



Local environmental conditions structured discrete fish assemblages in Arctic lagoons

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Abstract

Rapid changes in sea ice extent and changes in freshwater inputs from land are rapidly changing the nature of Arctic estuarine ecosystems. In the Beaufort Sea, these nearshore habitats are known for their high productivity and mix of marine resident and diadromous fishes that have great subsistence value for Indigenous communities. There is, however, a lack of information on the spatial variation among Arctic nearshore fish communities as related to environmental drivers. In summers of 2017–2019, we sampled fishes in four estuarine ecosystems to assess community composition and relate fish abundance to temperature, salinity, and wind conditions. We found fish communities were heterogeneous over larger spatial extents with rivers forming fresh estuarine plumes that supported diadromous species (e.g., broad whitefish *Coregonus nasus*), while lagoons with reduced freshwater input and higher salinities were associated with marine species (e.g., saffron cod *Eleginops gracilis*). West–East directional winds accounted for up to 66% of the community variation, indicating importance of the wind-driven balance between fresh and marine water masses. Salinity and temperature accounted for up to 54% and 37% of the variation among lagoon communities, respectively. Recent sea ice declines provide more opportunity for wind to influence oceanographic conditions and biological communities. Current subsistence practices, future commercial fishing opportunities, and on-going oil and gas activities benefit from a better understanding of current fish community distributions. This work provides important data on fish spatial distributions and community composition, providing a basis for fish community response to changing climatic conditions and anthropogenic use.

Keywords Beaufort Sea · Community composition · Estuarine · Salinity · Wind

Introduction

Rapid warming in the Arctic has resulted in noticeable declines in the extent, thickness, and volume of sea ice over the last 40 years (Meredith et al. 2019; Thoman et al. 2020). On average, monthly sea ice declined 12.6% per decade from 1979 to 2022 compared to the 1981–2010 baseline [National Snow and Ice Data Center (NSIDC) 2023]. Ice loss has created an ocean environment with considerably more open water, which reduces the albedo effect of the ice and further enhances warming of marine ecosystems (Timmermans and

Labe 2020). Additionally, storm related wave action is projected to increase along Arctic coastlines (Casas-Prat and Wang 2020), which could favor along-shore currents, lead to higher coastal erosion rates, and change nearshore water turbidity and primary production (Bonsell and Dunton 2018; Gibbs et al. 2021). Climate change effects on terrestrial landscapes also have measured consequences for Arctic estuarine systems (Meredith et al. 2019), including changes in quantity and form (i.e., snow versus rain) of over-land precipitation, magnitude and duration of the spring freshet, and delivery of carbon and nutrients from permafrost thaw to brackish systems (Ahmed et al. 2020; Beel et al. 2021). Longer ice-free seasons will also enable access to the Arctic, allowing for increased opportunities of resource development or commercial fishing (NPFMC 2009; Meredith et al. 2019). Little information, however, on the biotic response to marine and freshwater inputs is available for Arctic estuarine systems, even before effects of climate change are considered. Yet,

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this information can inform the management and conservation of estuarine fish species that are important to Indigenous communities, marine mammals, and birds (Rizzolo et al. 2015; Choy et al. 2020; Bilous et al. 2022).

The factors that organize fish communities in estuarine environments of the Beaufort Sea are relatively unknown; in part due to numerous challenges in studying Arctic estuarine fish communities, including accessibility of remote coastal locations and sampling highly mobile species (i.e., diadromous migrants) in shallow water (Roux et al. 2016; Khalsa et al. 2021; Bilous et al. 2022). A few foundational papers linked the presence and distribution of diadromous and marine species to various environmental factors, including temperature, the presence of rivers, wind-driven current systems, and the arrangement and size of barrier islands (e.g., Craig 1984; Craig et al. 1985; Fechhelm and Fissel 1988; Fechhelm et al. 1989). With few exceptions, however, there is little information on how fish community composition varies longitudinally among spatially distinct Beaufort Sea lagoons [for individual lagoons, see Barton et al. (2020) for Elson Lagoon, Alaska, U.S.A.; Craig et al. (1985) for Simpson Lagoon, Alaska, U.S.A.; Priest et al. (2022) for Prudhoe Bay, Alaska, U.S.A.; and Roux et al. (2016) for Husky Lakes, Northwest Territories, Canada].

Beaufort Sea lagoons offer relatively warm habitats compared to the adjacent marine environment (Craig 1984; Harris et al. 2017). For example, in August 2019, offshore sea surface temperatures were $< 5^{\circ}\text{C}$ (Timmermans and Ladd 2019), while adjacent Alaskan lagoons ranged from 5 to 17°C (Khalsa et al. 2021; Stanek et al. 2024). With air and sea surface temperatures increasing over several decades, fish are expected to respond by changing their habitat use and distribution (Ballinger et al. 2020; Timmermans and Labe 2020; von Biela et al. 2023). Recent investigations suggest that some fish species with boreal zoogeography are becoming more abundant [e.g., saffron cod, uugaq, (common name in English and Iñupiaq, upon introduction) *Eleginops gracilis*] or changing their seasonal distribution patterns (e.g., Dolly Varden, iqalukpik, *Salvelinus malma*) in response to warmer temperatures and sea ice extent (Gallagher et al. 2021; Priest et al. 2022; von Biela et al. 2023).

The presence of several species, including diadromous ciscoes (*Coregonus* spp.) and estuarine fourhorn sculpin, kanayuq (*Myoxocephalus quadricornis*), have been found to be limited by salinity gradients and are rarely captured outside barrier islands (Barton et al. 2020). Other species, like Dolly Varden, are tolerant to salinity variation and can be found in marine surface waters ($< 2\text{ m}$) up to 152 km from shore (Craig 1984; Gallagher et al. 2021). Winds also influence fish communities by moving water masses and juvenile fishes. For example, young-of-the-year Arctic cisco, qaaktaq (*Coregonus autumnalis*) rely on wind facilitated movement for recruitment to Alaska's nearshore and river habitats from

the Mackenzie River plume in the Canadian Beaufort Sea (Zimmerman et al. 2013). To improve our understanding, we ask, how do lagoon-specific environmental characteristics (i.e., temperature and salinity) and meteorology (i.e., wind speed and direction) influence fish community composition over 300 km of Alaska's coastline? This question is important because recent changes in fish abundance have a direct effect on the ability of subsistence fishers and marine predators to access desired fish species (Divoky et al. 2021; von Biela et al. 2023). Further, variation in the physical, chemical, and ecological system can influence the structure of fish communities, which can have profound feedback effects on lagoon food web dynamics and energy flow (Stanek et al. 2022a).

We examined spatial variation in nearshore fish community composition among four Beaufort Sea lagoons in relation to local oceanic and meteorological conditions. The lagoons vary in their proximity to large rivers and connectivity to the Beaufort Sea. Specifically, we looked for correlations between fish relative abundance and community composition with gradients in water temperature, salinity, and wind speed and direction. Based on the importance of these abiotic factors to fish populations, we expected to see correlations between (1) warmer water temperatures and species with a boreal zoogeography, (2) higher salinities and marine species, and (3) wind velocity and species that rely on winds and currents for recruitment or movement. We aim to demonstrate how communities reflect their contemporary local environment, as generalized in an early review documenting fish use of estuarine water along the Alaskan coast prior to the mid-1980s and the now rapid pace of climate change (Craig 1984; Rantanen et al. 2022).

Methods

Study area

The lagoons sampled in this study are located along the Beaufort Sea coast of Alaska, U.S.A., and span $\sim 300\text{ km}$ (Fig. 1). Stefansson Sound and Simpson Lagoon lie in the central region (Fig. 1b), near Prudhoe Bay, approximately halfway between Point Barrow and the border with Canada. Extensive oil and gas facilities have been developed around Simpson Lagoon. Drilling islands and causeways have also been constructed in Stefansson Sound. These structures and the fish communities around them have been the subject of study since the 1980s (Fechhelm et al. 1989; Priest et al. 2022). Jago and Kaktovik lagoons are to the east (Fig. 1c), within the bounds of the Arctic National Wildlife Refuge (ANWR) and near Kaktovik Village, Barter Island, Alaska. Lagoon regions will be classified as "central" and "eastern" hereafter. Within ANWR, the Alaska National Interest Land

