch rate. For example, we found no evidence that capelin were now thriving in the lagoons even though they were common in Jago Lagoon during 2003–2005 sampling and continue to occur throughout the Beaufort Sea (McNicholl et al., 2018; Priest et al., 2022). Preferences for specific types of nearshore habitat likely explain why capelin were not a part of our borealization story

TABLE 4 Sample sizes for length distribution histograms for each of three period and six common nearshore species in Kaktovik lagoon and Jago lagoon, eastern Beaufort Sea, Alaska, USA. Zero indicates a lack of length measurements because the species was not captured in the time period; dashes indicate a lack of length measurements when the species was present and not measured

Lagoon	Species	1988–1991	2003–2005	2017–2019
Kaktovik	Arctic cod	568	20	0
	Arctic cisco	1493	336	573
	Fourhorn sculpin	3804	—	81
	Arctic flounder	2714	979	417
	Saffron cod	432	300	651
	Dolly Varden	1342	293	10
Jago	Arctic cod	628	12	0
	Arctic cisco	2618	1540	961
	Fourhorn sculpin	4038	81	156
	Arctic flounder	1481	502	409
	Saffron cod	460	254	694
	Dolly Varden	952	267	127

as capelin use a combination of open bays and glacial fjords rather than the shallow, protected lagoons examined here (McNicholl et al., 2018; Priest et al., 2022).

The shifts in length distribution over time revealed a near-universal trend toward longer individuals regardless of whether the species was Arctic or Arctic-boreal. The magnitude of the changes in length distributions was large enough to imply the presence of additional older age classes in the lagoons and more older fishes. A shift toward more older fishes implies that survival has increased over time. One implication of the shift in length distribution is the increased opportunity to grow beyond sizes targeted by some piscivores such as seabirds (Divoky et al., 2021; Gall et al., 2017) and large predatory fishes (e.g., Dolly Varden; Thorsteinson & Love, 2016), although not adult marine mammals (Bluhm & Gradinger, 2008). Piscivorous seabirds declines in the Pacific Arctic have been interpreted as changes in the abundance of key fish species (Divoky et al., 2021; Gall et al., 2017; Poessel et al., 2020), but the shifts in the size distributions we documented here may also contribute to poor foraging. Relatively little is known about predator–prey interactions among Arctic fishes, although at least one study has indicated that borealization can amplify the direct effects of climate warming through the northward range extension of larger boreal gadid species that consume Arctic cod and may contribute to limits on their distributions (Marsh & Mueter, 2020).

This study is among the first to confirm a long-term increase in saffron cod abundance and size in the Arctic, as projected by Laurel et al. (2016) based on the results of temperature manipulation experiments. Given the high commercial and ecological importance of cod species in the North Pacific and Arctic, these results—of more and larger saffron cod—provide evidence for the plausibility of a future commercial cod fishery in the Pacific Arctic (NPFMC, 2009). Concerns have already been raised over how to juggle economic development opportunities and conservation concerns in a warming Arctic with increases in commercial fishing, vessel traffic, and overall industrial activity (Fauchald et al., 2021; Hauser et al., 2018). For local Iñupiaq people, specific concerns for vessel strikes and fisheries gear entanglement of bowhead whales (*Balaena mysticetus*, Aġviq) exist because bowhead whales are a culturally important subsistence resource (Reeves et al., 2012). Local subsistence fishers may eventually seek out saffron cod as a food resource, but harvest reporting suggests Arctic cisco and Dolly Varden remain far more important (2007–2012 subsistence use reported by Harcharek et al., 2018). For now, large saffron cod could be viewed as a nuisance species by some subsistence fishers if they prefer Arctic cisco or Dolly Varden. Our finding of Dolly Varden catch rate decline in Kaktovik Lagoon raises alarm about fishing access to this subsistence species even though the decline may reflect changes in marine distribution in response to sea ice loss (Gallagher et al., 2021) rather than declining populations.

The commonly captured nearshore fish species in the Beaufort Sea lagoons are members of self-sustaining Arctic populations. Species tolerate either several months of overwintering in subzero temperatures in marine habitats or near-zero temperatures in freshwater habitats (Thorsteinson & Love, 2016). Population sinks are often a concern for northward range expansions because pulses of water thought to draw species northward through the Bering Strait offer a dispersal route to suitable summer habitats (Moore et al., 2018). But, access to suitable winter habitats and survival of immigrants could be limited or unavailable for boreal marine resident species or diadromous species that remain in the ocean during winter (e.g., Pacific salmon; Carey et al., 2021; Irvine et al., 2009). Thus, the borealization described here, where the catch rate increased for existing Arctic-boreal species in relative proportion to Arctic specialists, is not a population sink where individuals distribute from core boreal habitats to marginal Arctic habitats in fruitless cycles that end with poor survival, little reproduction, and an inability to complete a life cycle (Kawecki, 2008; Spies et al., 2020).

