

## RESEARCH ARTICLE

# Shifts in the composition and distribution of Pacific Arctic larval fish assemblages in response to rapid ecosystem change

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## Abstract

The Pacific Arctic marine ecosystem has undergone rapid changes in recent years due to ocean warming, sea ice loss, and increased northward transport of Pacific-origin waters into the Arctic. These climate-mediated changes have been linked to range shifts of juvenile and adult subarctic (boreal) and Arctic fish populations, though it is unclear whether distributional changes are also occurring during the early life stages. We analyzed larval fish abundance and distribution data sampled in late summer from 2010 to 2019 in two interconnected Pacific Arctic ecosystems: the northern Bering Sea and Chukchi Sea, to determine whether recent warming and loss of sea ice has restricted habitat for Arctic species and altered larval fish assemblage composition from Arctic- to boreal-associated taxa. Multivariate analyses revealed the presence of three distinct multi-species assemblages across all years: (1) a boreal assemblage dominated by yellowfin sole (*Limanda aspera*), capelin (*Mallotus catervarius*), and wall-eye pollock (*Gadus chalcogrammus*); (2) an Arctic assemblage composed of Arctic cod (*Boreogadus saida*) and other common Arctic species; and (3) a mixed assemblage composed of the dominant species from the other two assemblages. We found that the wind- and current-driven northward advection of warmer, subarctic waters and the unprecedented low-ice conditions observed in the northern Bering and Chukchi seas beginning in 2017 and persisting into 2018 and 2019 have precipitated community-wide shifts, with the boreal larval fish assemblage expanding northward and offshore and the Arctic assemblage retreating poleward. We conclude that Arctic warming is most significantly driving changes in abundance at the leading and trailing edges of the Chukchi Sea larval fish community as boreal species increase in abundance and Arctic species decline. Our analyses document how quickly larval fish assemblages respond to environmental change and reveal that the impacts of Arctic borealization on fish community composition spans multiple life stages over large spatial scales.

## KEYWORDS

Arctic, borealization, Chukchi Sea, distribution shifts, ecosystem change, ichthyoplankton, larval fish communities, northern Bering Sea

## 1 | INTRODUCTION

Climate change and concomitant ocean warming are driving rapid poleward shifts of many marine species that quickly alter their distributions to remain within their preferred thermal and environmental conditions (Cheung et al., 2013; Simpson et al., 2011). Shifts in marine species distributions are particularly rapid and apparent in the Arctic, which has experienced warming at greater than twice the rate of the global average in recent decades (Danielson et al., 2020; Overland et al., 2018; Rantanen et al., 2022). The interplay of localized ocean warming, sea ice loss (Drinkwater et al., 2021), and increasing advection of subarctic waters into both the Atlantic Arctic and Pacific Arctic (Hunt et al., 2016; Woodgate, 2018) has culminated in declines in geographic range and biomass of Arctic marine species (Eriksen et al., 2015; Hop & Gjørseter, 2013) and northward shifts of subarctic (boreal) species into the Arctic from the Atlantic (Fosshiem et al., 2015; Husson et al., 2022) and Pacific Oceans (Marsh et al., 2020; Mueter & Litzow, 2008). This combination of factors has contributed to the reorganization of the Arctic toward a more physically and biologically temperate state, collectively known as the “borealization” of the Arctic (Mueter et al., 2021; Polyakov et al., 2020).

In the Pacific Arctic, which encompasses the Chukchi Sea and northern Bering Sea (>60°N), marine fish communities are strongly influenced by the seasonal advance and retreat of sea ice (Drinkwater et al., 2010; Grebmeier, Cooper, et al., 2006). Ecosystem transformation stemming from sea ice loss and unprecedented warming of the region, particularly from 2017 to 2019 (Baker, Kivva, et al., 2020; Stabeno & Bell, 2019; Thoman et al., 2020), is leading to the breakdown of the north–south boundaries delineating Arctic and subarctic environments (Huntington et al., 2020). In response, juveniles and adults of several boreal fish species such as walleye pollock (*Gadus chalcogrammus*, hereafter pollock), Pacific cod (*Gadus macrocephalus*), and northern rock sole (*Lepidopsetta polyxystra*) have moved northward into the northern Bering and southern Chukchi seas (Eisner et al., 2020; Spies et al., 2019; Stevenson & Lauth, 2019; Thorson et al., 2019), despite their historical associations with the eastern Bering Sea. In contrast, Arctic fish species such as Arctic cod (*Boreogadus saida*, also referred to as polar cod) and small (<15 cm) benthivorous fishes (Norcross et al., 2013), historically associated with the northern Bering and Chukchi seas, are retreating poleward in response to rising ocean temperatures and a receding ice edge (Baker, 2021; Marsh et al., 2020; Marsh & Mueter, 2019). Distributional shifts of juvenile and adult fish populations in the Pacific Arctic are becoming increasingly well documented, yet the impacts of the recent and abrupt ecosystem-wide changes of 2017–2019 on the earliest life stages (particularly larvae) remain uncertain.

The influence of environmental change on the larval stage of life can provide important insights into potential vulnerabilities of marine fish species and assemblages in response to Arctic borealization and climate change. Egg and larval production can be indicative of local spawning activity for many pelagic fish species and can be utilized as a proxy for estimating the abundance and distribution of adult

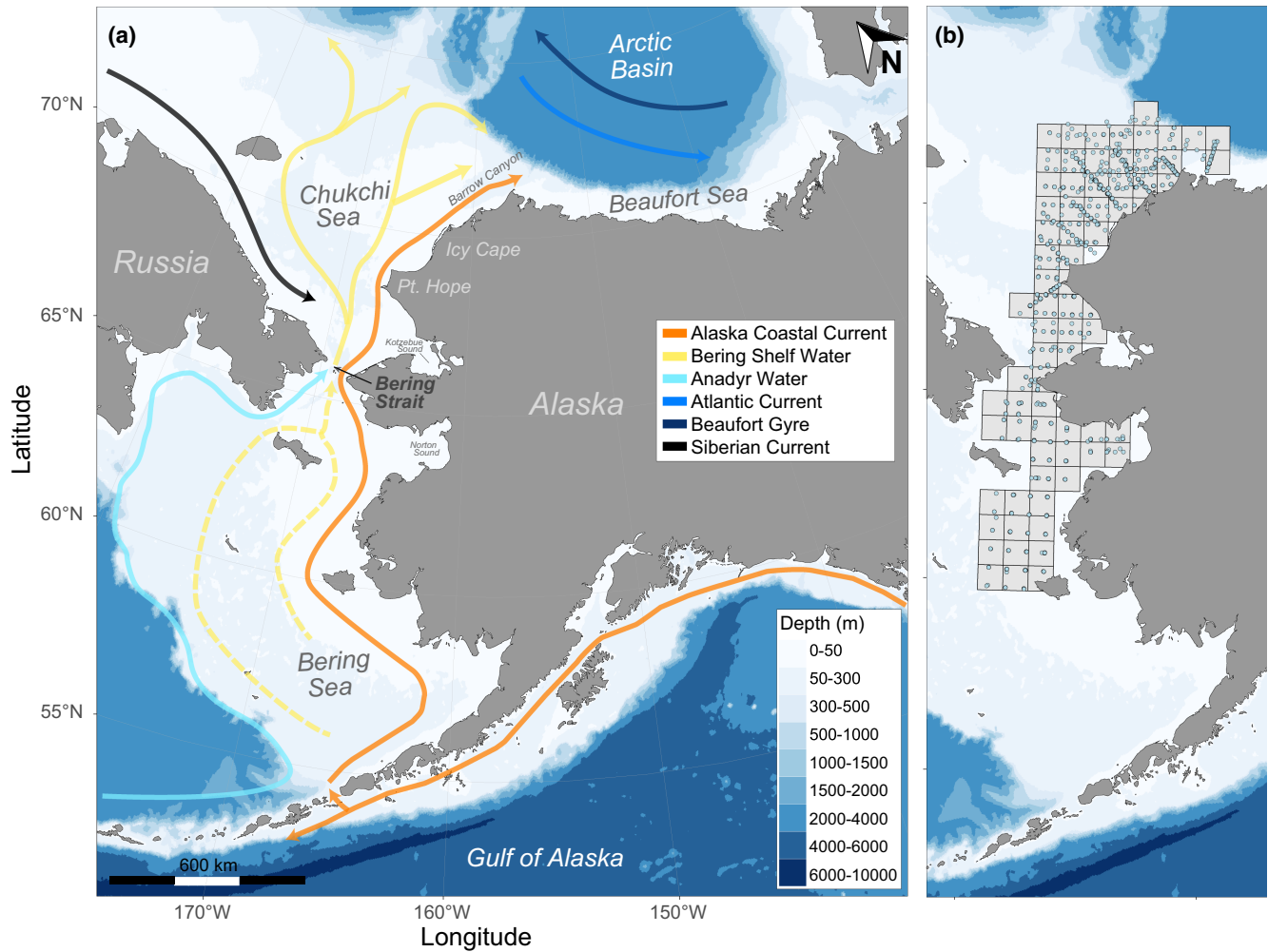
spawning stocks (Lasker, 1985; Ralston et al., 2003). This attribute is inherently useful because seasonal ice cover and a lack of commercial fishing have impeded consistent, long-term monitoring of adult fish populations in the Chukchi Sea. Within a warming Pacific Arctic, boreal fish populations are expected to continue expanding northward, while Arctic species may retreat poleward to remain within their preferred thermal habitat (Hollowed et al., 2013). This should result in an increase in spawning and egg and larval production of boreal species in the Arctic and potentially a decrease in Arctic fish eggs and larvae. Ichthyoplankton analyses can help elucidate the magnitude, extent, and likelihood of persistence of boreal species within a new habitat, particularly where adult species data are lacking. In addition, due to their small size and limited swimming ability, pelagic marine fish larvae are strongly influenced by the prevailing oceanography (Duffy-Anderson et al., 2006; Norcross et al., 2010; Siddon et al., 2011) and thus ichthyoplankton abundance and distribution dynamics not only provide insight into future recruitment potential for adult fish stocks (Houde, 2009), but also serve as early indicators of range expansions or contractions in response to large-scale environmental changes (Brodeur et al., 2008).

To assess the impacts of Arctic ecosystem change on the early life stages of marine fish communities in the northern Bering and Chukchi seas, we examined a 10-year time-series (2010–2019) of ichthyoplankton data that encompassed a period of warmer (2017–2019) and relatively colder (2012–2013) climate conditions. Specifically, we sought to (1) characterize the spatial and temporal distribution of larval fish assemblages in the northern Bering and Chukchi seas; (2) identify environmental drivers that influence Pacific Arctic larval fish assemblages in warm and cold climate conditions; and (3) assess species-specific abundance responses to Arctic warming in the Chukchi Sea. Ocean warming, sea ice loss, and associated changes in oceanographic circulation (stronger northward advection into the Chukchi Sea) are expected to continue yet the impacts on Arctic fish assemblages remain poorly understood. Developing a clearer understanding of how the early life stages of fishes respond to this oceanographic variability will help address some of these knowledge gaps and enable better evaluation of future climate change impacts on species' distributions and ecosystem structure in a rapidly changing Arctic.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

The Pacific Arctic was delineated by a 60°N southern boundary that encompassed the northern Bering Sea, the Bering Strait (66°N), and the broad, mostly shallow (<60 m deep; Hunt et al., 2013) Chukchi Sea continental shelf (≥66°N; Figure 1a). The northern extent of the study region stretched to the shelf break just beyond Barrow Canyon (>300 m) in the northeast Chukchi Sea. The narrow Bering Strait connects the North Pacific Ocean to the Pacific Arctic, funneling heat, freshwater, nutrients, plankton, and pelagic fishes northward from



**FIGURE 1** (a) Map of the study region showing primary current systems and typical water mass pathways in the northern Bering and Chukchi seas. (b) Locations of stations sampled for fish larvae and associated hydrographic conditions during late summer (August–September) in 2010–2019 (circles;  $n = 1114$ ) overlaid on a regular grid spanning the study region (squares;  $75 \times 75$  km per cell).

the northern Bering Sea to the southern Chukchi Sea (Woodgate et al., 2015) and driving the structure of three primary water masses: Anadyr Water, Alaskan Coastal Water, and Bering Shelf Water (Coachman et al., 1975). Cold, saline Anadyr Water is typically found along the Siberian coast and the western portion of the Bering Strait (Danielson et al., 2017). Warmer, nutrient-poor Alaskan Coastal Water, or warm Coastal Water (Danielson et al., 2020), is transported by the generally northward-flowing Alaska Coastal Current (Figure 1a) alongshore in summertime, separated from offshore waters by a strong density front (Coachman et al., 1975). Colder, nutrient-rich Bering Shelf Water, comprised of warm and cool Shelf Water (Danielson et al., 2020), flows further offshore than warm Coastal Water and eventually transforms into Chukchi Summer Water as it moves north over the Chukchi shelf. Cold Ice Melt Water can be encountered in the northwestern Chukchi Sea in summer and fall, while Modified Winter Water and Atlantic Water can be found at the edge of the Arctic basin (Danielson et al., 2020). Sea ice covers the northern Bering and Chukchi seas each winter with a maximum extent in March, and by late summer, sea ice retreats and open water occurs over most of the shelf with ice only remaining in the northern

Chukchi and Beaufort seas, reaching the minimum ice extent for the region by September (Frey et al., 2015).