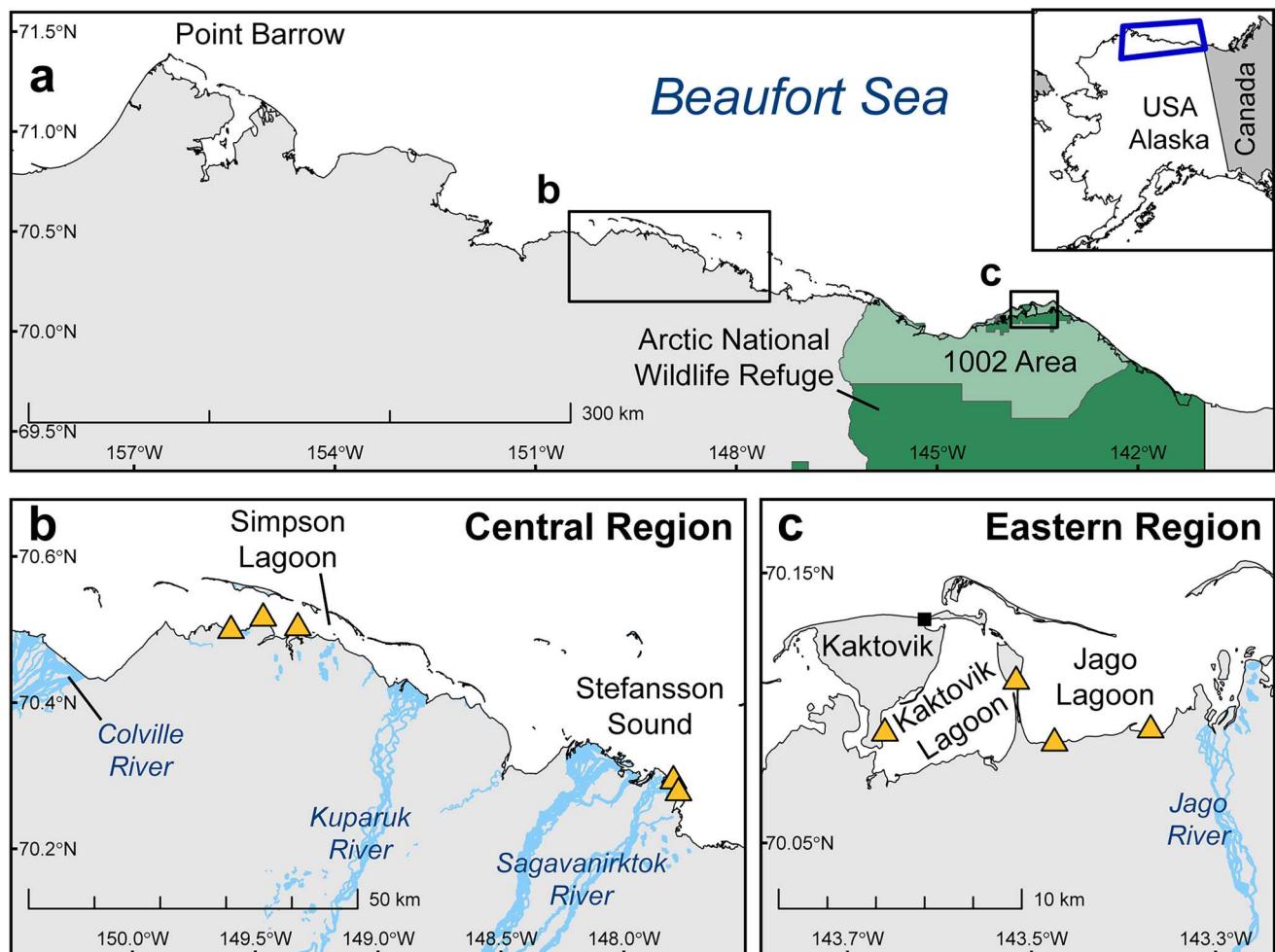


Fig. 1 Lagoons on **a** Alaska's Beaufort Sea coast are found between Point Barrow and Canada. The **b** central region lagoons are adjacent to large rivers and are relatively exposed to the marine environment,

while the **c** eastern region lagoons are adjacent to small rivers and are protected from the marine environment by barrier islands

Conservation Act of 1980, 16 U.S.C. § 3101–3233 aims to provide opportunities for subsistence and maintenance of healthy fish and wildlife populations. Currently, there is no offshore industrial development in marine waters adjacent to the 1002 area of ANWR.

The lagoons of the central region experience high influx of water from nearby rivers, with the largest of the North Slope rivers, the Colville River, discharging ~15 km to the west of Simpson Lagoon. The Kuparuk and Sagavanirktok rivers flow directly into Simpson Lagoon and Stefansson Sound, respectively. Simpson Lagoon and Stefansson Sound have a relatively open exchange with the Beaufort Sea due to wide spacing among barrier islands. The eastern region lagoons experience freshwater inflow from diffuse runoff and small rivers like the Jago River, which flows directly into Jago Lagoon. Kaktovik Lagoon is the least connected to freshwater and marine fish habitat as it is the only of the four lagoons without a major river and

no direct connection to the open ocean, its waters pass through Jago Lagoon, which is connected to the Beaufort Sea through a 200 m wide channel. During the open water season, wind-driven currents bring water masses of varying salinity and temperature into the lagoon systems (Dunton et al. 2006). Moderate and strong easterly winds ($> 5.4 \text{ m}\cdot\text{s}^{-1}$) favor coastal upwelling, pushing warmer fresh waters away and drawing cold, saline water from the deep into the nearshore (Okkonen et al. 2018). Fluctuating winds lead the lagoons to experience substantial seasonal variability, with temperatures ranging from -2 to 14°C and salinities from 0 to > 45 (Dunton et al. 2006, 2009; Harris et al. 2017). Substrate tends to be uniform in this region, mostly mud and sand (Craig 1984), interspersed with beaches of small gravel. There are no seagrass beds and macroalgae is limited to discrete boulder and cobble patches at depths > 5 m in Stefansson Sound where the

protection of barrier islands limits ice scour of the seabed (Dunton 1982).

Data collection

Two stations, established in each of the four lagoons [see Craig and Haldorson (1981) and Underwood et al. (1995)] were sampled during this study. One station in Simpson Lagoon was exposed to extreme changes in wind-forced water depth that submerged the fyke net in 2018, preventing collection of comparable fish abundance data; it was relocated in 2019. In total, fish data were collected from fyke nets deployed in Simpson Lagoon during late July of 2019, in Stefansson Sound during late July 2018 and 2019, and in Jago and Kaktovik lagoons during early August 2017, 2018, and 2019. Nets consisted of a 2.5 cm stretch mesh for lead (61 m length) and wings (15 m) attached to a trap with 1.3 cm stretch mesh and an opening of 1.5 m by 1.2 m (Underwood et al. 1995). Traps had two collection chambers, one for each side of the lead net. Set within 60 m and perpendicular to shore in water depths of about 1 m, traps fished continuously for one to six days (weather depending) with checks made approximately every 24 h. Each 24 h set was considered a “net-day” of fishing. We counted and identified all captured fishes to species or lowest taxonomic level. Volumetric estimates of abundance were used as necessary for large numbers (1000s) of juvenile Arctic cisco (Underwood et al. 1995; Brown 2008). Fish catch data that support the findings of this publication are available in Stanek et al. (2022b).

Analytical methods

The catch per unit effort (CPUE) of each fish species was determined for each independent fyke net collection chamber (two per apparatus), which separated fish traveling from opposing directions along the shore, as the number of fish captured per net-day (CPUE_{net}). Any fish not identified to species were excluded from these analyses (0.14% of total catch). In addition to the CPUE_{net}, data were summarized to determine differences among lagoons and to examine the association between lagoon communities and the environment. First, species CPUEs were averaged across all nets and years within each lagoon (CPUE_{lagoon}), so that proportional differences in species composition among lagoons could be visualized over the time frame of the study. Second, to relate the communities to environmental variables, we examined the mean CPUE of each species at the station (two net-days at each station) and year when data were available (CPUE_{y,station}). Using the average CPUE_{y,station} allowed for spatial comparisons without confounding relationships of in-year temporal or

spatial autocorrelation. All analyses were performed using R Statistical Software (v4.2.2; R Core Team 2021).

Community ordination

Using CPUE_{net}, we examined the community dissimilarity of all daily samples in ordination space. Community data were subject to a Wisconsin double standardization and square root transformation using the metaMDS function in R package vegan (R package version 2.5–7; Oksanen et al. 2020), and non-metric multidimensional scaling (NMDS) was used to examine communities in ordination space on three dimension ($k=3$) using Bray–Curtis dissimilarities. Convex hulls were drawn around each of the lagoons to visualize separation of lagoon communities and show the spread of individual community samples. Species scores are shown (as the abbreviated species name) in the ordination at their optimum, with abundance decreasing in all directions from that point.

Species contributions

The contributions of individual species to community similarity (rather, the Bray–Curtis dissimilarity of the community matrix [Clarke 1993]) were determined using CPUE_{net}. Comparisons were made on a pairwise basis, for example, comparing Jago Lagoon to Kaktovik Lagoon, Jago Lagoon to Simpson Lagoon, and Jago Lagoon to Stefansson Sound. The function simper in R package vegan (R package version 2.5–7; Oksanen et al. 2020) provides a cumulative contribution based on species abundances. Permutations tests ($n=1000$) were used to discover for which species the difference in abundance among lagoons were a consistently important component of their contribution to dissimilarities, rather than contributions due to variation in individual species abundance (e.g., 0–146 Arctic cisco per day in Jago Lagoon). Contributions were considered important for permutation p -values <0.05 .

Environmental associations

Measurements of water temperature and salinity associated with each station were collected using data loggers (HOBO Salt Water Conductivity/Salinity Data Logger, U24-002-C, Onset Computer Corporation, Bourne, Massachusetts, USA) attached to the fyke net. Data loggers recorded temperature (°C) and conductivity every 5 min during net deployment, the mean and maximum temperature and mean salinity were calculated for net-day. Salinity was determined from conductivity using the function gsw_SP_from_C in the gsw package (Kelley et al. 2022)

with the corresponding temperature (°C) and given a pressure of 10.6351 dbar at 0.5 m depth. All temperature, conductivity, and salinity data that support the findings of this publication can be found in Stanek et al. (2024).

Wind speed and direction data, downloaded from Mesowest (University of Utah 2019), were gathered for Barter Island, Alaska (station PABA) and employed for fyke net stations in Kaktovik Lagoon and Jago Lagoon, and from Deadhorse, Alaska (station PASC) for Simpson Lagoon and Stefansson Sound. Data were downloaded beginning 72 h prior to the first net-day through to the end of sampling. Typically, measurements were available at 5-min intervals, although additional and missing times are present in the dataset. Data were converted to metric using standard formulas. Wind u (west–east) and wind v (south–north) vectors were calculated from the wind speed ($\text{m}\cdot\text{s}^{-1}$) and direction. Lagged wind u and v were determined as the average wind condition three days prior to the net-day of interest for all sampling events (Barton et al. 2020). Relationships between the variables were assessed using pairwise Spearman correlations between maximum temperature, mean temperature, mean salinity, mean wind speed, mean wind u, mean wind v, mean lag wind speed, mean lag wind u, and mean lag wind v.

A second NMDS ordination of the entire fish community (19 species) was evaluated using the same methods as above, but mean values ($\text{CPUE}_{y,\text{station}}$) were used in order to meet the assumptions of independence for linear modeling. Here, a smoothed surface for each environmental variable was examined using the ordisurf function in R package vegan (R package version 2.5–7; Oksanen et al. 2020). For each station and year combination, we determined the average value of maximum temperature and mean temperature, salinity, wind speed, wind u, wind v, lagged wind speed, lagged wind u, and lagged wind v; individually, these variables were fit to the ordination surface using a generalized additive model (GAM). All GAMs used a thin plate regression spline with four knots. GAMs of environmental variables were examined on each pair of NMDS axes (i.e., 1 and 2, 2 and 3, 1 and 3) and diagnostic plots checked for goodness of fit. Select species scores, based on contributions, are shown in the ordinations at their optimum, with abundance decreasing in all directions from that point.