4.1 | Arctic-boreal species

Saffron cod and Dolly Varden were both influential species in the community transition found in this study. Both species share Arctic-boreal Pacific geographic ranges stretching from the Beaufort Sea in the north to the Gulf of Alaska in the south (Thorsteinson & Love, 2016; Wolotira, 1985). Saffron cod community proportions increased 6- and 18-fold and catch rates increased 19- and 18-fold over the study period in Jago and Kaktovik lagoons, respectively. Catch rates of Dolly Varden declined in proportion to the community in both Kaktovik and Jago lagoons from the early to middle periods, although declines in catch rates were only persistent in Kaktovik Lagoon. Additional context from other studies can explain this discrepancy in warming response between boreal species and provides

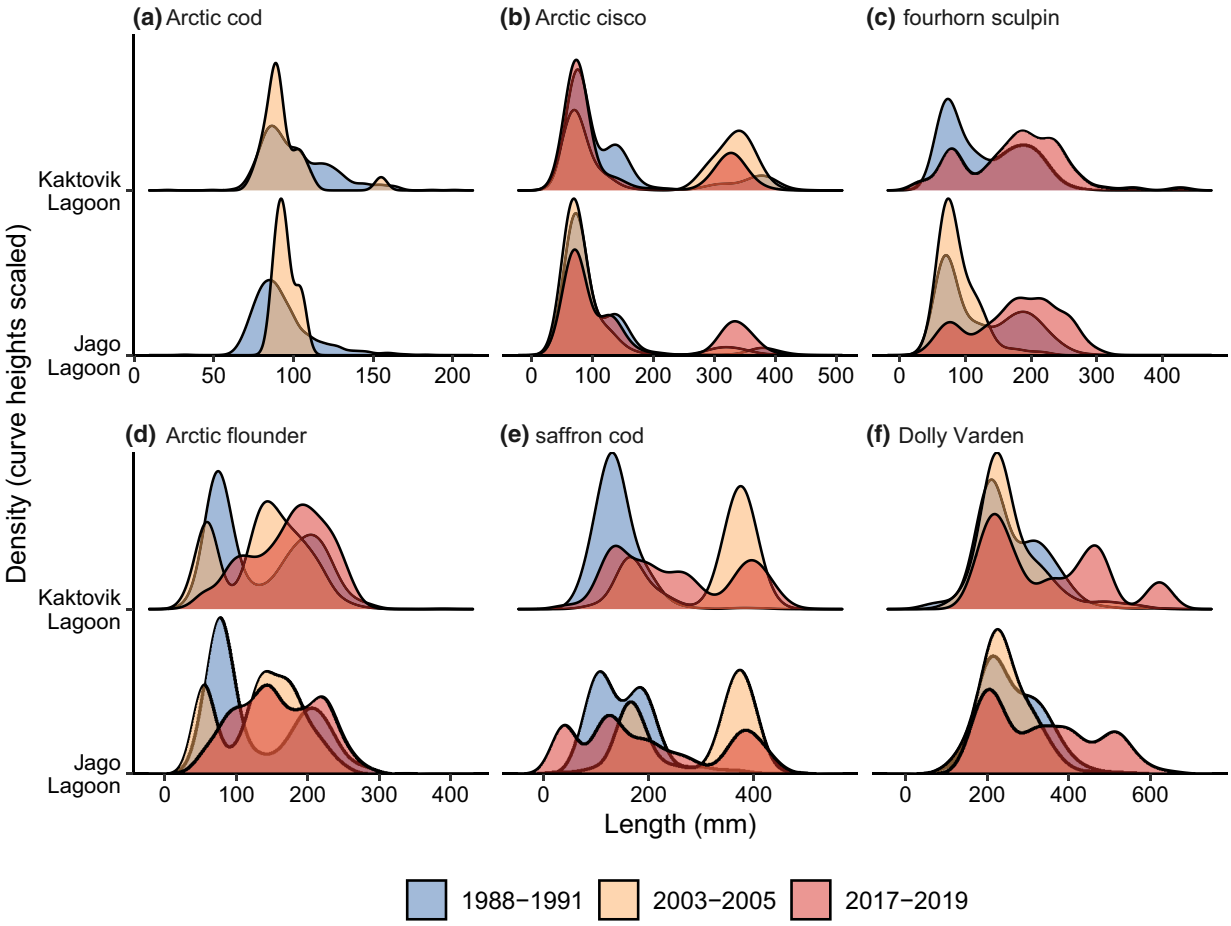

FIGURE 6 Length distribution for six fish species in each of three periods from Beaufort Sea, Alaska, USA. Fill color denotes time period (blue, 1988–1991; orange, 2003–2005; red, 2017–2019) and data from Kaktovik Lagoon and Jago Lagoons are shown separately. Plots show length distributions as densities to account for difference in sample size among periods. Species are ordered from Arctic to boreal: Arctic cod (a), Arctic cisco (b), fourhorn sculpin (c), Arctic flounder (d), saffron cod (e), and Dolly Varden (f). Length measurements for fourhorn sculpin were not collected in early August for the 2003–2005 period in Kaktovik Lagoon.

useful information to refine our expectations for diadromous boreal species.

Saffron cod is a marine resident species that received recent attention because of their potential to support a future commercial fishery in US Arctic waters (Bluhm & Gradinger, 2008; Mueter et al., 2020; NPFMC, 2009). The dramatic increases in saffron cod along with a shift toward larger individuals agrees with the spatial distribution of the species with higher abundance in warmer Arctic waters (Vestfals et al., 