## 2.2 | Environmental data collection

Field collections of environmental and ichthyoplankton datasets (Axler, 2023) were conducted by a variety of research programs across the eastern (U.S.) region of the northern Bering–Chukchi seas in August and September of 2010–2019, and included coordinated efforts by the Distributed Biological Observatory (<https://www.pmel.noaa.gov/dbo>), North Pacific Research Board's Arctic Integrated Ecosystem Research Program (Baker, Farley, et al., 2020; <http://www.nprb.org/arcticprogram>), and the National Oceanic and Atmospheric Administration's Alaska Fisheries Science Center. Hydrographic data were collected using a lowered conductivity–temperature–depth (CTD) profiler (SeaBird Electronics 911 plus) and in-line CTD system (SeaBird Electronics FastCAT SBE 49) attached to the ichthyoplankton nets to provide in situ temperature and salinity measurements from surface to bottom. If hydrographic

data were not collected at a station, data from the nearest station and closest date in time were used. CTD-derived temperature and salinity measurements at each station were averaged over the entire water column to align with ichthyoplankton sampling protocols.

To determine whether changes in larval fish assemblages were related to variable environmental conditions, we collated regional climate data sets (Axler, 2023) from the National Centers for Environmental Prediction reanalysis project (<https://www.esrl.noaa.gov/psd/cgi-bin/data/timeseries/timeseries1.pl>). Monthly estimates of sea surface temperature (SST) and surface wind velocities (meridional [south–north] and zonal components [west–east],  $\text{m s}^{-1}$ ) were acquired for the northern Bering Sea (60–65.9°N, 155–170°W) and Chukchi Sea (66–74°N, 155–170°W). The National Snow and Ice Data Center provided estimates of sea ice concentration (%; Cavalieri et al., 1996; DiGirolamo et al., 2022; <https://nsidc.org/data/nsidc-0051>), sea ice area ( $\text{km}^2$ ), and sea ice extent ( $\text{km}^2$ ) (Fetterer et al., 2017; <https://nsidc.org/data/g02135/versions/3>). The ice retreat index was estimated as the time (day of year; DOY) from January 1 to July 15 when ice coverage consistently reached values below 15% in the Bering Sea based on the 7-day running mean of the daily sea ice data. Bering Strait advective transport (Sv) was acquired from a year-round subsurface Acoustic Doppler Current Profiler moored ~35 km north of the strait (Woodgate & Peralta-Ferriz, 2021). All environmental data were averaged over the period of larval fish collection for each year of the study (August and September) to provide annual estimates of late summer ocean and climate conditions for each region.

## 2.3 | Larval fish data collection

Ichthyoplankton sampling was conducted in late summer of 2010–2019 using paired 60-cm diameter bongo nets towed obliquely from the surface to a maximum depth of 300 m deep or 10 m off the bottom, whichever was shallower (only  $n = 11$  of 1114 stations [ $<1\%$ ] were  $>300$  m). In 2010–2016, a few stations were also sampled using a 1- $\text{m}^2$  Tucker trawl affixed to a sled frame that was lowered to the seafloor and towed obliquely to the surface with a messenger-based opening-closing net system (Sameoto & Jarozynski, 1976). The bongo nets and Tucker trawls were equipped with either 333- or 505- $\mu\text{m}$  mesh before switching to only 505- $\mu\text{m}$  mesh beginning in 2015. All sampling configurations were used for analysis since previous studies showed no significant differences in ichthyoplankton catch rates between these gear types and mesh sizes (Boeing & Duffy-Anderson, 2008; Shima & Bailey, 1994). Flowmeters (General Oceanics) attached to each net were used to calculate volume filtered for each net tow, enabling larval abundance estimation ( $\text{ind. } 10\text{m}^{-2}$ ; Matarese et al., 2003). Samples were preserved in 5% formalin buffered with sodium borate and seawater and identified to the lowest taxonomic level at the Plankton Sorting and Identification Center in Szczecin, Poland. Taxonomic verifications took place at the

National Oceanic and Atmospheric Administration, Alaska Fisheries Science Center in Seattle, WA, USA.

To minimize bias due to interannual differences in larval development and to obtain more consistent temporal coverage, we only included taxa identified to the species and genus level and data sampled within a restricted temporal window based on sampling consistency within each region. In the northern Bering Sea, samples for analysis were restricted to a date range from day of year (DOY) 241 (August 28) to 272 (September 29). In the Chukchi Sea, the date range was truncated to DOY 221 (August 8) to 273 (September 30). On average, the northern Bering Sea was sampled ~10 days later than the Chukchi Sea across the study period. To account for slight differences in survey date, mean DOY of sampling was included as a parameter in our partial least squares analyses (see Section 2.5) and was found to not significantly contribute to the fit of any of the models except for one.

Larval fish abundances ( $\text{ind. } 10\text{m}^{-2}$ ) were fourth-root transformed to reduce the influence of highly abundant species and to equalize variances among species (Clarke & Warwick, 2001). To further reduce bias associated with sampling effort and spatial coverage of the surveys, which varied slightly among years, we generated a regular grid spanning the northern Bering–Chukchi seas (60–74°N, 155–170°W) and averaged species abundances using all stations within each 75 × 75 km grid cell (Figure 1b). In situ temperature, salinity, and bottom depth measurements were similarly averaged by grid cell using all stations present within each cell and each grid cell was classified as a particular water mass following Danielson et al. (2020). Only grid cells that had data for at least 2 years of the 10-year time series were included. Species present in  $<1\%$  of sampling units (grid cells) were removed to eliminate bias from rarely occurring taxa.

## 2.4 | Larval fish assemblage analysis

Non-metric multidimensional scaling (NMDS) analysis was used to characterize the larval fish community for all years pooled using the gridded data ( $n = 390$  grid cells). NMDS analysis was conducted in R (version 3.6.1; R Core Team, 2021) using the “vegan” package (Oksanen et al., 2020). Dissimilarities between sample units were calculated using “metaMDS” function with the Bray–Curtis distance measure (McCune et al., 2002). Three axes were appropriate for the data set (stress  $< 0.15$ ) and the greatest variation in the data was represented by axis 1. The final ordination was overlaid with relevant explanatory variables using the “envfit” function to show linear relationships (Pearson's correlations) with ordination axes. Variables significantly related to NMDS axes ( $p < .05$ ) were presented with vectors showing the direction of the relationship and strength of the correlation. Measures of fit (i.e.,  $R^2$ ) were used to evaluate variation in the overall species ordination explained by each environmental variable. To indicate the distribution of species across temperature, a two-dimensional smooth surface contour of in situ water temperature was fit to the ordination space using the “ordisurf” function, which plots thin-plate splines

from a generalized additive model (GAM; Marra & Wood, 2011; Wood, 2003).

## 2.5 | Environmental determinants of Pacific Arctic larval fish assemblages

To determine whether distinct larval fish assemblages were associated with particular ocean and climate conditions, the NMDS axis scores for each grid cell were used as numerical response variables and in situ water temperature ( $^{\circ}\text{C}$ ), salinity, and bottom depth (m) as predictor variables in a regression tree analysis using the “rpart” package (Breiman et al., 1984; Therneau & Atkinson, 2019). Pairwise correlation coefficients (Pearson's) among covariates included in the analysis were assessed according to Zuur et al. (2010) and ranged from 0.25 to 0.51, while observed variance inflation factors were all below established threshold values for collinearity ( $<3$ ; Zuur et al., 2010). Resulting trees were pruned to minimize misclassification error and model complexity using 10-fold cross-validation (De'ath & Fabricius, 2000; Loh, 2011). Each NMDS axis was modeled separately, but axis 2 and axis 3 scores were uninformative (no splits) and likely represent assemblage characteristics that were associated with environmental variables unaccounted for in our conceptual model. Axis 1 scores from the pruned regression tree resulted in three distinct leaves, hereafter referred to as larval fish assemblages. To determine the species composition by assemblage type, the average contribution (%) of all individual species to each assemblage was calculated across all years pooled.

To evaluate potential spatial shifts in assemblages over time while accounting for the heterogeneity of the data set, each  $75 \times 75$  km grid cell was classified according to the assemblage affiliations of the stations located in the cells. For grid cells where net tows and environmental sampling were performed but no fish were caught ( $n=73$  across all years), the final pruned regression tree model was used to predict fish assemblage type for each grid cell based on the associated environmental data. To set a conservative threshold for the remaining missing grid cells, only years that had data for  $\geq 60\%$  of the grid cells were included in the following analyses, resulting in the exclusion of 2010–2011 as well as 2014–2016 due to low sampling effort and inconsistent spatial coverage. Similar to the methodology of others (e.g., Fossheim et al., 2015), cells missing stations (14–39% of grid cells in the remaining years) were assigned the assemblage type (boreal, mixed, or Arctic) from the closest nearby grid cell using the midpoint coordinates of the cells for the nearest neighbor calculations (Figure S1). The now complete matrix was analyzed for changes in latitudinal distribution ( $^{\circ}\text{N}$ ) and the proportion of area covered (%) relative to the total area considered for each assemblage in focal years (2012–2013, 2017–2019). In addition, the center of distribution (COD; average latitude and longitude) of each assemblage was compared between warm (2018–2019) and cold years (2012–2013). Warm and cold year designations for the northern Bering and Chukchi seas were based on previous literature (Huntington

et al., 2020) and corroborated by regional estimates of SST being  $\sim 0.5$ – $2^{\circ}\text{C}$  above or below the time-series average (2010–2019) in both surveyed regions. Finally, the frequency of occurrence (%) of fish assemblage type was calculated for each water mass by region (northern Bering Sea or Chukchi Sea) across all years pooled.