Results

In Jago and Kaktovik lagoons, Arctic cisco was the most abundant fish species, comprising 75% and 54% of the average catch, respectively (Fig. 2a, b). Other captured fishes with marine affinity included Arctic flounder, nataaqnaq (*Liopsetta glacialis*); Arctic smelt, ilhuaqniq (*Osmerus dentex*); fourhorn sculpin, and saffron cod. These fishes were

prevalent in the eastern Beaufort Sea region, collectively making up 23% of the average catch in Jago Lagoon and 45% of the average catch in Kaktovik Lagoon; < 0.5% of the average catch in these lagoons included fish with a strong freshwater affinity [i.e., broad whitefish, aanaaktliq (*Coregonus nasus*); humpback whitefish, pikuktuuq (*Coregonus pidchian*); and least cisco, iqalusaaq (*Coregonus sardinella*)]. In the central Beaufort Sea region, fishes with a freshwater affinity had higher average CPUEs (Table 1) and comprised greater proportions of the catch (Fig. 2c, d) compared to eastern Beaufort Sea lagoons. Thirteen percent of the average catch in Simpson Lagoon and 60% of the average catch in Stefansson Sound included broad whitefish, humpback whitefish, least cisco, and threespine stickleback, kakilasak (*Gasterosteus aculeatus*). Simpson Lagoon had higher proportions of fourhorn sculpin (20%) and Arctic flounder (55%) than other lagoons. Polar cod, iqaluqaq (*Boreogadus saida*, sometimes called Arctic cod) comprised small proportions of the catch in the central region only (Table 1). Dolly Varden were captured in both regions, but made up less than 2% of the total catch. Other species, which cumulatively made up less than 1% of the catch in any lagoon, included Arctic grayling, sulukpaugaq (*Thymallus arcticus*); Arctic sand lance, pañmaksraq (*Ammodytes hexapterus*); Arctic staghorn sculpin, kanayuq, (*Gymnoanthus tricuspidis*); chum salmon, qalugruaq (*Oncorhynchus keta*); ninespine stickleback, kakalisauraq (*Pungitius pungitius*); Pacific capelin, pañmaksraq (*Mallotus catervarius*); Pacific herring, uqsruqtuuk (*Clupea pallasi*); or pink salmon, amaqtuuq (*Oncorhynchus gorbuscha*) (see Table 1 for mean CPUEs across lagoons).

Community ordination & species contributions

NMDS ordination (stress = 0.14) indicated clear separation of central (Simpson Lagoon and Stefansson Sound) and eastern (Jago and Kaktovik lagoons) lagoon communities along the first NMDS axis (Fig. 3a). Broad whitefish and humpback whitefish presence was associated with the central lagoons, while saffron cod and Arctic flounder presence was associated with the eastern lagoons. Among the freshwater associated fishes, least cisco contributed 18–24% and broad whitefish contributed 11–14% of the variation between the central Beaufort Sea and eastern Beaufort lagoon communities (Table 2; “Between regions”). Among the marine fishes, Arctic flounder contributed 29–33% and fourhorn sculpin contributed 12–15% of the variation between central Beaufort Sea lagoon communities and eastern Beaufort Sea lagoon communities (Table 2; “Between regions”). Polar cod, which was associated with Stefansson Sound, contributed little (1%) to the variation between regions and was captured only in the central Beaufort Sea lagoons.

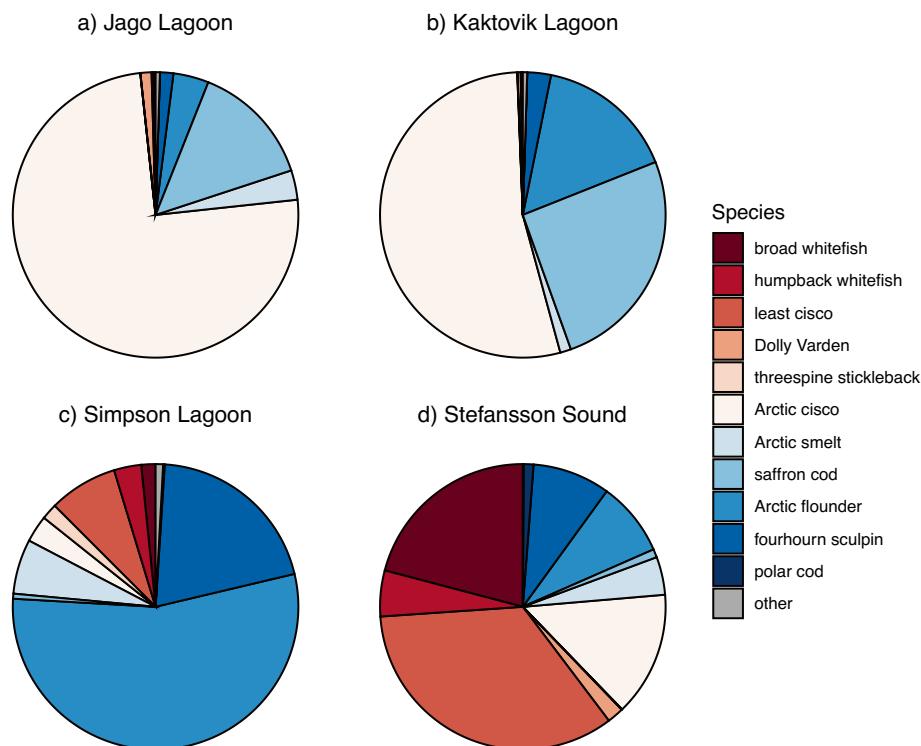


Fig. 2 Fish species proportions in nearshore communities—**a** Jago Lagoon, **b** Kaktovik Lagoon, **c** Simpson Lagoon, and **d** Stefansson Sound—based on the mean catch per unit effort (CPUE_{lagoon}) of all sampled dates in 2017, 2018, and 2019. Species shaded in reds [broad whitefish (*Coregonus nasus*), humpback whitefish (*Coregonus pidgichian*), least cisco (*Coregonus sardinella*), Dolly Varden (*Salvelinus malma*), threespine stickleback (*Gasterosteus aculeatus*), and Arctic cisco (*Coregonus autumnalis*)] are diadromous, likely using river habitats and lagoons as adults; species shaded in blues are marine [Arctic smelt (*Osmerus dentex*), saffron cod (*Eleginops gracilis*), Arctic

tic flounder (*Liopsetta glacialis*), fourhorn sculpin (*Myoxocephalus quadricornis*), and polar cod (*Boreogadus saida*)]. Species in the “other” category may include <1% combined of Arctic grayling (*Thymallus arcticus*), Arctic staghorn sculpin (*Gymnocephalus tricuspidatus*), Arctic sand lance (*Ammodytes hexapterus*), chum salmon (*Oncorhynchus keta*), pink salmon (*Oncorhynchus gorbuscha*), ninespine stickleback (*Pungitius pungitius*), Pacific capelin (*Mallotus catervarius*), or Pacific herring (*Clupea pallasii*). Fish CPUE data from Stanek et al. (2022b)

The convex hulls for the central Beaufort Sea lagoons were distinct along the third NMDS axis (Fig. 3b, c). Arctic flounder, fourhorn sculpin, threespine stickleback, and pink salmon contributed to differences between the Simpson Lagoon and Stefansson Sound communities (Table 2; “Within regions”). Arctic flounder accounted for the greatest percent contribution at 41%, followed by fourhorn sculpin (17%), threespine stickleback (2%) and pink salmon (<1%). Species associations can be seen for pink salmon and fourhorn sculpin in Stefansson Sound and threespine stickleback in Simpson Lagoon (Fig. 3b, c). Arctic flounder, which was relatively abundant in Simpson Lagoon (Table 1), was an important contributor to the variation between Simpson Lagoon and all other lagoons (see also Table 2; “Between regions”).

The convex hulls for Jago and Kaktovik lagoons, where three years of data were collected, were larger than those for Simpson Lagoon (one year of data) and Stefansson Sound (two years of data); additionally, the eastern Beaufort Sea lagoons did not show clear separation on any axis (Fig. 3).

Seven fish species contributed to minor differences between the communities in Kaktovik and Jago lagoons (Table 2; “Within regions”). The top three contributors from the similarity percentages were Arctic cisco (51%), saffron cod (22%) and Dolly Varden (3%). Several species, like Arctic sand lance and Pacific capelin, accounted for small proportions of the catch and small percent contributions to the variability (Table 2), but were captured only in Jago Lagoon. The association of Dolly Varden with Jago Lagoon also appeared to contribute to slight separation from the Kaktovik Lagoon community on the first and second axes (Fig. 3b, c), and the association of saffron cod in Kaktovik Lagoon contributed to separation on the second axis (Fig. 3c).