2019) and predictions from temperature-dependent growth experiments in laboratories (Laurel et al., 2016). Saffron cod growth rate, body condition, and survival were high in a 16°C treatment, near the current water temperature maximums, and even at 20°C survival and body condition were maintained and suggested that additional warming would not be detrimental (Laurel et al., 2016).

The length range of saffron cod described here includes individuals smaller and larger than those observed in the past. The smallest fish (~50 mm) were only present in Jago Lagoon during the most recent period. This size is associated with age-0 fish (Copeman et al., 2016) and their appearance may indicate that a spawning area is now close to Jago Lagoon. The presence of many large (>300 mm) saffron cod suggests the possibility that Beaufort Sea saffron cod now have higher survival rates and live longer. It appears that some combination of in situ increases in growth rates, higher survival, and more age classes explains the increase in saffron cod catch rates and community proportion.

Saffron cod were also part of community reorganization in a southerly portion of their range in the boreal Pacific in two Gulf of Alaska nearshore areas (60°N; Prince William Sound and Cook Inlet) during sampling in 2006–2007 (Johnson et al., 2009). The circumstance surrounding this saffron cod increase were distinct from our Beaufort Sea example because it was restricted to juveniles (<220 mm), no obvious climate driver, and was strongly tied to the eelgrass *Zostera marina* habitat (Johnson et al., 2009). Saffron cod in the Gulf of Alaska are genetically distinct from those in the Arctic and it is possible that they are a different species (Sme et al., 2018).

For Dolly Varden, the general expectation that boreal species would increase in abundance or proportion with climate warming cannot be easily tested because their use of lagoon habitats and catch are unlikely to track population abundance. This is because of