Partial least squares regression (PLSR) was used to summarize the shared variability across environmental covariates and identify environmental drivers of the mean latitudinal distribution ( $^{\circ}\text{N}$ ) and areal coverage (%) of each larval fish assemblage across focal years. PLSR is a multivariate modeling approach that searches for a set of components (latent variables) and performs a simultaneous dimension reduction such that the latent variables of the independent data matrix are uncorrelated with one another, but are correlated with the dependent data set (Abdi, 2003; Geladi & Kowalski, 1986). This method is particularly useful when predictor variables are highly correlated (i.e.,  $r > 0.70$ ) and when there are few observations relative to the number of predictor variables (Carrascal et al., 2009). We defined 10 predictor variables indicative of environmental conditions for each of the focal years (2012–2013, 2017–2019): northern Bering and Chukchi SSTs, Bering Strait advection (Sv), northern Bering and Chukchi meridional (northward) and zonal (eastward) surface wind velocities ( $\text{m s}^{-1}$ ), spring Bering Sea ice retreat index (d), and late summer Chukchi Sea ice area and extent ( $\text{km}^2$ ). Mean DOY of sampling was also included in each model to account for any potential differences in species occurrence due to slight differences in survey date. Separate PLSR models were developed for areal coverage and latitudinal distribution of each larval fish assemblage. Because PLSR produces a reduced dimension linear representation of the independent data set, each component can be used to model the biological parameter (dependent variable) using simple linear regression (Takahashi et al., 2012; Wells et al., 2008). The correlation coefficients ( $R^2$ ) and loadings of each predictor variable onto the first PLSR component were used to assess the relationship (positive or negative) with the dependent variable (Wells et al., 2008). Square weights ( $\text{weight}^2$ ) were used to assess the amount of variation in areal coverage and latitudinal distribution accounted for by a particular predictor variable and similar to Carrascal et al. (2009) and Fennie et al. (2023), we defined “significant” predictor variables as those explaining more than 15% of the original variance in the dependent variable ( $\text{weight}^2 \geq 0.15$ ).

Finally, to assess the impacts of warming in the Arctic on individual species over the entire study period (2010–2019), we subset the data to the northeast Chukchi Sea only ( $\geq 67.5^{\circ}\text{N}$ ) and calculated nonparametric Spearman's rank correlation coefficients to quantify the association of mean annual abundance with in situ temperature data for each  $75 \times 75$  km grid cell ( $n=211$ ). One sample  $t$ -tests were used to identify species where the correlation coefficients were significantly different from zero, indicating a positive or negative relationship with in situ temperature. Significance was determined to be  $p < .05$  using the “rcorr” function in the “Hmisc” package in R (Harrell et al., 2021) and taxa were sorted based on their mean latitudinal distribution in cold years (i.e., 2012–2013).

### 3 | RESULTS

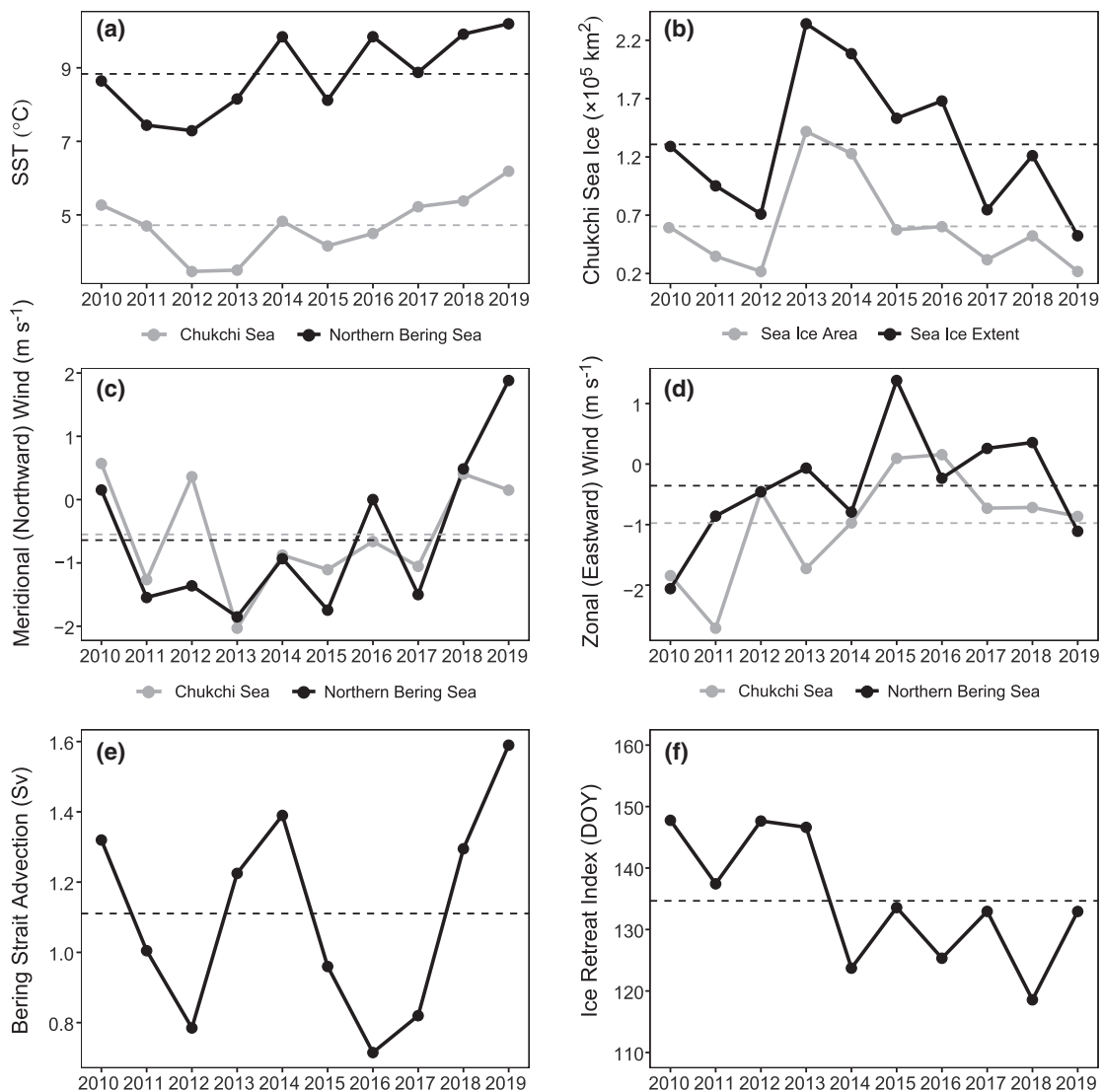
#### 3.1 | Environmental conditions in the Pacific Arctic in late summer (2010–2019)

Environmental conditions in late summer varied greatly over the 10-year study period in the northern Bering–Chukchi Sea marine ecosystem. SSTs fluctuated during the first 6 years of the time series but increased in 2017 and were  $-0.5$ – $1.5^{\circ}\text{C}$  above the time-series average in 2018 and 2019 (warm years), yet  $-1$ – $2^{\circ}\text{C}$  below average in 2012 and 2013 (cold years) in both surveyed regions (Figure 2a). Sea ice area and extent ( $\text{km}^2$ ) were both below average in recent warm years (2017–2019) and above average in the cold year of 2013 (Figure 2b). Annual estimates of surface wind magnitude and direction varied widely among regions and years and though winds were generally light and variable (typical for the late summer season), recent warm years (2018–2019) were notably characterized by

slightly stronger meridional (northward-flowing) winds in both regions (Figure 2c). Regional zonal winds (eastward) were similar to the time-series averages in both warm and cold years (Figure 2d). Mean northward advective transport (Sv) through the Bering Strait was above average in warm years (2018–2019) and below average in the cold year of 2012 (Figure 2e). The ice retreat index varied (Figure 2f) but showed sea ice to retreat increasingly earlier in the latter half of the study period (e.g., late April to early May [DOY 119–134]) relative to the start of the time series in 2010 (e.g., late May [DOY 148]).

#### 3.2 | Larval fish assemblage composition and structure

NMDS ordination of the gridded larval fish species matrix resulted in a three-dimensional solution that was sufficient to explain most of the variability in the data set ( $R^2 = .92$ , final stress = 0.14



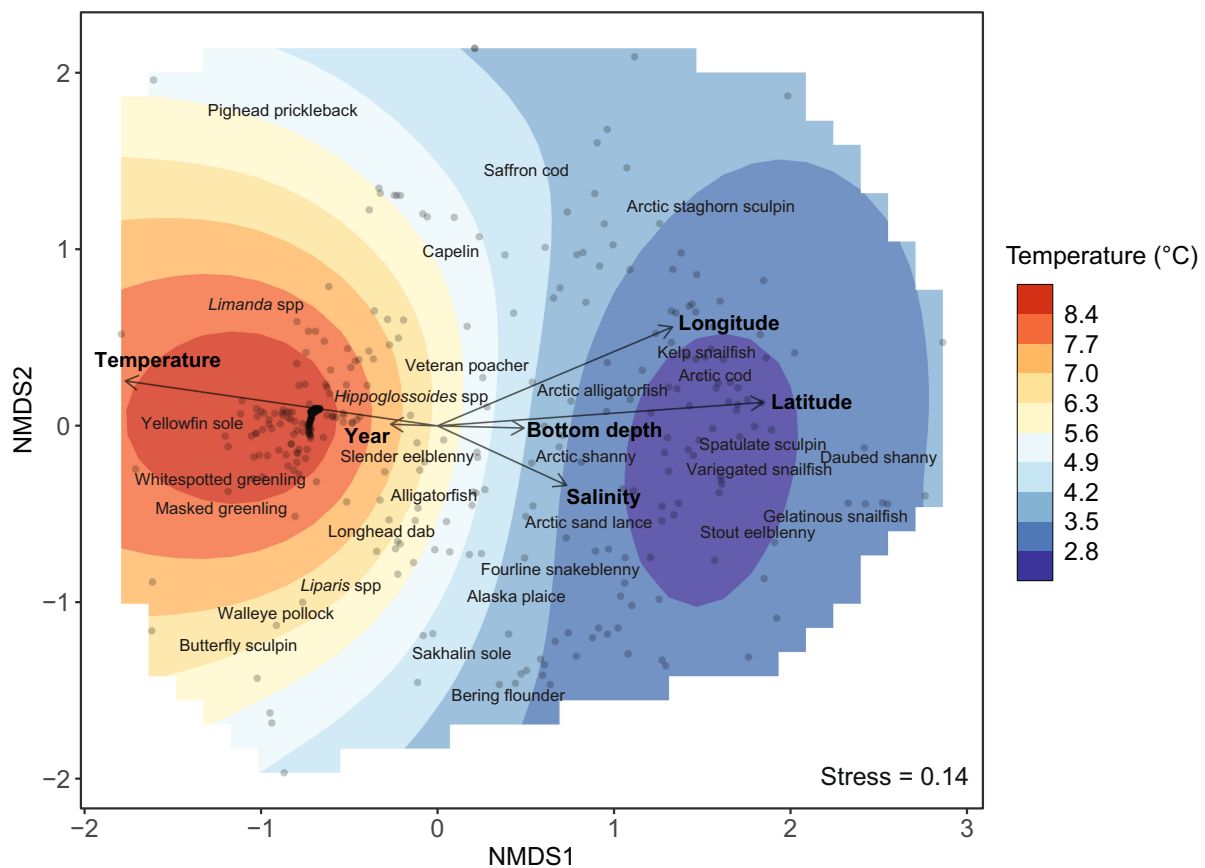
**FIGURE 2** Mean environmental conditions (a–f) during late summer (August–September averaged) in the northern Bering–Chukchi Sea region (2010–2019). The dashed line shows the 10-year time-series average of each variable. SST, Sea surface temperature; Sv, Sverdrup; DOY, day of year.

after 352 iterations of real data). Variability in NMDS axis 1 was strongly associated with in situ temperature ( $R^2 = .51$ ) as indicated by the temperature gradient from low (min =  $-1.19^\circ\text{C}$ , blue) to high (max =  $13.76^\circ\text{C}$ , red; Figure 3). Species with an affinity for warmer water such as yellowfin sole (*Limanda aspera*) and whitespotted greenling (*Hexagrammos stelleri*) ordinated toward the negative side of axis 1 while species with an affinity for colder water (e.g., Arctic cod) ordinated toward the positive side of axis 1.