Environmental associations

During sampling events, differences in temperature, salinity, and wind speed and direction were evident among years and sites (Fig. 4). Several variables were strongly correlated ($|r| \geq 0.600$) including daily maximum and mean water

Table 1 Mean (standard error) catch per unit effort (CPUE_{lagoon}) for fish species captured in nearshore regions of the central and eastern Beaufort Sea coast

Common name	Scientific name	Life history ^a	Zoogeographic pattern	Central		Eastern	
				Simpson Lagoon (n=11)	Stefansson Sound (n=19)	Jago Lagoon (n=32)	Kaktovik Lagoon (n=32)
Arctic grayling	<i>Thymallus arcticus</i>	F	Predominantly boreal ^b	0	0	0.001 (0.001)	0
Broad whitefish	<i>Coregonus nasus</i>	D	Predominantly Arctic	0.256 (0.070)	0.999 (0.279)	0.037 (0.018)	0.001 (0.001)
Humpback whitefish	<i>Coregonus pid-schian</i>	D	Predominantly Arctic	0.486 (0.083)	0.248 (0.053)	0	0
Least cisco	<i>Coregonus sardinella</i>	D	Predominantly Arctic	1.236 (0.257)	1.636 (0.269)	0.026 (0.005)	0.008 (0.003)
Dolly Varden	<i>Salvelinus malma</i>	D	Arctic-boreal Pacific	0	0.090 (0.018)	0.175 (0.031)	0.015 (0.005)
Ninespine stickleback	<i>Pungitius pungitius</i>	D	Predominantly boreal	0.009 (0.009)	0	0.023 (0.007)	0.006 (0.003)
Threespine stickleback	<i>Gasterosteus aculeatus</i>	D	Predominantly boreal	0.284 (0.095)	0.002 (0.002)	0.001 (0.001)	0.001 (0.001)
Arctic cisco	<i>Coregonus autumnalis</i>	D	Arctic	0.483 (0.143)	0.675 (0.119)	10.441 (4.690)	2.269 (0.916)
Chum salmon	<i>Oncorhynchus keta</i>	A	Predominantly boreal Pacific	0	0	0.001 (0.001)	0.003 (0.002)
Pink salmon	<i>Oncorhynchus gorbuscha</i>	A	Predominantly boreal Pacific	0.124 (0.055)	0.002 (0.002)	0.020 (0.008)	0
Arctic smelt	<i>Osmerus dentex</i>	D	Arctic-boreal Pacific	0.981 (0.289)	0.206 (0.065)	0.465 (0.163)	0.052 (0.018)
Saffron cod	<i>Eleginops gracilis</i>	M	Arctic-boreal Pacific	0.089 (0.035)	0.044 (0.027)	1.939 (0.759)	1.082 (0.229)
Arctic flounder	<i>Liopsetta glacialis</i>	M	Predominantly Arctic	8.647 (3.664)	0.403 (0.151)	0.560 (0.100)	0.669 (0.105)
Arctic staghorn sculpin	<i>Gymnocanthus tricuspidis</i>	M	Arctic	0	0	0.004 (0.002)	0.007 (0.004)
Fourhorn sculpin	<i>Myoxocephalus quadricornis</i>	M	Predominantly Arctic	3.210 (1.339)	0.420 (0.084)	0.211 (0.035)	0.113 (0.014)
Pacific capelin	<i>Mallotus catervarius</i>	M	Arctic-boreal	0	0	0.004 (0.003)	0
Arctic sand lance	<i>Ammodytes hexapterus</i>	M	Arctic-boreal Pacific	0	0	0.009 (0.006)	0
Pacific herring	<i>Clupea pallasii</i>	M	Arctic-boreal Pacific	0	0.002 (0.002)	0.004 (0.003)	0.006 (0.004)
Polar cod	<i>Boreogadus saida</i>	M	Arctic	0.028 (0.024)	0.053 (0.028)	0	0

Sample sizes (n) are provided for lagoons where fish collection occurred. Zeroes are shown when no fish were captured. Fish are arranged in descending order from those with greater freshwater affinity to marine affinity. Zoogeographic patterns from Thorsteinson and Love (2016) and fish CPUE data from Stanek et al. (2022b)

^aLife history: A anadromous, D diadromous, F freshwater, M marine

^bAuthor defined

temperature ($r_s=0.971$, $n=16$, $p<0.0001$), lag wind u and lag wind speed ($r_s=0.841$, $n=16$, $p<0.0001$), wind u and salinity ($r_s=-0.785$, $n=16$, $p=0.0005$), wind v and maximum temperature ($r_s=0.768$, $n=16$, $p=0.0008$), lag wind v and maximum temperature ($r_s=0.729$, $n=16$, $p=0.0019$),

lag wind v and mean temperature ($r_s=0.726$, $n=16$, $p=0.0020$), wind v and mean temperature ($r_s=0.697$, $n=16$, $p=0.0036$), lag wind u and wind speed ($r_s=0.688$, $n=16$, $p=0.0042$), wind speed and mean temperature

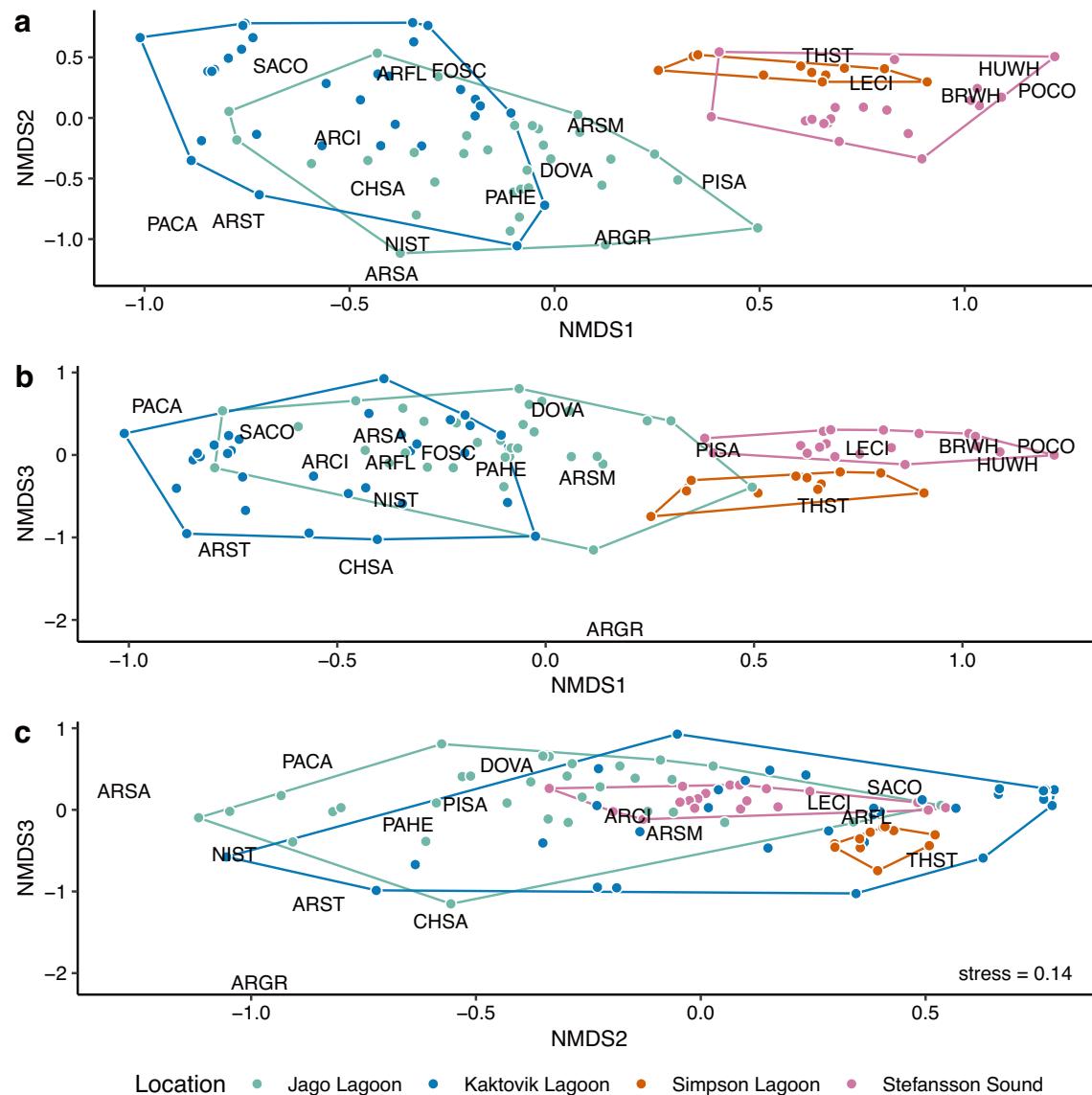


Fig. 3 Ordination of all axis pairs (a—NMDS 1 and 2, b—NMDS 1 and 3, and c—NMDS 2 and 3) for fish communities represented by individual sampling events during 2017, 2018, and 2019; each point represents the community based on the catch per unit effort (CPUE_{net}) of 19 species. Species include ARCI Arctic cisco (*Coregonus autumnalis*), ARFL Arctic flounder (*Liopsetta glacialis*), ARGR Arctic grayling (*Thymallus arcticus*), ARSA Arctic sand lance (*Ammodytes hexapterus*), ARSM Arctic smelt (*Osmerus dentex*), ARST Arctic staghorn sculpin (*Gymnocephalus tricuspidis*), BRWH broad whitefish (*Coregonus nasus*), CHSA chum salmon (*Oncorhynchus keta*), DOVA Dolly Varden (*Salvelinus malma*), FOSC

fourhorn sculpin (*Myoxocephalus quadricornis*), HUWH humpback whitefish (*Coregonus pidschian*), LECI least cisco (*Coregonus sardinella*), NIST ninespine stickleback (*Pungitius pungitius*), PACA Pacific capelin (*Mallotus catervarius*), PAHE Pacific herring (*Clupea pallasi*), PISA pink salmon (*Oncorhynchus gorbuscha*), POCO polar cod (*Boreogadus saida*), SACO saffron cod (*Eleginops gracilis*), and THST threespine stickleback (*Gasterosteus aculeatus*). Convex hulls encompass all points within a location: Jago Lagoon, Kaktovik Lagoon, Simpson Lagoon, and Stefansson Sound. POCO and BRWH (overlapped LECI), and HUWH and FOSC (overlapped ARFL) were removed from panel c for legibility

($r_s = -0.612, n = 16, p = 0.0136$), and wind speed and maximum temperature ($r_s = -0.600, n = 16, p = 0.0160$).