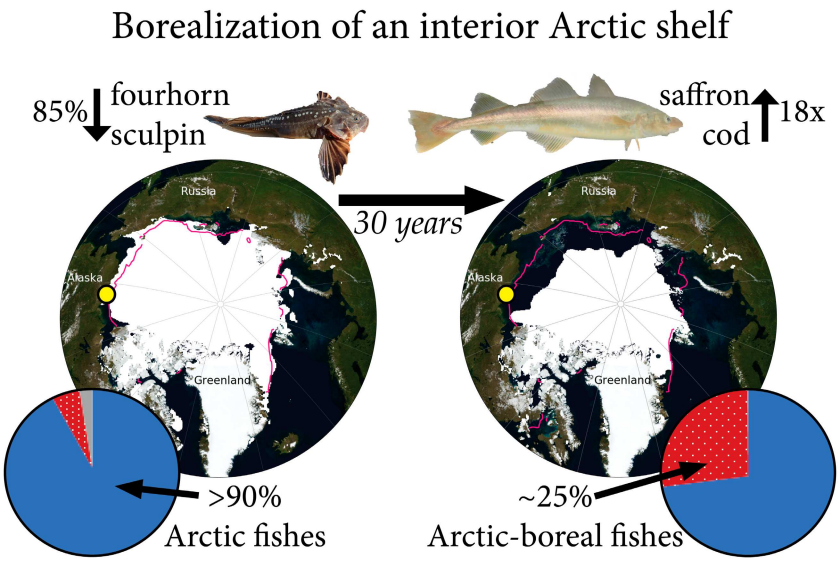

FIGURE 7 Graphical abstract summarizing nearshore Arctic borealization as documented in lagoons near Kaktovik Alaska, Beaufort Sea, USA. Sea ice extent maps on 15 August of 1988 (left) and 2019 (right). The solid line (pink) is the median ice edge 1981–2010. Images from the National Snow and Ice Data Center/NASA Earth Observatory. Yellow circle on map added to denote the study location. Pie charts summarize the relative contributions of Arctic (blue; fourhorn sculpin, Arctic cod, Arctic cisco, and Arctic flounder), Arctic-boreal (red dotted; saffron cod, Dolly Varden, and Pacific capelin), and boreal fishes (gray; ninespine stickleback) for 1988–1991 (left) and 2017–2019 (right) in Kaktovik Lagoon. Jago Lagoon similar, but not shown. Fish pictures show the two most influential species from the analysis: Arctic specialist fourhorn sculpin that declined 85% in catch per unit effort and the Arctic-boreal species, saffron cod, that increased 18-fold in catch per unit effort.

the flexibility in their use of marine habitats as diadromous species. Dolly Varden are notable for their life history plasticity and facultative use of marine feeding that ranges from a complete absence of marine feeding (i.e., freshwater resident form) to annual migrations that can occur any time after 1–5 years of freshwater residency (Armstrong & Morrow, 1980; Brown et al., 2019; Courtney et al., 2018; Decicco, 1992; Gallagher et al., 2020; Underwood et al., 1996). Even when Dolly Varden makes marine feeding migrations, their feeding in the Beaufort Sea is restricted and closer to shore in cold years with more sea ice (Gallagher et al., 2021). Therefore, in the early period, the higher catch rate of Dolly Varden in nearshore could be explained by confinement to warmer lagoons during summer seasons with extensive sea ice. A recent study indicates that Dolly Varden are foraging farther from shore, seeking out a preferred water temperature range of 5–10°C (Gallagher et al., 2021). A long-term shift in the marine distribution of Dolly Varden from nearshore to offshore waters is consistent with our central idea that borealization can arise from the nearshore.

Our results suggest that changes in saffron cod and Dolly Varden abundance are related to borealization. Our overall expectation that boreal species would increase with ocean warming was too simplistic for diadromous species because it overlooked limitations of freshwater overwinter and spawning habitat (Craig, 1989; Reist et al., 2006; Shuter et al., 2012), which likely changed very little over this study period because winter air temperatures are still cold enough to lock up much of the freshwater in rivers as ice. The shifting length distributions of both saffron cod and Dolly Varden suggest that more age classes are now common and raise questions about increased survival rates in a warmer Arctic.

4.2 | Arctic species

This study included four species with Arctic (Arctic cod, Arctic cisco) or predominantly Arctic distributions (fourhorn sculpin, Arctic flounder) with the analysis suggesting that the response of fourhorn sculpin was the most distinct. Fourhorn sculpins are common across their circumpolar distribution and have been used as an indicator species for ecosystem health due to their ease of capture and limited movements (Bengtsson et al., 1988; Dietz et al., 2019; Underwood et al., 1995). The decline in the proportion of fourhorn sculpin was a major contributor to the long-term shift in the nearshore fish assemblage and fits with the general expectation of a negative impact on species with a stronger affinity to the Arctic. Thorsteinson and Love (2016) suggested that the fairly limited occurrence of fourhorn sculpin south of the Bering Strait indicated that the species may have more stenothermic preferences than generally appreciated. At least one study provided evidence of the species preference for colder and saltier waters including higher catch rates with increasing salinity near Prudhoe Bay (Griffiths et al., 1998), but more recent studies found an opposite water temperature relationship with higher catch rates on warmer days (Khalsa et al., 2021; Priest et al., 2022). Arctic flounders were identified as an influential species in the community

analysis, but there was no evidence of persistent shifts in their community proportion or catch rate.