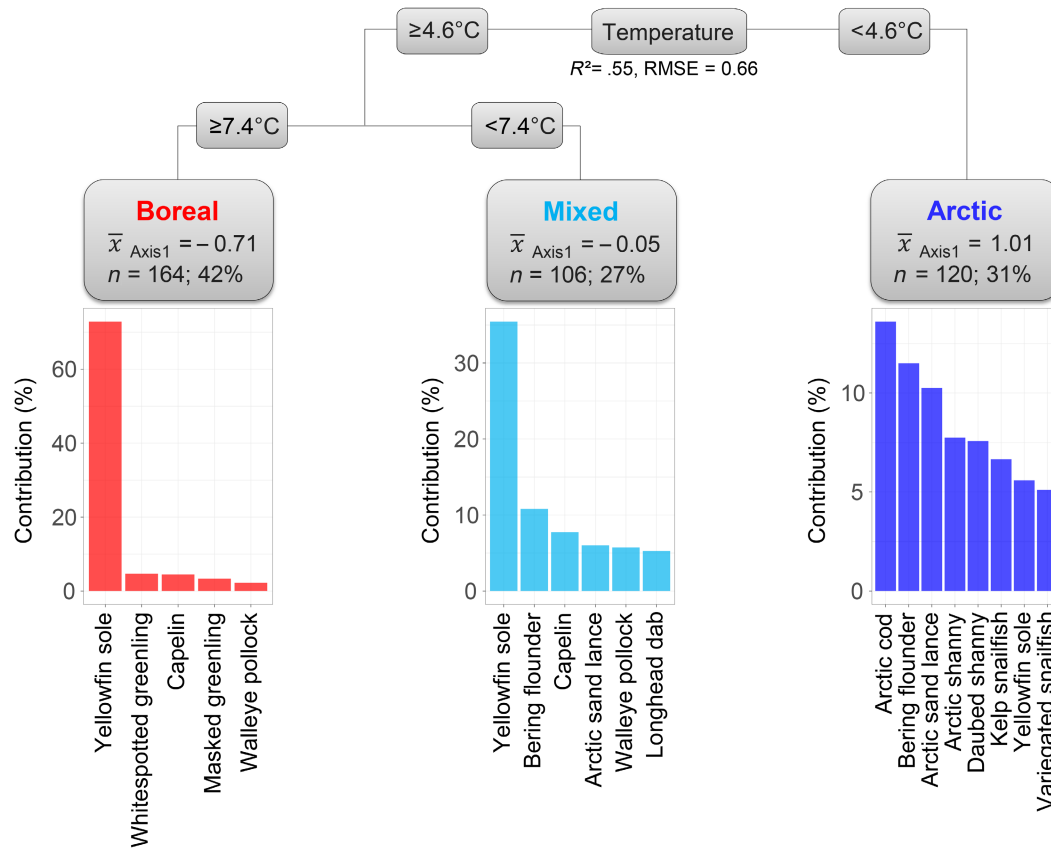
Regression tree analysis revealed in situ water temperature to be the only significant predictor of larval fish assemblage type (of the variables analyzed) and the resulting pruned regression tree predicted three distinct, multispecies assemblages across all years ( $R^2 = .55$ , RMSE = 0.66, Figure 4). The first regression tree split was represented by a temperature threshold where 69% of samples were associated with temperatures  $\geq 4.6^\circ\text{C}$  and the remaining 31% of samples ( $n = 120$ ) with temperatures  $< 4.6^\circ\text{C}$  (hereafter, called the “Arctic” assemblage). The second split in the regression tree distinguished 42% of the samples ( $n = 164$ ) to be associated with relatively high temperatures ( $\geq 7.4^\circ\text{C}$ ; hereafter called the “boreal” assemblage), while the remaining 27% of samples ( $n = 106$ ) were

associated with moderate temperatures ( $4.6\text{--}7.4^\circ\text{C}$ ; hereafter called the “mixed” assemblage).

The boreal assemblage was widely prevalent throughout the northern Bering Sea and in the nearshore waters of our surveyed area, including Norton Sound and Kotzebue Sound (Figure 5). This assemblage inhabited the warmest, shallowest, and freshest waters on average (mean  $\pm$  SD) across all years (in situ temperature =  $9.6 \pm 1.47^\circ\text{C}$ , bottom depth =  $26.8 \pm 7.9$  m, salinity =  $29.9 \pm 1.7$ ) and was primarily associated with warm Coastal Water ( $\sim 65\text{--}75\%$  of the surveyed area by region; Table 1), which was widespread throughout the nearshore northern Bering and southern Chukchi seas (Figure S2). This lower-latitude assemblage was dominated by yellowfin sole, which comprised 72.9% of the assemblage in all years, while whitespotted greenling, capelin (*Mallotus catervarius*), masked greenling (*Hexagrammos octogrammus*), and pollock contributed an additional 14.8% to the assemblage structure (Figure 4; see Table S1 for complete species composition). The boreal assemblage appeared mostly inshore in 2012 and 2013 (cold years), but shifted its latitudinal distribution ( $^\circ\text{N}$ ) slightly northward and expanded in areal coverage (%) further offshore in warm years, particularly in



**FIGURE 3** Non-metric multidimensional scaling (NMDS) ordination of larval fish species composition in the northern Bering and Chukchi seas using a Bray–Curtis distance measure of the gridded abundances during late summer 2010–2019 ( $n = 390$  grid cells, grey circles). Environmental vectors for water temperature, salinity, bottom depth, year, longitude, and latitude show the direction of maximum association with the ordination axes and the vector length corresponds with the strength of the correlation. A generalized additive model (GAM) of temperature was fit to the ordination space using a two-dimensional smooth surface contour (high temperature = red, low temperature = blue).



**FIGURE 4** Pruned multivariate regression tree analysis of the non-metric multidimensional scaling (NMDS) axis 1 scores of larval fish abundances (ind.  $10\text{ m}^{-2}$ ) revealed three distinct assemblages in the northern Bering–Chukchi Sea region during late summer (2010–2019): boreal (red), mixed (light blue), and Arctic (dark blue). Assemblage type was significantly explained by in situ temperature (cross-validated error = 0.018). Values in each assemblage box represent mean NMDS axis 1 scores and the number and percentage of samples allocated to each assemblage type. Bar plots show the relative contribution (%) of different larval fish species to each assemblage. Only species contributing  $\geq 2\%$  to the boreal assemblage and  $\geq 5\%$  to the mixed and Arctic assemblages are shown here. See Table S1 for the full species composition of each assemblage.

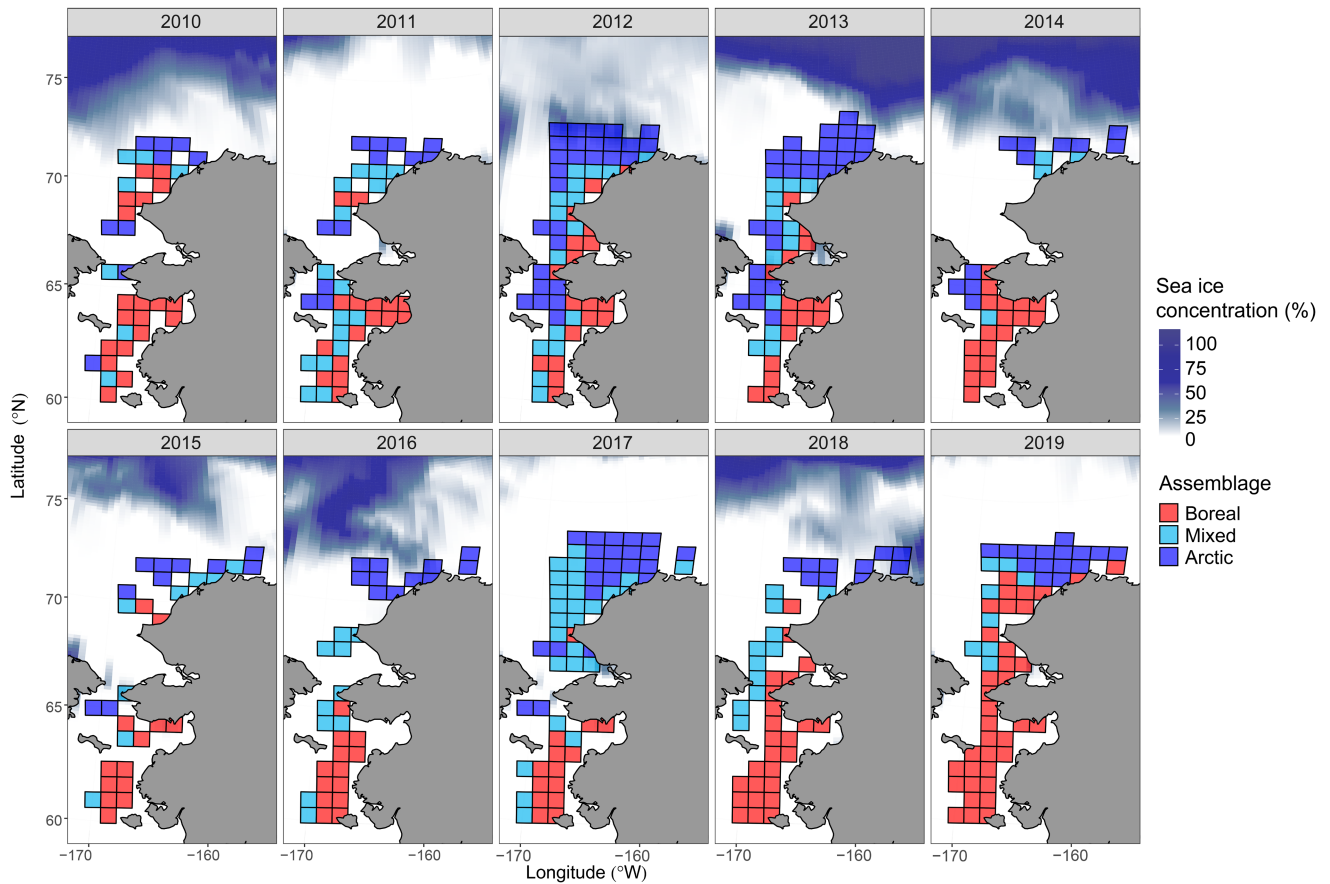
2019 (Figure 6a,b). Furthermore, the assemblage's COD shifted approximately 75 km northward from the northern Bering Sea toward the southern Chukchi Sea between averaged cold (2012–2013) and warm years (2018–2019; Figure 6c).

In contrast, the Arctic assemblage was predominantly distributed in the northeast Chukchi Sea and closest to the ice edge (Figure 5), inhabiting the coldest, deepest, and most saline waters on average (in situ temperature =  $2.3 \pm 1.7^\circ\text{C}$ , bottom depth =  $99.7 \pm 201.1\text{ m}$ , salinity =  $31.6 \pm 0.7$ ). In the Chukchi Sea, the Arctic assemblage was primarily associated with cool Shelf Water (which accounted for  $\sim 37\%$  of surveyed area), warm Shelf Water ( $\sim 37\%$ ), Ice Melt/coastal Water ( $\sim 11\%$ ), and Modified Winter Water ( $\sim 8\%$ ; Table 1). The primary contributors to this higher-latitude, cold water assemblage were Arctic cod, Bering flounder (*Hippoglossoides robustus*), Arctic sand lance (*Ammodytes hexapterus*), Arctic shanny (*Stichaeus punctatus*), daubed shanny (*Leptoclinus maculatus*), and kelp snailfish (*Liparis tunicatus*), altogether contributing 57.4% to the assemblage structure (Figure 4). In most years, the Arctic assemblage's range extended south through the Bering Strait and into the northern

Bering Sea, yet in the two warmest years (2018–2019) its range was constrained to the northeastern Chukchi Sea (Figure 6a,b). On average, the Arctic assemblage's COD shifted  $\sim 253\text{ km}$  northeastward between cold and warm years (Figure 6c).