In Jago and Kaktovik lagoons, conditions in August 2017 were relatively warm [mean \pm standard error (se) maximum temperatures: Jago Lagoon 12.9 ± 0.2 °C, $n = 12$; Kaktovik Lagoon 13.2 ± 0.2 °C, $n = 12$; Fig. 4a] and saline (mean \pm se salinity: Jago Lagoon 19.6 ± 0.5 ,

$n = 12$; Kaktovik Lagoon $23.6 \pm 0.5, n = 12$; Fig. 4b), when winds were relatively calm and vector components did not differ from zero (Fig. 4c, d). During sampling in August 2018, Jago and Kaktovik lagoons were cooler (mean \pm se maximum temperatures: Jago Lagoon 5.6 ± 0.4 °C, $n = 16$; Kaktovik Lagoon 6.4 ± 0.2 °C, $n = 16$) and brackish (mean \pm se salinity: Jago Lagoon 7.5 ± 1.1 ,

Table 2 Fish species that contributed to between lagoon differences as determined by a permutation ($n_{iter}=1000$) analysis of similarity percentages

	Lagoon pair	Species	% Contribution
Between regions	Jago & Simpson	Arctic flounder	29
		Fourhorn sculpin	12
		Humpback whitefish	4
		Threespine stickleback	2
		Pink salmon	1
	Jago & Stefansson	Least cisco	18
		Broad whitefish	11
		Humpback whitefish	3
		Polar cod	1
	Kaktovik & Simpson	Arctic flounder	33
		Fourhorn sculpin	15
		Humpback whitefish	5
		Threespine stickleback	2
		Pink salmon	1
	Kaktovik & Stefansson	Least cisco	24
		Broad whitefish	14
		Humpback whitefish	4
		Polar cod	1
Within regions	Jago & Kaktovik	Arctic cisco	51
		Saffron cod	22
		Dolly Varden	3
		Ninespine stickleback	< 1
		Arctic sand lance	< 1
		Arctic grayling	< 1
		Pacific capelin	< 1
	Simpson & Stefansson	Arctic flounder	41
		Fourhorn sculpin	17
		Threespine stickleback	2
		Pink salmon	1

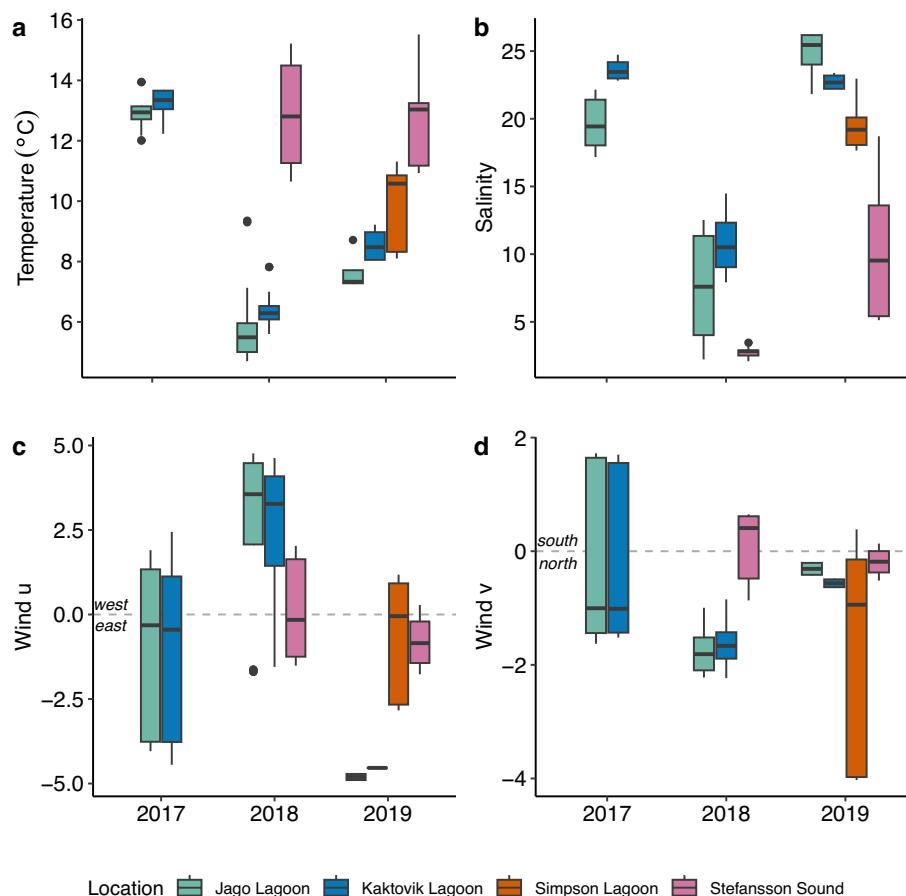
Only significant contributions ($p < 0.05$) are shown. The percent contribution to variation in the communities was determined on a pairwise basis. Contributions are shown for pairs that occur between regions (central versus eastern Beaufort Sea) and within regions. Arctic cisco (*Coregonus autumnalis*), Arctic flounder (*Liopsetta glacialis*), Arctic grayling (*Thymallus arcticus*), Arctic sand lance (*Ammodytes hexapterus*), broad whitefish (*Coregonus nasus*), Dolly Varden (*Salvelinus malma*), fourhorn sculpin (*Myoxocephalus quadricornis*), humpback whitefish (*Coregonus pidschian*), least cisco (*Coregonus sardinella*), ninespine stickleback (*Pungitius pungitius*), Pacific capelin (*Mallotus catervarius*), pink salmon (*Oncorhynchus gorbuscha*), polar cod (*Boreogadus saida*), saffron cod (*Eleginops gracilis*), and threespine stickleback (*Gasterosteus aculeatus*)

$n=16$; Kaktovik Lagoon 10.7 ± 0.5 , $n=16$; Fig. 4b), with stronger winds from the west and north (Fig. 4d). In August 2019, Jago and Kaktovik lagoons were relatively cold (mean \pm se maximum temperatures: Jago Lagoon 7.7 ± 0.4 °C, $n=4$; Kaktovik Lagoon 8.6 ± 0.3 °C, $n=4$) and saline (mean \pm se salinity: Jago Lagoon 24.7 ± 1.0 , $n=4$; Kaktovik Lagoon 22.7 ± 0.3 , $n=4$; Fig. 4b), with stronger winds from the east and north (Fig. 4c, d). In July 2018 and 2019, Stefansson Sound was warm (mean \pm se maximum temperatures: 12.9 ± 0.5 °C, $n=12$, in 2018; 12.3 ± 0.4 °C, $n=8$, in 2019; Fig. 4a) and relatively fresh to brackish (mean \pm se salinity: 2.8 ± 0.1 , $n=12$, in 2018; 10.2 ± 2.1 , $n=8$, in 2019; Fig. 4b). Simpson Lagoon was

cooler (mean \pm se maximum temperatures 9.9 ± 0.4 °C, $n=12$) and saline (mean \pm se salinity 19.3 ± 0.05 , $n=12$) compared to Stefansson Sound, but with variable northerly winds compared to other locations in 2019 (Fig. 4c, d).

The NMDS ordination (stress = 0.08) of the average fish community at all stations for each location and year, showed similar separation patterns as the ordination of all samples. Across all NMDS axes, GAMs were compared for each individually assessed variable (Table 3). Significant ($p < 0.05$) and marginally significant ($p = 0.05$) variables were visualized in plots (Figs. 5, 6, 7, 8, 9), with species that contributed to notable differences among locations and years indicated in multivariate space (not all

Fig. 4 Environmental conditions of **a** maximum temperature, **b** salinity, and sign and magnitude of wind vectors (**c**—west–east, **d**—south–north) in nearshore lagoons of the Beaufort Sea during sampling in 2017, 2018, and 2019. Vectors of wind speed indicate the direction and magnitude (speed) of the wind; positive values indicate a west (u) or south (v) wind while negative values indicate an east (u) or north (v) wind. Box-and-whisker plots show the median (line in the box), interquartile range (IQR, box), and whiskers extending above and below to 1.5(IQR). Outliers included as points. Temperature and salinity data can be found in Stanek et al. (2024), wind data are from MesoWest (University of Utah 2019)



species are shown). For six of nine variables – salinity, wind speed, wind u, lag wind u, wind v, and maximum water temperature – we found agreement between the community patterns (represented by species CPUEs) and the environment. On two NMDS axes pairs (1 and 2, 2 and 3), the correlated variables salinity and wind u both related to the community ordination, but their effects cannot be fully parsed. Surface fits of mean temperature, lagged wind speed and lagged wind v did not project meaningfully onto the community ordination, explaining little of the community patterns seen among lagoons (Table 3).

The surface fit of salinity was associated with the community ordination on two of three axes pairs and described about 53% of the community variation in ordination space (Table 3, Fig. 5). Communities containing higher abundances of least cisco and broad whitefish clustered together on the first and second axes, near points representing Stefansson Sound, Simpson Lagoon, and Kaktovik and Jago lagoons during 2018 at locations and time periods of lower salinity (Fig. 5a). Arctic cisco and saffron cod, which were separated from one another on the second and third ordination axes, were associated with higher salinities found in Kaktovik and Jago lagoons in 2017 and 2019 (Fig. 5b). Along the third axes, separation of Simpson Lagoon and

Stefansson Sound communities were associated with high abundances of Arctic flounder and fourhorn sculpin in the relatively salty Simpson Lagoon, compared to fresher Stefansson Sound (Fig. 5b).

Similar surface fits were found for wind u (west–east) on the same axes (Fig. 6a, b), although wind u appeared to explain about 10% more variation than salinity alone—61% for the first and second axes and 66% on the second and third axes (Table 3). Positive values of wind u indicate a west wind, which was more often associated with Stefansson Sound and Kaktovik and Jago lagoons in 2018 and the presence of Dolly Varden (Fig. 6a, b). Strong easterly winds in 2017 and 2019 (negative wind u values) were associated with high abundances of Arctic cisco, saffron cod, and pink salmon in Jago and Kaktovik lagoons (Fig. 6a, b). Similarly, strong winds in Stefansson Sound during 2019 correlated with polar cod (Fig. 6a). Lagged wind u explained about 45% of the variation on the first and third axes. Stronger lagged west winds associated with least cisco in Stefansson Sound and saffron cod in Kaktovik Lagoon (Fig. 6c). Lagged easterly winds differentiated the Simpson Lagoon communities, which were associated with higher threespine stickleback abundance (Fig. 6c).