We predicted that Arctic cod and Arctic cisco contributions to the community and catch rates would be highly variable and prevent any detection of long-term change. Indeed, nearshore catch rates of Arctic cod were episodic, and likely related to ice, wind, water temperature, and salinity (Craig et al., 1982). Arctic cod have a strong preference for cold, high-salinity waters, and wind and ice play an important role in the nearshore temperature and salinity conditions (Craig et al., 1982; Logerwell et al., 2011; Marsh & Mueter, 2020; Vestfals et al., 2019). Past sampling in Kaktovik and Jago lagoons included episodic events where Arctic cod were extremely abundant in the early August study period, but sampling efforts during August 2017–2019 did not capture a single Arctic cod. The lower fishing effort during the 2017–2019 period is an important caveat of this temporal comparison since the detection of episodic events, such as Arctic cod influx, is likely sensitive to differences in sampling effort. Arctic cod were the exception to the overall shift in length distribution toward larger, and older fishes. The larger size class of Arctic cod (>130 mm) was already missing by the middle period (2003–2005).

A lack of Arctic cod in nearshore lagoons is consistent with the broader understanding that Arctic cod distribution is responding to environmental changes in the Pacific Arctic (Logerwell et al., 2011; Marsh et al., 2020; Marsh & Mueter, 2020). As sea ice retreats further offshore each summer, it is likely that Arctic cod are also further offshore and beyond the range where wind events could advect Arctic cod into nearshore lagoons. Indeed, a dramatic reduction of Arctic cod in the diet of Mandt's black guillemot (*Cepphus grylle mandtii*) nesting in the nearshore western Beaufort Sea coincided with warmer water temperatures and a longer travel distance to the sea ice edge with the decline in summer sea ice extent (Divoky et al., 2021).

For Arctic cisco, catch rates varied widely over years as anticipated, given wind-driven recruitment processes of juveniles from the Mackenzie River, Northwest Territories, Canada (Fechhelm & Griffiths, 1990; Zimmerman et al., 2013). Unlike Arctic cod, there is no hint of long-term decline for Arctic cisco in the nearshore Beaufort Sea. Our finding agrees with previous studies indicating that Arctic cisco prefers water temperatures that remain within the warmer part of the summer temperature range (11–16°C; Fechhelm & Gallaway, 1982). The increase in the growth rate of young-of-year Arctic cisco from the late 1970s to the early 2000s (von Biela et al., 2011) further supports this hypothesis. Length distributions in more recent periods had a more prominent mode of larger individuals (300–400 mm), associated with mature fish (Brown, 2008) that are likely headed toward Mackenzie River spawning grounds. This could indicate a shift in the timing of the spawning migration or stronger recruitment from the juveniles rearing in Alaska. Taken together, it appears that Arctic cisco are resilient to a warming Arctic and that the Arctic distribution of this species did not arise because of a cold stenothermic temperature tolerance or association with sea ice.

4.3 | Conclusions

Our results reveal a temporal trend toward borealization of an Arctic marine fish community on an interior Arctic shelf. Range expansion from southerly waters was not necessary for this community reorganization, because fish assemblages in Beaufort Sea nearshore waters have long included species with distributions that span the Arctic and boreal latitudes. In this example, the Arctic-boreal Pacific species, saffron cod, was well positioned to exploit the changing Arctic ecosystem and still tolerate subzero winter water temperatures. This general pattern of borealization in nearshore waters is likely common throughout the Arctic because the contiguous panarctic Riverine Coastal Domain provided a route for the dispersal of and habitat for boreal species that predated recent warming (Carmack et al., 2015). Additionally, borealization of interior Arctic shelves may expand from nearshore waters, as warmer conditions provide opportunities for species that have historically been relatively restricted to warmer nearshore habitats to move farther offshore, which appears to be the case for Beaufort Sea Dolly Varden (Gallagher et al., 2021). Within the existing circumpolar literature, distinct fish communities between the nearshore and shelf are well described, but little is known about the transition of fish communities between the two areas (Alabia et al., 2020). Thus, understanding of Arctic marine ecosystems could benefit from studies focused on identifying the location and physicochemical drivers (e.g., ice, water temperature, salinity) that characterize biogeographic transition zones between the nearshore and shelf akin to the studies examining the transition from boreal to Arctic communities. The localized expansion of fish from nearshore to shelf waters may result in persistent community reorganization. Species and individuals of local origin are equipped with life-history strategies to survive Arctic winter compared with those fishes that episodically migrate northward to the northern edges of their boreal distributions. Such episodic migrations by boreal fishes are more likely to face high mortality risks because of unsuitable overwinter habitats.

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DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are openly available in Stanek et al. (2022) at https://doi.org/10.5066/P9120X5B.

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