The mixed assemblage generally inhabited slightly cooler waters further offshore and north of the boreal assemblage (Figure 5), often at the interface of the boreal and Arctic assemblages (in situ temperature =  $6.0 \pm 0.8^\circ\text{C}$ , bottom depth =  $39.8 \pm 8.6\text{ m}$ , salinity =  $31.3 \pm 1.1$ ) in warm Shelf Water ( $\sim 76\text{--}87\%$  of surveyed area; Table 1). Accordingly, the mixed assemblage was composed of dominant taxa from both the boreal and Arctic assemblages, including yellowfin sole, Bering flounder, capelin, pollock, Arctic sand lance, and longhead dab (*Limanda proboscidea*), which comprised 71.0% of the assemblage structure (Figure 4). The mixed assemblage displayed its highest areal coverage in 2017 before decreasing the following two (warm) years (Figure 6b). Despite having a smaller distributional range in 2018 and 2019, the mixed assemblage's COD shifted  $\sim 310\text{ km}$  northeastwards relative to cold (2012–2013) years (Figure 6c).





**FIGURE 5** Annual distributions of the larval fish assemblage identified for each grid cell (75 × 75 km) during late summer (August–September) in the northern Bering–Chukchi Sea region. The boreal assemblage is shown in red, the mixed assemblage in light blue, and the Arctic assemblage in dark blue. Blue shading shows the mean sea ice concentration (%) at the approximate time of sampling each year.

**TABLE 1** Frequency of occurrence (%) of each larval fish assemblage (boreal, mixed, and Arctic) in each water mass by region (northern Bering Sea or Chukchi Sea) during late summer 2010–2019.

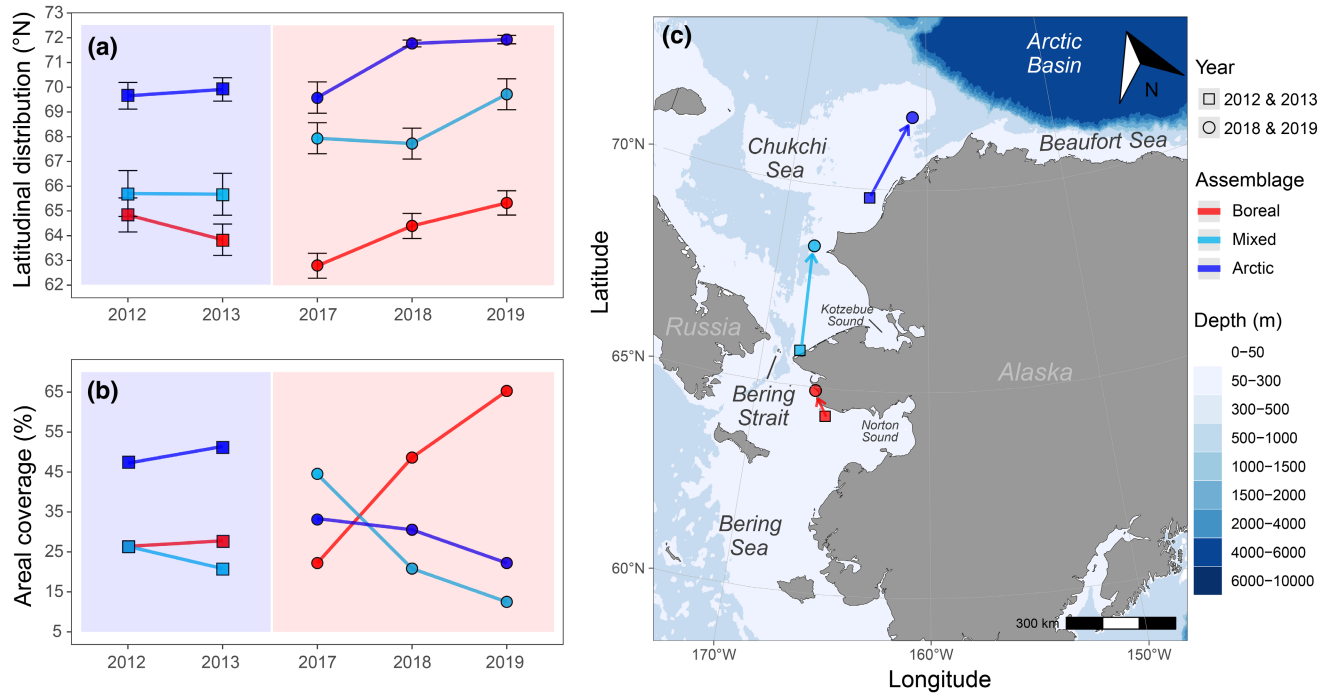
Water mass type	Northern Bering Sea			Chukchi Sea		
	Boreal	Mixed	Arctic	Boreal	Mixed	Arctic
Anadyr Water	0	0	4.0	0	0	3.0
Atlantic Water	0	0	0	0	0	0.8
Cool Shelf Water	0	0	19.2	0	0	36.8
Ice Melt Water/cool Coastal Water	0	0	0	0	0	11.4
Modified Winter Water	0	0	0	0	0	8.4
Warm Coastal Water	74.6	24.1	0	65.2	13.4	3.0
Warm Shelf Water	25.4	75.9	76.8	34.8	86.6	36.6

Note: Water mass designations were identified using gridded water column temperature (°C) and salinity following Danielson et al. (2020).

### 3.3 | Environmental determinants of larval fish assemblage distributions in the Pacific Arctic

Partial least squares regression revealed a significant relationship between the fit of the first PLSR component (which explained the greatest variability in the data set) to the areal coverage (%) of the boreal assemblage ( $R^2=.85$ ,  $p=.017$ ), mixed assemblage ( $R^2=.77$ ,  $p=.031$ ), and Arctic assemblage ( $R^2=.94$ ,  $p=.004$ ; Table 2). The

boreal assemblage's areal coverage was significantly ( $\text{weight}^2 \geq 0.15$ ) explained by the presence of northward winds in the northern Bering Sea, increased northward advection via the Bering Strait, and warmer northern Bering Sea SSTs (Figure 7a, Table 3). In contrast, the Arctic assemblage's areal coverage receded in those warm, highly advective years, instead expanding in years with colder SSTs, later spring ice retreat, and greater late summer sea ice area and extent (Figure 7c, Table 3). The mixed assemblage's areal coverage



**FIGURE 6** (a) Mean ( $\pm$ SE) latitudinal distribution ( $^{\circ}$ N) and (b) areal coverage (%) of each larval fish assemblage in the northern Bering–Chukchi Sea region during late summer in the focal years of 2012–2013 (blue panels; colder climate conditions) and 2017–2019 (red panels; warmer climate conditions). (c) Shifts in the centers of distribution (COD) of each larval fish assemblage between cold years (2012–2013; squares) and the two warmest years (2018–2019; circles). Vectors show the mean shift in latitude and longitude for the boreal (red), mixed (light blue), and Arctic (dark blue) assemblages.

**TABLE 2** Partial least squares regression (PLSR) model results relating each larval fish assemblage's areal coverage (%) to the first PLSR component.

Variable	Estimate	SE	t-value	Pr(> t )	R <sup>2</sup>	F	p
Boreal areal coverage (%)							
(Intercept)	38.1	3.20	11.9	0.001	.85	23.2	.017
t1	8.06	1.67	4.82	0.017	—	—	—
Mixed areal coverage (%)							
(Intercept)	25.0	2.54	9.84	0.002	.77	14.7	.031
t1	6.85	1.79	3.83	0.031	—	—	—
Arctic areal coverage (%)							
(Intercept)	36.9	1.31	28.3	<0.001	.94	65.6	.004
t1	5.25	0.65	8.09	0.004	—	—	—

Note: Statistics include model estimates, standard error (SE), test statistic (t-value), probability of the test statistic (Pr(>t)), and model coefficient of determination (R<sup>2</sup>), F-statistic (F), and probability of F (p).

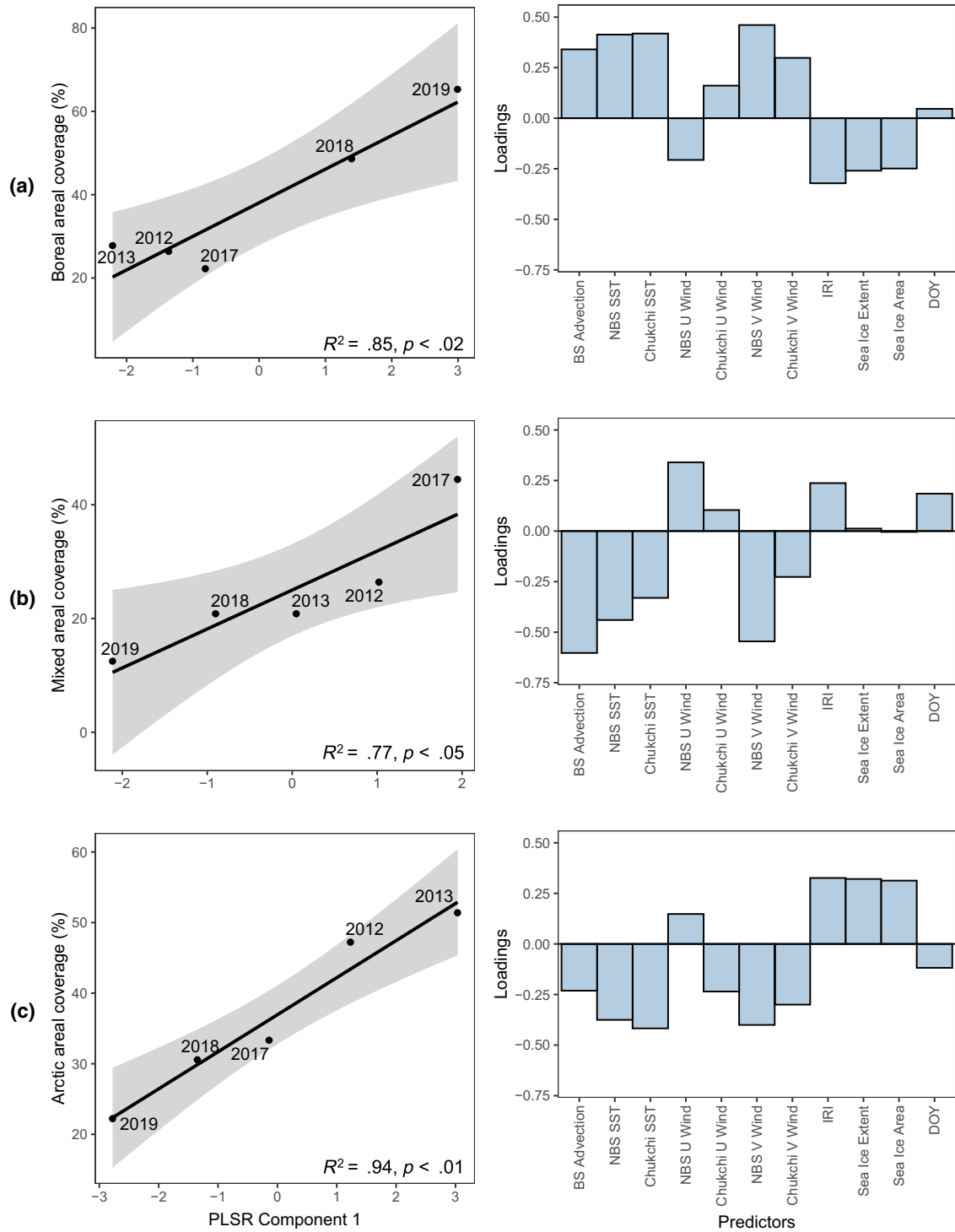
increased in years of stronger southward and eastward winds and lower advection (Figure 7b, Table 3).

Mean latitudinal distribution ( $^{\circ}$ N) was similarly modeled for each larval fish assemblage and a significant relationship was found between the PLSR first component and the latitudinal distribution of the mixed (R<sup>2</sup> = .88, p = .012) and Arctic assemblage (R<sup>2</sup> = .85, p = .017), though not for the boreal assemblage (R<sup>2</sup> = .60, p = .078; Table 4). In general, however, the PLSR loadings showed a similar pattern across all three assemblages in that latitudinal distributions increased in warm years characterized by north-northeastward-flowing winds

and advection, an earlier spring ice retreat, and low summer sea ice area and extent (Figure 8a–c, Table 5).