Table 3 Significance and deviance explained for Generalized Additive Models of environmental variables, fit as a smoothed surface over the existing ordination

NMDS axes	Variable	edf	Ref. df	F	p-value	Deviance Explained (%)
1 & 2	Max. temperature	0.934	3	0.628	0.1590	16.7
	Mean temperature	0.431	3	0.252	0.2050	7.5
	Salinity	2.425	3	3.860	0.0190	52.7
	Wind speed	2.255	3	4.471	0.0090	54.7
	Wind u	2.516	3	5.768	0.0060	61.4
	Wind v	1.469	3	2.294	0.0240	38.2
	Lag wind speed	4.65×10^{-5}	3	0	0.4910	0
	Lag wind u	0.245	3	0.093	0.3460	3.4
	Lag wind v	2.58×10^{-5}	3	0	0.8140	0
	Max. temperature	0.719	3	0.852	0.0800	18.6
2 & 3	Mean temperature	0.445	3	0.268	0.1990	7.9
	Salinity	2.076	3	4.330	0.0080	53.8
	Wind speed	0.937	3	4.972	0.0010	53.0
	Wind u	2.476	3	7.219	0.0020	65.8
	Wind v	0.275	3	0.106	0.3400	3.9
	Lag wind speed	0.508	3	0.340	0.1760	9.6
	Lag wind u	0.686	3	0.727	0.0960	16.7
1 & 3	Lag wind v	0.064	3	0.023	0.3180	0.9
	Max. temperature	1.730	3	1.975	0.0510	36.6
	Mean temperature	0.697	3	0.768	0.0910	17.3
	Salinity	1.308	3	1.260	0.0890	27.1
1 & 3	Wind speed	1.666	3	3.330	0.0140	46.6
	Wind u	0.612	3	0.294	0.2700	9.4
	Wind v	0.150	3	0.059	0.2950	2.2
	Lag wind speed	0.861	3	0.484	0.2120	14.1
	Lag wind u	0.913	3	3.495	0.0040	44.7
	Lag wind v	3.95×10^{-5}	3	0	0.7350	0

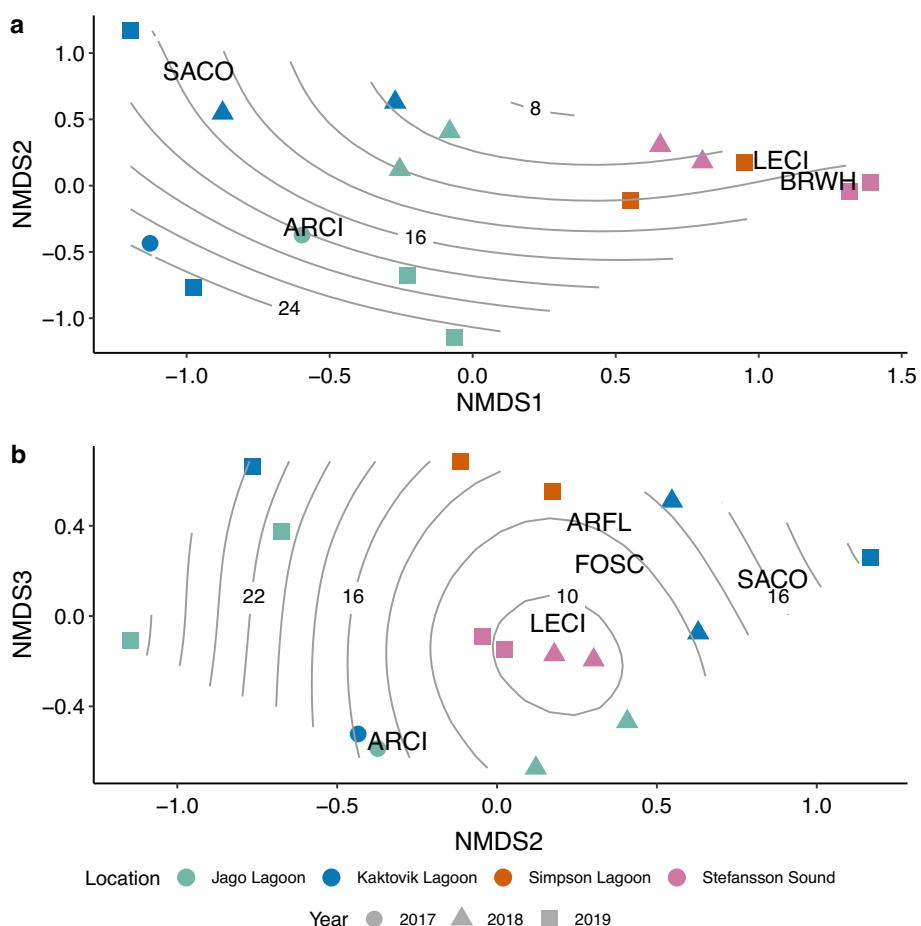
Each variable was fit independently and examined on nonmetric multidimensional scaling (NMDS) axes pairs (1 and 2, 2 and 3, 1 and 3). The most influential variables on axes pairs are bold. Wind u describes west–east vectors of wind speed and direction, and wind v describes south–north vectors of wind speed and direction. Lag wind values represent the value from three days prior to sampling. Effective degrees of freedom: edf; reference degrees of freedom: Ref. df

The wind v (south–north) component centered around the communities in Jago Lagoon in 2018, which were associated with Arctic flounder, and experienced the strongest average northerly winds. Communities in 2019 at all locations correlated with higher, but still negative, wind v values, but species associations varied across ordination space, with wind v explaining up to 38% of the variation on only the first and second axes (Table 3; Fig. 7). Lastly, average maximum water temperature, which was positively correlated with wind v, explained 37% of the community variation on the first and third axes (Table 3). Warmer water temperatures were associated with communities in Stefansson Sound, while cooler temperatures were associated with communities in Kaktovik Lagoon during 2019 (Fig. 8). This separation aligned with the arrangement of freshwater-leaning species (e.g., least cisco) and marine species (e.g., saffron cod). Average wind speed

was the only variable correlated with the ordinations of fish communities on all three axes pairs, explaining between 47 and 55% of the variation in communities (Table 3; Fig. 9). The ordination of the fish community, particularly the first axes, showed clear separation between the central and eastern Beaufort Sea lagoons (Fig. 9a, c), and average wind speed correlated well with the distribution of marine and freshwater favoring species (Fig. 9b). Greater average wind speed was associated with marine species like Pacific capelin and Arctic sand lance that were encountered infrequently during sampling and only at Jago Lagoon. Higher wind speed was also associated to the presence of abundant Arctic cisco, a species that relies on winds for recruitment to the region.

Fig. 5 Contour lines represent the smoothed generalized additive model fit of salinity to the fish communities in ordination space for the **a** first and second non-metric multidimensional scaling (NMDS) axes and the **b** second and third NMDS axes. Each point represents the average fish community (includes 19 species) for a station within a location and year (CPUE_{y,station}) when collection occurred.

Select species associations are shown for visual clarity, including ARCI Arctic cisco (*Coregonus autumnalis*), ARFL Arctic flounder (*Liopsetta glacialis*), BRWH broad whitefish (*Coregonus nasus*), FOSC fourhorn sculpin (*Myoxocephalus quadricornis*), LECI least cisco (*Coregonus sardinella*), and SACO saffron cod (*Eleginops gracilis*)



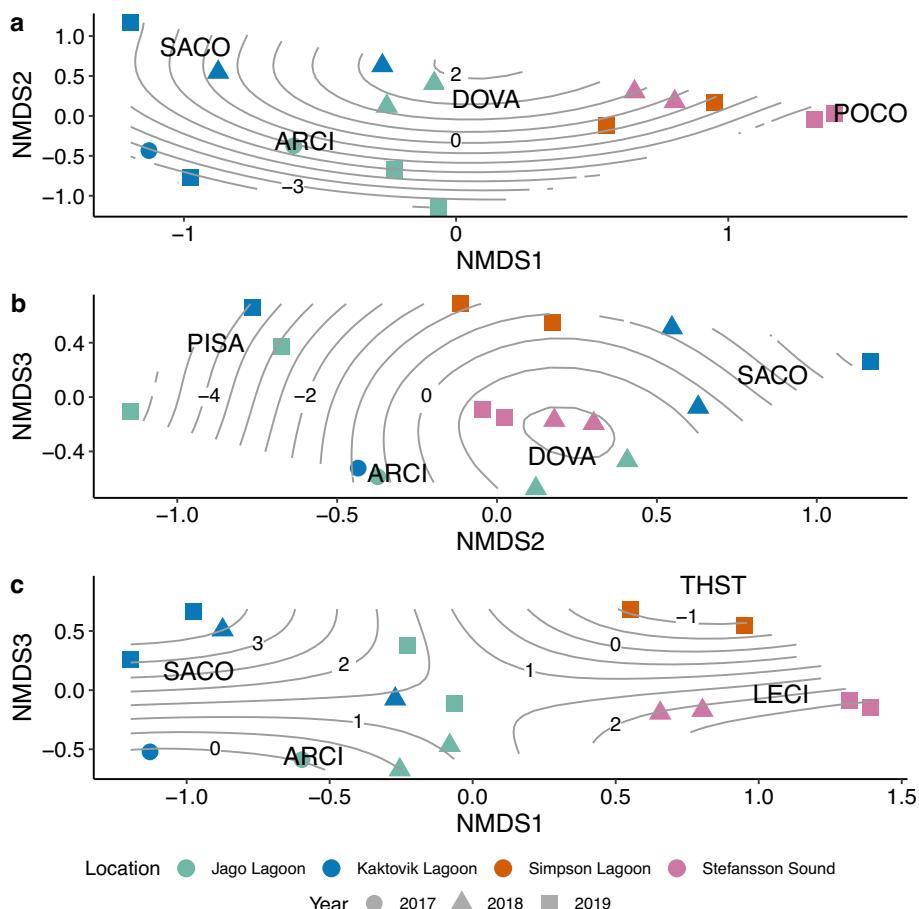
Discussion

Composition of fishes in Beaufort Sea lagoons

The spatial distribution of fish communities highlighted the effects of wind, salinity, and temperature on the coexistence of diadromous and marine fishes among Beaufort Sea lagoons and demonstrated the importance of the local environment in supporting distinct lagoon communities. In agreement with earlier studies, diadromous species with strong freshwater affinity were common to the central region, where large coastal plain rivers are used for spawning, rearing, and overwintering (Craig 1984; Craig et al. 1985). Thus, landscape features like large Arctic rivers and their nearshore freshwater plumes may represent a dominant structuring force among Arctic estuarine communities that has been maintained during a period of rapid climate change (Rantanen et al. 2022). The recently documented community reorganizations, which are primarily driven by sea ice loss and warmer water temperatures (Priest et al. 2022; von Biela et al. 2023), appear to be nested within the spatial framework that exists along the Beaufort Sea coast.