### 3.4 | Species-level abundance responses to Pacific Arctic warming

Spearman rank correlation coefficients of individual species-level abundance responses to temperature revealed that Pacific Arctic warming is most significantly driving changes at the leading and



**FIGURE 7** Panels on the left show the fits of the mean annual areal coverage (%) of the (a) boreal, (b) mixed, and (c) Arctic larval fish assemblages to the first component score calculated from partial least squares regression (PLSR). Panels on the right show the loadings of the predictor variables on the first PLSR component. NBS, Northern Bering Sea; BS, Bering Strait; U Wind, Zonal (eastward) wind component, V Wind, Meridional (northward) wind component, IRI, ice retreat index, DOY, day of year.

trailing edges of the larval fish community. In the northeast Chukchi Sea, significant positive associations between larval fish annual abundance and increasing in situ temperatures were observed for 9 of the 30 species (30%), whereas 5 species (17%) showed significant declines in abundance in response to higher water temperatures

(Figure 9). In total, ~47% ( $n = 14$  of 30) of the larval fish taxa sampled during late summer in the northeast Chukchi Sea significantly changed in abundance in response to Arctic warming over the study period (2010–2019). More specifically, lower-latitude, boreal species such as yellowfin sole, capelin, pollock, and whitespotted greenling

**TABLE 3** Correlation coefficients ( $R^2$ ), loadings, and square weights (weight<sup>2</sup>) of all predictor variables calculated using the first component score calculated from partial least squares regression (PLSR) for each larval fish assemblage's areal coverage (%).

Predictor	Boreal areal coverage (%)			Mixed areal coverage (%)			Arctic areal coverage (%)		
	$R^2$	Loading	Weight <sup>2</sup>	$R^2$	Loading	Weight <sup>2</sup>	$R^2$	Loading	Weight <sup>2</sup>
NBS V Wind	.99	0.46	<b>0.24</b>	-.87	-0.55	<b>0.20</b>	-.90	-0.40	<b>0.15</b>
BS Advection	.73	0.34	<b>0.20</b>	-.96	-0.60	<b>0.32</b>	-.52	-0.23	0.06
NBS SST	.89	0.41	<b>0.17</b>	-.70	-0.44	0.06	-.85	-0.38	<b>0.17</b>
Chukchi SST	.90	0.42	0.14	-.53	-0.33	0.01	-.94	-0.42	<b>0.20</b>
NBS U Wind	-.44	-0.21	0.08	.54	0.34	<b>0.17</b>	.33	0.15	0.01
Chukchi V Wind	.64	0.30	0.07	-.36	-0.23	0.04	-.68	-0.30	0.05
IRI	-.69	-0.32	0.07	.38	0.24	0.00	.73	0.33	0.12
Sea Ice Extent	-.56	-0.26	0.03	.02	0.01	0.01	.72	0.32	0.09
Sea Ice Area	-.53	-0.25	0.02	-.01	0.00	0.02	.71	0.31	0.08
Chukchi U Wind	.34	0.16	0.00	.17	0.10	0.03	-.53	-0.24	0.03
DOY	.10	0.00	0.05	.29	0.14	<b>0.18</b>	-.27	0.03	-0.12

Note: Bolded values show 'significant' predictor variables (weight<sup>2</sup> ≥ 0.15) of each assemblage's areal coverage.

Abbreviations: BS, Bering Strait; DOY, day of year; IRI, ice retreat index; NBS, Northern Bering Sea; U Wind, Zonal (eastward) wind component; V Wind, Meridional (northward) wind component.

**TABLE 4** Partial least squares regression (PLSR) model results relating each larval fish assemblage's latitudinal distribution (°N) to the first PLSR component.

Variable	Estimate	SE	t-value	Pr(> t )	$R^2$	F	p
Boreal latitudinal distribution (°N)							
(Intercept)	64.2	0.28	230.9	<0.001	.60	6.94	.078
t1	0.45	0.17	2.63	0.078	—	—	—
Mixed latitudinal distribution (°N)							
(Intercept)	67.4	0.26	255.9	<0.001	.88	30.5	.012
t1	0.73	0.13	5.52	0.012	—	—	—
Arctic Latitudinal Distribution (°N)							
(Intercept)	70.6	0.21	343.3	<0.001	.85	23.2	.017
t1	0.52	0.11	4.81	0.017	—	—	—

Note: Statistics include model estimates, standard error (SE), test statistic (t-value), probability of the test statistic (Pr(>|t|)), and model coefficient of determination ( $R^2$ ), F-statistic (F), and probability of F (p).

increased in abundance in the region in response to higher temperatures, while higher-latitude, Arctic species such as Arctic cod, daubed shanny, and gelatinous snailfish decreased in response to higher temperatures. Mid-latitude species responses to warming conditions varied, but were generally far less extreme than high-latitude and low-latitude Arctic species.

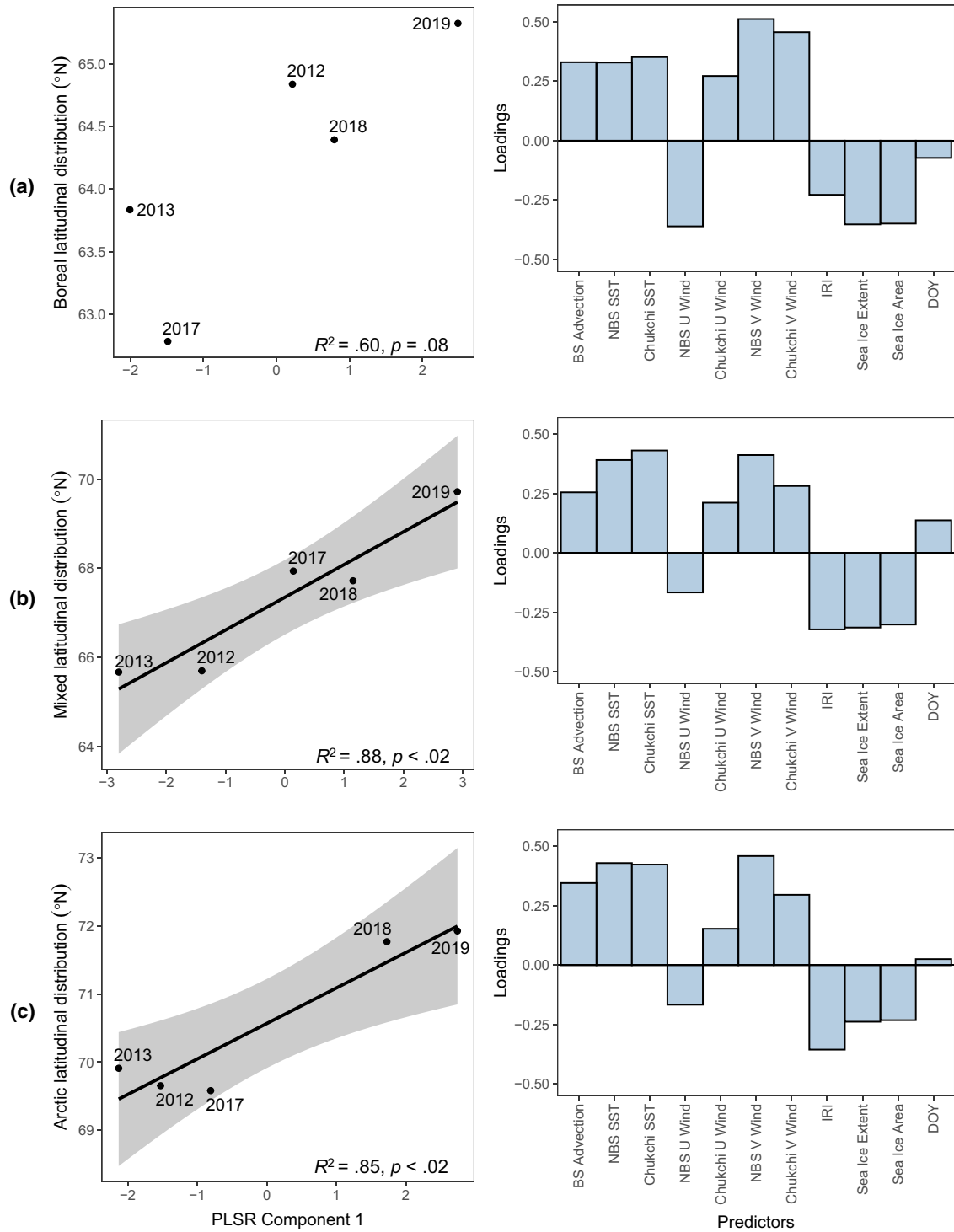
## 4 | DISCUSSION

### 4.1 | Interannual variability in larval fish assemblage distributions in the Pacific Arctic

Analyses of late summer larval fish assemblages revealed striking shifts in distribution over a decade of oceanographic variability (2010–2019) in the northern Bering and Chukchi seas. Sea ice loss

and the wind- and current-driven northward advection of warmer, subarctic waters from the northern Bering Sea expanded the range of boreal species into the Chukchi Sea and constricted spatial distributions of Arctic assemblages, resulting in mixed assemblages in some years and replacement of Arctic taxa in the warmest years. These findings concur with several recent studies, which have likewise found that the warmer seas, increased northward advection, and diminishing sea ice coverage of recent years (particularly since 2017) have perpetuated dramatic and extensive ecological shifts in communities of phytoplankton (Oziel et al., 2020), zooplankton (Huntington et al., 2020; Kimmel et al., 2023; Spear et al., 2019), juvenile and adult fishes (Baker, 2021; Eisner et al., 2020; Marsh et al., 2020; Wildes et al., 2022), and seabirds (Kuletz et al., 2020).

In all years, a warm water-associated boreal assemblage composed primarily of yellowfin sole, whitespotted greenling, capelin, masked greenling, and pollock dominated the nearshore portions of



**FIGURE 8** Panels on the left show the fits of the mean annual latitudinal distribution (°N) of the (a) boreal, (b) mixed, and (c) Arctic larval fish assemblages to the first component score calculated from partial least squares regression (PLSR). Panels on the right show the loadings of the predictor variables on the first PLSR component. NBS, Northern Bering Sea; BS, Bering Strait; U Wind, Zonal (eastward) wind component; V Wind, Meridional (northward) wind component; IRI, ice retreat index; DOY, day of year.

the northern Bering and southern Chukchi seas. These taxa have primarily boreal distributions concentrated in the North Pacific Ocean and eastern Bering Sea (Mecklenburg et al., 2018), and although some boreal species (including pollock and yellowfin sole) may move northward in summer via warm surface water masses (Barber

et al., 1997; Emelin et al., 2022), the cold bottom water temperatures of the Chukchi Sea have historically not been considered suitable spawning or feeding habitat for many of these species (Hollowed et al., 2013; Norcross et al., 2010). The boreal larval fish assemblage closely mirrored the distribution of warm water masses (i.e., warm

TABLE 5 Correlation coefficients ( $R^2$ ), loadings, and square weights (weight<sup>2</sup>) for all predictor variables calculated using the first component score calculated from partial least squares regression (PLSR) for each larval fish assemblage's latitudinal distribution (°N).