The seasonal accessibility of freshwater habitats in the central region is critical to diadromous fishes. In winter, when lagoon water temperatures are subzero, large river deltas provide overwintering areas or overwintering access for ciscoes, whitefishes, and Dolly Varden (Craig et al. 1985; Carey et al. 2021; Gallagher et al. 2021). While the seasonal migration movements of some diadromous species or life stages (e.g., Dolly Varden and Arctic cisco) are documented, information on the amount of time spent in varying estuarine habitats remains limited for most Arctic fishes including marine species (Craig 1984; Zimmerman et al. 2013; Gallagher et al. 2021). The presence or abundance of marine fishes increased in lagoons with greater connection to marine waters, that is when lagoons were more saline—typically later in the summer after the spring freshet or during periods of easterly winds (Craig 1984; Khalsa et al. 2021; Priest et al. 2022). Marine species can make up large proportions of the fish community's abundance in lagoons, though some species, like polar cod, are episodic in occurrence with their presence linked to strong winds, cold temperatures, and high salinity (Craig et al. 1982; Barton et al. 2020; von Biela et al. 2023). These findings support information generalized from early

Fig. 6 Contour lines represent the smoothed generalized additive model fit of the wind u vector to the communities in ordination space for the **a** first and second non-metric multidimensional scaling (NMDS) axes and the **b** second and third NMDS axes, and **c** fit of the three-day lagged wind u vector to the communities for the first and third NMDS axes. Wind u describes west (+) and east (−) vectors of wind speed and direction; larger values are associated with stronger wind speeds. Each point represents the average fish community (includes 19 species) for a station within a location and year (CPUE_{y,station}) when collection occurred. Select species associations are shown for visual clarity, including ARCI Arctic cisco (*Coregonus autumnalis*), DOVA Dolly Varden (*Salvelinus malma*), LECI least cisco (*Coregonus sardinella*), PISA pink salmon (*Oncorhynchus gorbuscha*), POCO polar cod (*Boreogadus saida*), SACO saffron cod (*Eleginops gracilis*), and THST threespine stickleback (*Gasterosteus aculeatus*)



studies (Craig 1984) and expand on our knowledge of spatial distributions and environmental correlates in Arctic estuarine communities that are experiencing rapid climate change (Meredith et al. 2019).

Distribution of Arctic estuarine fishes in relation to abiotic variables

The results of the generalized additive models on each pair of the three NMDS axes revealed that estuarine communities are most responsive to the west–east (u) wind component, salinity, and wind speed. To a lesser extent, south–north (v) winds and maximum temperature were correlated to the spatial distribution of the fish communities. Multicollinearity among the environmental variables, however, makes it difficult to parse specific effects, yet these analyses indicated that local fish communities respond to wind influenced marine and freshwater masses that determine salinity and temperature in the lagoons (Craig 1984; Valesini et al. 2014). As expected, higher salinities correlated with marine species like saffron cod, while low salinity conditions in the central region near the Sagavanirktok (Stefansson Sound) and Kuparuk (Simpson Lagoon) rivers were associated with freshwater-leaning diadromous species like least cisco. Strong

easterly winds were associated with Arctic cisco abundance, which we anticipated given the known recruitment patterns of young-of-the-year, which made up a large proportion of the catch in 2017 (Zimmerman et al. 2013; Stanek et al. 2022b). The response of fishes to the predominant regional water mass (i.e., river discharge versus marine water) and the accessibility of freshwater habitats for diadromous species may be the ultimate driver of coastal distribution patterns across Beaufort Sea lagoons (Craig 1984; Feyrer et al. 2015; Roux et al. 2016; Lundstrom et al. 2022). Changes to the timing or magnitude of river discharge events, or increased wave action from storms occurring over ice-free areas of the Arctic Ocean could have profound effects on the balance of water masses in lagoons (Casas-Prat and Wang 2020; Feng et al. 2021), potentially changing the relative abundance or presence of fish community members.

The west–east (u) wind component explained more community variation than temperature or salinity independently; temperature and salinity are important to the structure of fish communities in other Beaufort Sea estuarine studies (Roux et al. 2016; Barton et al. 2020; Priest et al. 2022). Strong easterly winds draw cold, saline water from depth onto the shelf (Schulze and Pickart 2012), drawing water away from the shoreline, resulting in decreased depth in lagoons and

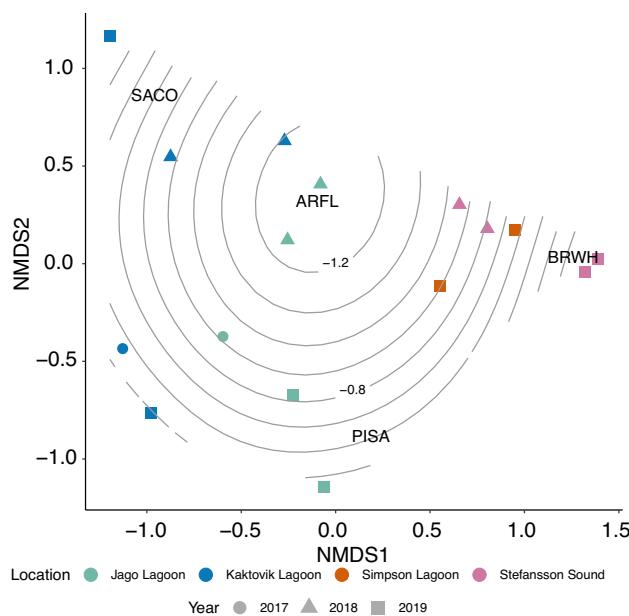


Fig. 7 Contour lines represent the smoothed generalized additive model fit of the wind v vector to the communities in ordination space on first and second non-metric multidimensional scaling axes. Wind v describes south (+) and north (−) vectors of wind speed and direction; larger values are associated with stronger wind speeds. Each point represents the average fish community (includes 19 species) for a station within a location and year ($CPUE_{y,station}$) when collection occurred. Select species associations are shown for visual clarity, including ARFL Arctic flounder (*Liopsetta glacialis*), BRWH broad whitefish (*Coregonus nasus*), PISA pink salmon (*Oncorhynchus gorbuscha*), and SACO saffron cod (*Eleginops gracilis*)

creating habitat for marine species (Okkonen et al. 2018). At Elson Lagoon, which lies directly east of Point Barrow, Alaska, easterly winds move water from the Beaufort Sea through barrier islands, advecting Arctic marine species (e.g., Pacific capelin) into the shallow water (Barton et al. 2020). Additionally, strong easterly winds in mid- to late-August promote transport of juvenile Arctic cisco into Alaskan waters (Fechhelm and Fissel 1988; Zimmerman et al. 2013; Priest et al. 2022), as witnessed through high abundance in Jago and Kaktovik lagoons in August of 2017 and 2019. Arctic cisco arrive in eastern lagoons earlier in August than to the central lagoons, which are farther from the Mackenzie River (Moulton 1989). July sampling in the central region likely resulted in missed detection of abundant recruits in Simpson Lagoon and Stefansson Sound. Still, our results are similar to those from season-long data sets (July–September), where marine species abundance is higher relative to freshwater/diadromous species in the eastern Beaufort Sea lagoons (Brown 2008) and marine species abundance is roughly equivalent to freshwater/diadromous species abundance in Prudhoe Bay (Priest et al. 2022).

Lagoon salinity was correlated strongly with regional differences in fish community composition. Salinity gradients

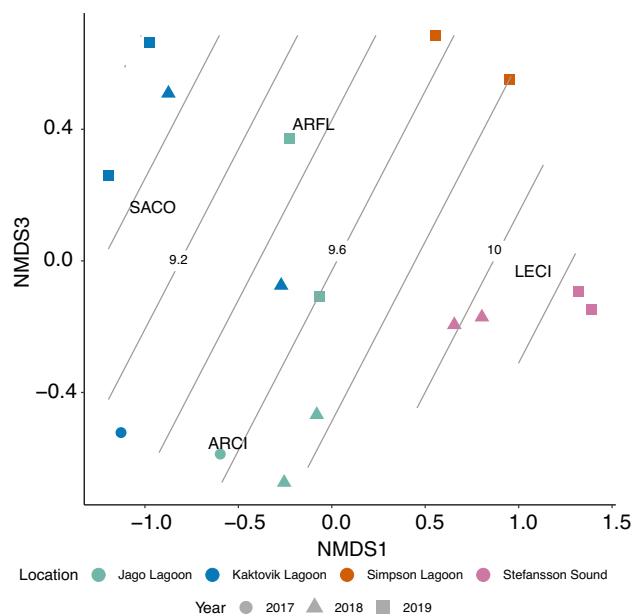
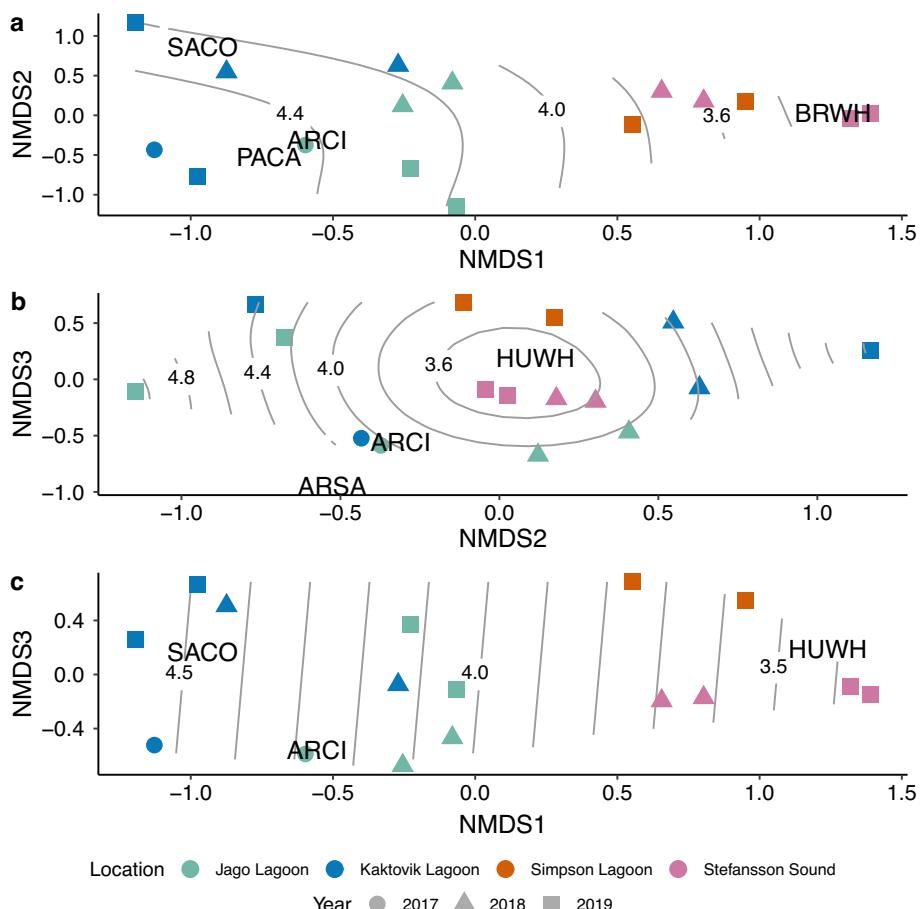