Predictor	Boreal latitudinal distribution (°N)			Mixed latitudinal distribution (°N)			Arctic latitudinal distribution (°N)		
	$R^2$	Loading	Weight <sup>2</sup>	$R^2$	Loading	Weight <sup>2</sup>	$R^2$	Loading	Weight <sup>2</sup>
Chukchi SST	.64	0.35	0.01	.96	0.43	<b>0.22</b>	.90	0.42	0.14
NBS SST	.60	0.33	0.02	.87	0.39	<b>0.18</b>	.91	0.43	<b>0.19</b>
NBS V Wind	.93	0.51	<b>0.20</b>	.91	0.41	<b>0.16</b>	.98	0.46	<b>0.22</b>
IRI	-.41	-0.23	0.00	-.71	-0.32	0.09	-.75	-0.36	0.13
BS Advection	.60	0.33	0.13	.57	0.25	0.08	.74	0.35	<b>0.19</b>
Sea Ice Extent	-.64	-0.35	0.04	-.70	-0.31	0.08	-.51	-0.24	0.01
Sea Ice Area	-.63	-0.35	0.04	-.67	-0.30	0.06	-.49	-0.23	0.01
DOY	-.13	-0.07	0.11	.30	0.14	0.06	.06	0.03	0.01
Chukchi V Wind	.83	0.46	<b>0.19</b>	.62	0.28	0.03	.63	0.30	0.07
NBS U Wind	-.65	-0.36	<b>0.25</b>	-.37	-0.17	0.03	-.35	-0.17	0.02
Chukchi U Wind	.49	0.27	0.02	.47	0.21	0.02	.33	0.15	0.00

Note: Bolded values show 'significant' predictor variables (weight<sup>2</sup> ≥ 0.15) of each assemblage's latitudinal distribution.

Abbreviations: BS, Bering Strait; DOY, day of year; IRI, ice retreat index; NBS, Northern Bering Sea; U Wind, Zonal (eastward) wind component; V Wind, Meridional (northward) wind component.

Coastal Water and Shelf Water) that originate from the Bering shelf and regularly intrude into the Chukchi Sea via the Alaska Coastal Current, yet are typically restricted to the nearshore regions of the eastern Chukchi Sea. In the two warmest years of the study period (2018 and 2019), these warm water masses expanded much further northward and offshore than usual (Danielson et al., 2020), coinciding with the largest expansion of the boreal assemblage into the northeast Chukchi Sea (as far north as 70–72°N).

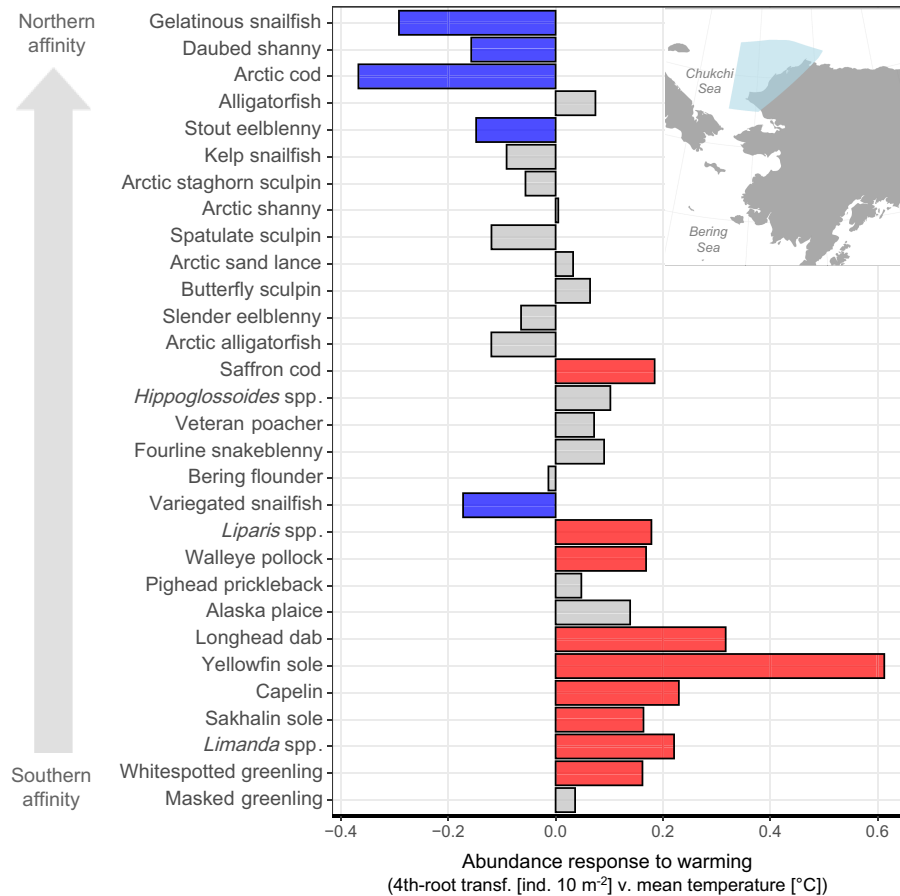
Arctic cod, Bering flounder, Arctic sand lance, Arctic shanny, and daubed shanny contributed most to the Arctic assemblage's structure, which is a typical summertime larval assemblage composition for the Chukchi Sea (Logerwell et al., 2020; Randall et al., 2019; Wyllie-Echeverria et al., 1997). The Arctic assemblage was widespread across the Chukchi shelf in the two coldest years of the study period (2012–2013) but retreated ~250 km northward in the two warmest years (2018–2019), closely tracking the distribution of colder, higher salinity water masses (e.g., Anadyr Water, cool Shelf Water, Ice Melt Water/cool Coastal Water, and Modified Winter Water) in the Chukchi Sea (Figure S2).

The mixed assemblage was comprised of a few of the most abundant boreal (e.g., yellowfin sole, capelin, pollock) and Arctic (e.g., Bering flounder, Arctic sand lance) species and most widely distributed throughout the study region in 2017, the same year that physical conditions in the Pacific Arctic shelf ecosystem underwent a dramatic warming-associated shift relative to historical conditions (Huntington et al., 2020). The prevalence of the mixed assemblage in 2017 thus likely reflected both a northward shift of boreal species as well as the persistence of Arctic species across the Chukchi shelf, resulting in a high degree of co-occurrence of Arctic and boreal taxa. Acoustic-trawl survey data likewise found higher densities of both age-0 pollock and Arctic cod co-occurring

in the Chukchi Sea in 2017 compared to previous years (Levine et al., 2023). Yet while the anomalous environmental changes that began in 2017 persisted into 2018 and 2019 (Huntington et al., 2020), 2018 and 2019 were also marked by earlier spring ice retreat, higher transport through the Bering Strait, and extensions of warm coastal water even farther north. Under such conditions, the Arctic larval fish assemblage retreated northeastward toward the Arctic Basin and Beaufort Sea, thereby reducing the Arctic-boreal spatial overlap and leaving primarily boreal species occupying the Chukchi shelf in 2018 and 2019.

## 4.2 | Climate-mediated drivers of Pacific Arctic larval fish assemblage distribution shifts

The poleward retreat of the Arctic larval fish assemblage and expansion of the boreal assemblage is indicative of considerable climate-mediated community restructuring in recent years. The strongest environmental predictors of the larval fish assemblage shifts were the northward-flowing surface winds and currents, as well as ocean warming. Seasonally strong currents carry warmer Pacific water northward into the Chukchi Sea during summer and fall (Stabeno et al., 2018; Woodgate et al., 2015), structuring water masses, zooplankton, and fish communities (Eisner et al., 2013). Increased wind- and current-driven poleward advection of warmer, subarctic waters into the Pacific Arctic in recent decades (Woodgate, 2018) is likely magnifying existing dispersal pathways (Levine et al., 2021), resulting in the expansion of the boreal larval assemblage into the northeast Chukchi Sea and poleward shifts of Arctic larval taxa toward the Arctic Basin and Beaufort Sea in 2018 and 2019 as cooler, Chukchi-resident water masses (e.g., Winter Water and Ice Melt/cool Coastal



**FIGURE 9** Mean species-level relationships between the abundance (fourth-root transformed ind.  $10\text{ m}^{-2}$ ) of larval fish taxa and in situ temperature ( $^{\circ}\text{C}$ ) for all years pooled (2010–2019) during late summer in the northeast Chukchi Sea ( $\geq 67.5^{\circ}\text{N}$ ; calculated region shown in the blue shaded polygon on the inset map). Spearman correlation coefficient values are given for each species' abundance and temperature pairing; positive correlations are displayed in red (indicating a significant increase in abundance in response to higher water temperatures), negative correlations in blue (indicating a significant decrease in response to warming), and grey indicates no significant response (correlations with  $p > .05$ ). Taxa are sorted based on their mean latitudinal distribution in cold years (i.e., 2012–2013).

Water) were increasingly displaced by warmer, Bering-origin water masses.

While dissimilarities in life stage (highly mobile adults vs. planktonic larvae) and scale (single species vs. community wide) make it difficult to directly compare range shift values to those from the literature, the  $\sim 75\text{ km}$  northward shift of the boreal assemblage between warm (2018–2019) and cold (2012–2013) years was on a similar scale as distribution shift estimates of marine communities in the Bering Sea ( $\sim 34 \pm 56\text{ km}$  [mean  $\pm$  SD] northward in 1982–2006; Mueter & Litzow, 2008). However, the displacement shift of the Arctic larval fish assemblage was far more dramatic ( $\sim 250\text{ km}$  northward) and even exceeded displacement estimates for adult Arctic fish communities in the Barents Sea (159 km shift in 2004–2012; Fossheim et al., 2015) and North Sea (169 km shift in 1977–2001; Perry et al., 2005). The magnitude and direction of latitudinal shifts of marine taxa are known to be tightly linked to the regional rates of temperature changes (e.g., Cheung et al., 2015; Pinsky et al., 2013) and larval fish assemblages appear to be no exception to this. Planktonic larval distributions are driven by ocean currents to a greater degree than adult fishes that can undergo active migration

toward more favorable conditions (Cowen & Sponaugle, 2009; Fuiman & Werner, 2002). Differences in current strength and direction, such as increasing northward-flowing currents in the Chukchi Sea, could increase the rates of larval range shifts in warm years. The larger displacement shift of the Arctic larval assemblage relative to the boreal is likely due to differing rates of transport as well as the Arctic assemblage's increased sensitivity to environmental change, particularly temperature and presence of sea ice, and the greater degree of change occurring at higher latitudes (Serreze & Francis, 2006).

Sea ice conditions influenced larval fish assemblage compositions and distributions but to a lesser degree than advection, wind, and SST according to our multivariate model estimates (weight<sup>2</sup>). Sea ice coverage and timing of ice retreat in the spring shape important biophysical processes in the northern Bering and Chukchi seas (Drinkwater et al., 2010; Grebmeier, Cooper, et al., 2006) by affecting SSTs and light availability, which regulate the timing of phytoplankton blooms and zooplankton productivity and reproduction in spring and summer (Hunt et al., 2002, 2011; Waga et al., 2021). This has cascading impacts for the broader ecological system

and biological processes such as feeding and growth (Grebmeier, Overland, et al., 2006; Wassmann & Reigstad, 2011), but potentially less direct effects on larval fish distributions than other physical processes such as transport and advection. Nevertheless, the largest areal coverage of the Arctic assemblage occurred when summertime sea ice areal coverage was greatest (2013) and when springtime sea ice retreat was latest (2012 and 2013). Sea ice cover at the time of sampling (late summer) explained less variation in the Arctic assemblage's spatial patterns than the timing of spring ice retreat, however. This suggests that the influence of sea ice on larval fish assemblage composition may be linked with the phenology of spring ice retreat to a greater degree than the persistence of summer ice. Indeed, adult fish spawn timing coincides with productivity pulses such as sea ice algae in the spring, which stimulates zooplankton productivity and thereby supports larval first feeding, growth, and survival (Grebmeier, 2012; Logerwell et al., 2020) and can accordingly be influenced by environmental conditions. Hatch timing is even more directly tied to sea ice retreat than spawning for some Arctic taxa (Bouchard et al., 2017; Bouchard & Fortier, 2011), suggesting that late summer larval assemblage composition may be indicative of range expansions as well as phenological shifts.

### 4.3 | Mechanisms behind the expansion of the boreal larval fish assemblage in the Chukchi Sea

The mechanisms driving the expansion of the boreal larval fish assemblage remain unclear, since the interplay of adult spawning behavior, advection, and phenology makes it difficult to determine whether boreal larvae in the Chukchi Sea resulted from local (Chukchi Sea) or remote (Bering Sea) spawning. Bottom water temperatures in the Chukchi Sea ( $\geq 66^\circ\text{N}$ ) have long been considered too cold to support the spawning of boreal species such as pollock and Pacific cod, and previous perspectives concluded that any sub-adult individuals caught in the Chukchi Sea were advected from spawning grounds in the Bering Sea (Hollowed et al., 2013, Hunt et al., 2013). A lack of consistent, long-term fisheries monitoring programs in the region has historically made this question difficult to assess. Yet, with the Pacific Arctic becoming more hospitable for some of these warmer water fishes (Alabia et al., 2020; Spies et al., 2019), reproduction of boreal fish species in the Chukchi Sea may already be a reality. In 2019, adult pollock were found in large numbers in the western Chukchi Sea (Orlov, Gorbatenko, et al., 2021; Orlov, Rybakov, et al., 2021), which is notable considering that adult pollock were previously thought to be scarce in shallow Chukchi Sea waters (Mecklenburg et al., 2018). Levine et al. (2023) and Wildes et al. (2022) similarly observed high densities of juvenile pollock in the eastern Chukchi Sea in recent warm years (2017 and 2019) relative to colder years (2012 and 2013). This study likewise recorded increasing abundances of boreal fish larvae (including pollock) in the Chukchi Sea over time and Cooper et al. (2023) reported the first occurrence of larval Pacific cod in the northeastern Chukchi Sea in August 2018. Since larval fish production can be indicative

of localized spawning (Fuiman & Werner, 2002), the prevalence of boreal fish larvae in 2018 and 2019 may reflect the beginnings of colonization of the Chukchi Sea by boreal fish stocks.

Logerwell et al. (2020) used estimates of along-shelf current speeds (i.e.,  $5\text{ cm s}^{-1}$ ) and pelagic larval durations ( $\sim 30\text{--}60$  days) to conclude that yellowfin sole larvae found in the Chukchi Sea in 2012 and 2013 were more likely to have been spawned locally than transported from remote spawning grounds in the south (Bartolino et al., 2011). However, in the northeastern Chukchi Sea in 2010–2015, mean northward current velocities across the mid and upper water column averaged  $\sim 9\text{ cm s}^{-1}$  and reached  $24\text{ cm s}^{-1}$  (Stabeno et al., 2018). Furthermore, mean northward current velocities through the Bering Strait ranged from  $\sim 18$  to  $28\text{ cm s}^{-1}$  in 1991–2015 (Woodgate, 2018) and have continued to increase (Woodgate & Peralta-Ferriz, 2021). Therefore, if transit times are updated to reflect the increasing trend in northward current speeds in the region in recent warm years (e.g.,  $\geq 12.5\text{ cm s}^{-1}$ ), it is feasible that boreal fish larvae captured in the northeastern Chukchi Sea could have been advected the  $\sim 650\text{ km}$  from the northern Bering Sea within a reasonable time period corresponding to a typical pelagic larval duration (e.g., 30–60 days). Taken together with the documented northward distribution shifts of adult boreal taxa from the eastern Bering Sea to the northern Bering Sea in 2017–2019 (Eisner et al., 2020; Stevenson & Lauth, 2019), we cannot rule out the possibility that boreal fish larvae are being spawned in the south (i.e., northern Bering Sea and Bering Strait [ $< 66^\circ\text{N}$ ]) and advected into the Chukchi Sea by the elevated northward-flowing currents in late summer of 2018 and 2019. Species-specific spawning behavior could further exacerbate northward dispersal of eggs and larvae as advection increases in warm years. For instance, populations of nearshore-spawning yellowfin sole and capelin (Nichol & Acuna, 2001; Ressel et al., 2019) may have a greater likelihood of eggs and larvae being entrained in the northward-flowing Alaska Coastal Current than species that spawn further offshore or along the continental slope (e.g., Pacific cod; Neidetcher et al., 2014).

Climate-mediated impacts on spawning phenology may have also contributed to the observed larval fish assemblage shifts. In 2018 and 2019, ocean temperatures were greater than average in winter and sea ice retreated north of the Bering Strait before spring (Siddon & Zador, 2018, 2019). These environmental changes could have triggered earlier spawning of boreal species such as yellowfin sole that follow the receding ice edge in their migration eastward in the spring (Bakkala, 1981) and have been observed spawning earlier in warm years in the Bering Sea (Nichol et al., 2019). Since our survey timing was fixed in August and September, and larval abundances and distributions are the result of both spawning and advection, it is plausible that earlier ice retreat could have shifted temporal patterns of seasonal assemblages. Earlier spawning or hatch of boreal species due to warm conditions could have resulted in increased abundances of boreal larvae in the Chukchi Sea at the time of sampling as boreal taxa were advected into the survey area. Similarly, early spawning or hatching of Arctic taxa could have resulted in advection outside of the sampling domain in the Chukchi Sea prior to the late summer



surveys. While we do not have sufficient data from this study to evaluate these questions, a species-specific ageing and ontogenetic analysis of a subset of larvae from each year could disentangle the influences of spawning phenology and advection on the observed spatial shifts.

#### 4.4 | Species-specific abundance responses to a warming Pacific Arctic

Species-specific responses to warming in the northeast Chukchi Sea indicate differing impacts on the leading and trailing edges of the Pacific Arctic larval fish community. We estimate that nearly half of larval fish taxa in the northeast Chukchi Sea have significantly changed in abundance in response to Arctic warming over the study period (2010–2019), with 30% of lower-latitude, boreal species (e.g., yellowfin sole, pollock, capelin, whitespotted greenling, longhead dab, and Sakhalin sole) increasing in abundance and 17% of the higher-latitude, Arctic species (e.g., Arctic cod, daubed shanny, stout eelblenny, and gelatinous snailfish) decreasing in abundance. These findings suggest that Arctic warming is leading to the local displacement of Arctic shelf taxa, as previous studies have predicted (Cheung et al., 2008; Wassmann et al., 2006). Similar to what has been found in other systems, mid-latitude species responses to warming were varied but typically less extreme than high-latitude and low-latitude taxa (e.g., Poloczanska et al., 2013; Robinson et al., 2015; Sunday et al., 2012), a phenomenon which has been attributed to the greater climatic sensitivity of individuals living closer to the edges of their distributional range relative to individuals at the center (La Sorte & Thompson, 2007; Viejo et al., 2011).

Species that significantly increased in abundance in response to warming were primarily boreal in distribution with relatively high thermal occupancy thresholds. For example, increased abundances of larval yellowfin sole have been linked to high (up to 10°C) near-bottom temperatures in the eastern Bering Sea, with the population expanding its distribution northwards and offshore in warm years relative to cold years (Porter, 2021). Similarly, pollock eggs and larvae are known to have a wide-ranging thermal tolerance (−1.0 to 12°C; Blood, 2002; Laurel et al., 2018) that likely reflects their broad latitudinal range (Puget Sound to the northern Bering Sea; Mecklenburg et al., 2011). In a warming Arctic, species with a higher and/or broader thermal range likely have competitive growth and survival advantages over those with lower thermal occupancy limits such as Arctic cod, which display reduced hatch success of eggs incubated at >2°C (Laurel et al., 2018) and elevated mortality rates of larvae incubated at >5°C (Koenker et al., 2018). Higher abundances of boreal species may also indicate improved egg and larval survivorship as the Chukchi Sea becomes an increasingly favorable thermal habitat. In contrast, multiple Arctic species significantly decreased in abundance in response to rapid warming in the northeast Chukchi Sea. Many Arctic taxa are constrained by temperature and bathymetry to cold, shallow-water habitats and are sensitive to habitat changes triggered by ocean warming and

sea ice loss (Kortsch et al., 2015; Marsh & Mueter, 2019; Planque et al., 2014). Species living near their thermal limits and those with restricted spatial ranges are far more likely to shift their distribution in response to climate warming (Campana et al., 2020). Indeed, the areal coverage of the Arctic larval fish assemblage was smallest in years with early spring ice retreat, low-ice cover, and when warm water masses were widely pervasive throughout the survey region. Fossheim et al. (2015) reported a similar decline of the Atlantic Arctic adult fish assemblage in the northern Barents Sea in response to a rapid influx of warmer water, predatory species from the south (e.g., Atlantic cod [*Gadus morhua*] and haddock [*Melanogrammus aeglefinus*]). In this study, Arctic cod—the most abundant fish in the Pacific Arctic (De Robertis et al., 2017; Logerwell et al., 2018) and the primary prey for many upper trophic level marine predators (Watson & Divoky, 1972; Welch et al., 1992)—decreased in larval abundance as in situ water temperatures and predatory boreal species such as pollock (Emelin et al., 2022) increased, mirroring observations of declining adult populations in the Atlantic Arctic (Eriksen et al., 2015; Hop & Gjørseter, 2013). Due to their small size and limited swimming ability, planktonic fish larvae are more vulnerable to predation, competition, and disruptions to their zooplankton prey field compared to later life stages that are capable of directed movement toward more favorable conditions. As boreal species infringe on the habitat of Arctic species, there is the potential for niche overlap, interspecific competition, and predation that could have far-reaching ecological consequences for Arctic biodiversity and food web functioning (Emblemsvåg et al., 2022; Frainier et al., 2017).

## 5 | CONCLUSIONS

Assessments of a 10-year ichthyoplankton time series revealed an abrupt northward range expansion of a boreal assemblage and a poleward range contraction of an Arctic assemblage in response to unprecedented ecosystem change in 2017–2019. Arctic warming significantly influenced larval fish abundances and distributions, as boreal species increased in abundance and areal coverage and Arctic species declined in the Chukchi Sea. Prevailing winds, advection, and sea ice dynamics also played a large role in structuring larval fish assemblage composition and distribution across the northern Bering and Chukchi seas. If earlier ice retreat and frequent and extended warming continues as is predicted (Baker, Kivva, et al., 2020; Wang et al., 2018; Woodgate & Peralta-Ferriz, 2021), shelf habitat for Arctic larval fish assemblages may continue to contract. Changes in advection, spawning, and phenology may further influence growth and survival of marine fish larvae with potentially significant impacts on fisheries recruitment dynamics in the Pacific Arctic. Prolonged shifts in species composition and the influx of new predatory species from the south (e.g., pollock and Pacific cod) that are well adapted to warmer conditions could impact food web functioning and trigger a cascade of consequences for upper trophic levels, Alaskan communities and subsistence users, and larger-scale fisheries (Huntington et al., 2020). Model-based predictions indicate that

Arctic borealization will continue under different global warming scenarios (Polyakov et al., 2020), ultimately emphasizing the need for expanded fisheries surveys and biological time series across all life stages within the Pacific Arctic to track and incorporate these ecological changes into future ecosystem management and climate adaptation programs. Results from our study expand our understanding of how changing climate and oceanographic processes are capable of restructuring Arctic fish assemblages over large spatial scales beginning with the earliest stages of life.

## ACKNOWLEDGMENTS

We thank the participating captains, crews, and scientific parties for the implementation of these oceanographic surveys and the Plankton Sorting and Identification Center (Poland) and Alaska Fisheries Science Center (USA) for their taxonomic expertise. We thank Rebecca Woodgate for providing Bering Strait transport data and Silvana Gonzalez, Robert Levine, Elizabeth Logerwell, and two anonymous reviewers for providing helpful feedback that greatly improved the manuscript. This research is contribution EcoFOCI-1027 to NOAA's Ecosystems and Fisheries Oceanography Coordinated Investigations program, the North Pacific Research Board (contribution no. ArcticIERP-50), and the Cooperative Institute for Climate, Ocean, & Ecosystem under NOAA Cooperative Agreement NA20OAR4320271 (contribution no. 2022-1227).

## CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at <https://doi.org/10.5061/dryad.9zw3r22jv>.

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**How to cite this article:** Axler, K. E., Goldstein, E. D., Nielsen, J. M., Deary, A. L., & Duffy-Anderson, J. T. (2023). Shifts in the composition and distribution of Pacific Arctic larval fish assemblages in response to rapid ecosystem change. *Global Change Biology*, 00, 1–22. <https://doi.org/10.1111/gcb.16721>