Fig. 8 Contour lines represent the smoothed generalized additive model fit of maximum temperature ($^{\circ}\text{C}$) to the communities in ordination space on first and second non-metric multidimensional scaling axes. Each point represents the average fish community (includes 19 species) for a station within a location and year ($CPUE_{y,station}$) when collection occurred. Select species associations are shown for visual clarity, including ARCI Arctic cisco (*Coregonus autumnalis*), ARFL Arctic flounder (*Liopsetta glacialis*), LECI least cisco (*Coregonus sardinella*), and SACO saffron cod (*Eleginops gracilis*)

have been associated with species replacement in coastal lagoon systems, with stronger effects found at larger spatial scales (Feyrer et al. 2015; Menegotto et al. 2019). Investigations in other Beaufort Sea lagoon systems indicated the presence of or distance to the river mouth was pivotal to the distribution and abundance of species and that salinity played an important role in community composition (Roux et al. 2016; Barton et al. 2020; Priest et al. 2022). Freshwater species, like Arctic grayling, are found in oligohaline (salinity < 5) waters of lagoons (Roux et al. 2016) and were rarely captured during this study since salinities were often higher–oligohaline conditions occurred only in Jago Lagoon (Arctic grayling captured) and Stefansson Sound in 2018. Diadromous species with higher salinity tolerance (< 25) were common and widespread, but some species, like humpback whitefish and Arctic cisco, appeared to sort along a gradient from west to east, which may be strongly related to their life histories. Humpback whitefish occurred only in the central region, and their absence from Kaktovik and Jago lagoons likely reflects true differences in occurrence given their known distribution and reliance on large river systems to complete their life history (Alt 1979; Craig 1984). Arctic cisco abundance was ~11 times higher on average in the eastern region compared to the central region, which

Fig. 9 Contour lines represent the smoothed generalized additive model fit of wind speed (m/s) to the communities in ordination space for the **a** first and second non-metric multi-dimensional scaling (NMDS) axes, the **b** second and third NMDS axes, and the **c** second and third NMDS axes. Each point represents the average fish community (includes 19 species) for a station within a location and year ($CPUE_{y, \text{station}}$) when collection occurred. Select species associations are shown for visual clarity, including ARCI Arctic cisco (*Coregonus autumnalis*), ARSA Arctic sand lance (*Ammodytes hexapterus*), BRWH broad whitefish (*Coregonus nasus*), HUWH humpback whitefish (*Coregonus pidschian*), PACA Pacific capelin (*Mallotus catervarius*), and SACO saffron cod (*Eleginops gracilis*)



may be related to the congruence of August sampling and migration timing of young-of-the-year fish in Kaktovik and Jago lagoons (Moulton 1989).

Marine species rare to the lagoons during sampling (e.g., polar cod, Arctic sand lance) supported differences in fish community composition between individual lagoons within and across regions, and were likely associated with sporadic events like storms, when strong wind-driven currents facilitate the movement of small marine fishes into open lagoons (Valesini et al. 2014; Barton et al. 2020). We may have failed to detect species like Arctic sand lance that burrow in soft sediments and require active sampling for capture (e.g., beach seine). Among sites near Point Barrow, Alaska, Arctic sand lance CPUE was at least 40 times higher outside of the lagoon compared to capture rates in the lagoon (Barton et al. 2020), suggesting capture of this species in lagoons would be rare even using different sampling methods. The absence of polar cod in the lagoons is more likely due to current environmental conditions (i.e., warmer and less sea ice) than from sampling methods, which historically used the same gear and readily captured polar cod when present (Priest et al. 2022; von Biela et al. 2023). Reduction of polar cod in seabird diets also indicates their decline in nearshore

areas as water temperatures increase and summer sea ice declines (Divoky et al. 2021).

In the Beaufort Sea's coastal waters, wind speed is correlated with nearshore current speeds, which are coupled to the size of the brackish water band in the coastal zone and to the advection of water masses (Craig 1984; Hale 1990; Dunton et al. 2006). Stronger winds in 2017 were associated with high Arctic cisco abundance in Jago and Kaktovik lagoons and with the presence of Arctic sand lance and Pacific capelin in Jago Lagoon. The average wind speeds included in this study were limited in magnitude ($3.4\text{--}5.0\text{ m}\cdot\text{s}^{-1}$) due to operational constraints of field sampling; storms with strong westerly winds ($22\text{ m}\cdot\text{s}^{-1}$) prevented multiple days of sampling in 2019. Although sustained ($> 72\text{ h}$) strong winds have been shown to affect nearshore conditions and communities days later (Hale 1990; Barton et al. 2020), we saw limited evidence of association between the three-day lagged west–east wind component and community composition. The effects of strong winds in the nearshore Beaufort Sea can be moderated by sea ice cover, but summer sea ice extent and concentration in the nearshore Arctic has declined over the past four decades (Perovich et al. 2020). Summer and fall winds are now poised to have much stronger effects on oceanography and biological communities than they have

in past decades with higher sea ice cover (Casas-Prat and Wang 2020; Falardeau et al. 2023).

Maximum temperature was less important to the distribution of fish communities across Beaufort Sea lagoons than anticipated, even though it was found to be important in studies within lagoons (e.g., Roux et al. 2016; Priest et al. 2022), or between lagoons and colder shelf waters (e.g., Barton et al. 2020). We attribute this to the relatively narrow range of average maximum temperatures (5.6–13.3 °C) experienced by fish during our July and August sampling windows or to the environmental tolerance of species present in our data set. In the Husky Lakes, some species that are encountered occasionally or rarely [e.g., pike (*Esox lucius*)] are cool-water fishes that reside primarily in freshwater and only visit Arctic lagoons during warmer periods (Roux et al. 2016). In warmer temperatures, upwards of 17 °C, like those experienced in Prudhoe Bay, Alaska, cold-water marine species likely remain outside of the lagoons (Barton et al. 2020; Khalsa et al. 2021). Polar cod, an ice-associated species, favors temperatures <6 °C and the sea ice edge (Laurel et al. 2016; Marsh et al. 2020). In recent sampling, this species has been found less often in lagoons during late summer, and access to suitable lagoon habitat may be restricted as waters continue to warm during summer months (Marsh et al. 2020; von Biela et al. 2023). Certainly, small climate change induced increases in lagoon summer water temperatures (to >10 °C) may affect the presence or distribution of fishes—promoting higher species richness in Arctic estuaries by way of range expansions or migrations of boreal species (Roux et al. 2016; Barton et al. 2020; Dunnall et al. 2022).

Conclusion

Our results showed fish community composition in Beaufort Sea lagoons depended on local geography and the wind-driven balance between freshwater and marine water masses that dictate salinity. As expected, higher salinities and associated easterly winds facilitated the arrival and abundance of marine species in the lagoons, but the relationship between community composition and warmer temperatures was weaker, and often covaried with winds and salinity making it difficult to parse these effects. The importance of easterly winds and salinity was evident during the brief summer period and agrees with other investigations in northern estuaries, some of which were conducted over longer time periods (e.g., Roux et al. 2016; Priest et al. 2022). Where long-term data collection exists, there is evidence of shifting communities, away from Arctic species and towards boreal species (Priest et al. 2022; von Biela et al. 2023). Changes in sea ice conditions and access to the Arctic, concurrent with increases in saffron cod abundance have added

focus to potential commercial cod fisheries in U.S. Arctic waters (NPFMC 2009). Not only will sea ice loss be dire for polar cod and the ice-associated food web (Huserbråten et al. 2019), but ice reductions will alter nearshore currents, increase wave action, and erode shorelines, all of which will increase variability in nearshore salinity (Falardeau et al. 2023). The intrusion of marine waters to lagoons during storms may decrease the habitat suitability for diadromous fishes. Conversely, increasing freshwater inputs, from thawing permafrost or increased precipitation, would supply fresh water and additional carbon and nutrients from terrestrial sources for use by estuarine species (Stanek et al. 2022a). Additional freshwater inputs may make more nearshore areas available to the freshwater-leaning diadromous species. Together, changes to Arctic estuarine environments could have profound effects on the make up of the community, biological function, and energy flow. Improved understanding of lagoon community structure and the drivers supporting species presence and abundance may inform the management and conservation of estuarine fish species in a rapidly changing environment.

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Author contributions SML, VRV, KHD conceived the research. SML, VRV, AES conducted field investigations and curated data. AES assisted with visualization and coding. SML analyzed the data and wrote the manuscript. All authors contributed to reviewing and editing. All authors read and approved the manuscript.

Declarations

Competing interests The authors declare that they have no competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Ethical approval Sample collection and animal handling were conducted in accordance with the Animal Care and Use Policy of the Institutional Animal Care and Use Committee (IACUC), U.S. Geological Survey Alaska Science Center (2017-07).

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