

Understanding transboundary stocks' availability by combining multiple fisheries-independent surveys and oceanographic conditions in spatiotemporal models

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Shifts in the distribution of groundfish species as oceans warm can complicate management efforts if species distributions expand beyond the extent of existing scientific surveys, changing the proportion of groundfish available to any one survey each year. We developed the first-ever model-based biomass estimates for three Bering Sea groundfishes (walleye pollock (*Gadus chalcogrammus*), Pacific cod (*Gadus macrocephalus*), and Alaska plaice (*Pleuronectes quadrituberculatus*)) by combining fishery-independent bottom trawl data from the U.S. and Russia in a spatiotemporal framework using Vector Autoregressive Spatio-Temporal (VAST) models. We estimated a fishing-power correction to calibrate disparate data sets and the effect of an annual oceanographic index to explain variation in groundfish spatiotemporal density. Groundfish densities shifted northward relative to historical densities, and high-density areas spanned the international border, particularly in years warmer than the long-term average. In the final year of comprehensive survey data (2017), 49%, 65%, 47% of biomass was in the western and northern Bering Sea for pollock, cod, and plaice, respectively, suggesting that availability of groundfish to the more regular eastern Bering Sea survey is declining. We conclude that international partnerships to combine past data and coordinate future data collection are necessary to track fish as they shift beyond historical survey areas.

Keywords: Bering Sea, bottom-trawl, catchability, cold pool index, model-based index, VAST.

Introduction

The movement of global taxa as a consequence of warming conditions across global ecosystems as the climate changes is well documented (Visser, 2008; Thomas, 2010; Pinsky *et al.*, 2013). Taxa are shifting their locations beyond historical ranges in response to climate change (Chen *et al.*, 2011; Pinsky *et al.*, 2013), with many marine fishes moving to higher latitudes or deeper waters (Perry *et al.*, 2005; Dulvy *et al.*, 2008; Pinsky *et al.*, 2013). Consequently, many species are leaving their historical scientific survey and management areas (Currie *et al.*, 2019). The Pacific Arctic, a historically cold-dominated ecosystem that is now warming, is an example of an ecosystem where empirical evidence suggests that many groundfish species are tracking their preferred temperature niche, resulting in poleward distribution shifts for some ecosystems (Fredston *et al.*, 2021).

Sea ice coverage in the Pacific Arctic has reached historic lows in the recent years (Thoman and Walsh, 2019). This reduction of sea ice has led to a series of changes in this system, including weakened water column stratification, delayed spring bloom, and low abundances of large crustacean zooplankton (Duffy-Anderson *et al.*, 2019; Huntington *et al.*, 2020). The weakened water column stratification and reduced sea ice resulted in historic lows in the spatial extent of the cold pool, a subsurface feature in the Bering Sea, typically defined by temperatures below 2°C that is one of the main physical barriers preventing northward movement of groundfish (Thoman and Walsh, 2019).

Studies and observations suggest that groundfish such as walleye pollock (Gadus chalcogrammus), Pacific cod (Gadus macrocephalus), and Alaska plaice (Pleuronectes quadrituberculatus) are responding to reductions in sea ice and cold pool extent (Kotwicki and Lauth, 2013; Stevenson and Lauth, 2019), although it is unknown if these changes are temporary or long-term (Eisner et al., 2020). Evidence of distribution shifts can be found in a mixture of genetic and observational data, including evidence that pollock distribution is expanding (Eisner et al., 2020), cod are moving northward into the northern Bering Sea (NBS) during summer months (Spies et al., 2020), and the proportion of Alaska plaice in the NBS relative to the eastern Bering Sea (EBS) has increased from 2017 to 2019 (Wilderbuer and Nichol, 2019; O'Leary et al., 2021). Changes in groundfish distribution can potentially impact commercial and subsistence fishing effort and food web dynamics (Haynie and Huntington, 2016; Eisner et al., 2020). As such, it is crucial to track groundfish as they shift their distributions in response to climatic, biological, and environmental drivers to effectively monitor and manage these species.

One of the main difficulties in managing marine taxa as the climate changes is tracking their movements into new habitat areas beyond historical survey extents or across political boundaries. Fisheries data are typically collected within fixed

Received: December 2, 2021. Revised: March 1, 2022. Accepted: March 2, 2022

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spatial units that reflect relatively static management areas. Therefore, accurately tracking where and how many individuals have moved is difficult if fish leave or enter historical survey extents or international boundaries (Pinsky et al., 2018). Furthermore, extending surveys or adding additional data collection points is seldom possible because organizational budgets are static and personnel are limited (ICES, 2020). Therefore, there is a need to combine resource-monitoring efforts and promote international partnerships to share information across political borders and scientific survey extents to assess and manage transboundary species. Ongoing efforts record the global coverage of existing data sets and highlight that on average 18 scientific bottom-trawl surveys are needed to cover 50% of most commercial demersal fish species ranges, but that a majority of the global datasets are not publicly available (Maureaud et al., 2020). Improving data availability and collaboration while developing methods to combine surveys is therefore crucial to adequately monitor the full extent of fish distributions. This information and collaboration is vital under a changing climate to understand the economic and ecological risks of managed species and to continue to manage sustainably and accurately.

We outline a spatiotemporal modelling approach to combine multiple bottom trawl datasets collected by the US and Russian national organizations. We apply this framework to combine fishery-independent bottom trawl data sets from the US National Oceanic and Atmospheric Administration's (NOAA) Alaska Fisheries Science Center (AFSC) and Pacific branch of the Russian Federal Research Institute of Fisheries and Oceanography VNIRO (TINRO). Together, these data cover the entire Bering Sea shelf region, including the eastern (EBS), western (WBS), and northern (NBS) Bering Sea (Fig. 1). The analyses focus on three commercially valuable groundfish species, pollock, cod, and plaice, which represent differing life-history strategies. We estimate catchability parameters to combine data sets and spatial covariances to interpolate across missing data. We also incorporate a metric of oceanographic conditions, the cold pool index, to provide additional information to estimate spatially-explicit groundfish densities based on previous work that ties pollock and cod to physical drivers in their habitat (Thorson, 2019a; Thorson et al., 2017, 2020a, 2020b; Eisner et al., 2020; O'Leary et al., 2020). This analysis demonstrates that spatiotemporal modelling can combine multiple surveys to track changes in fish densities across time and space. As the ocean continues to warm, increased efforts for data sharing and international collaboration will be needed to support effective transboundary fisheries management

Methods

We aimed to combine fishery-independent bottom trawl data that span the entire Bering Sea shelf to provide annual Bering Sea shelf-wide biomass estimates. We also sought to answer the following questions:

- (1) What is the effect of oceanographic conditions on biomass and derived quantity estimates, their uncertainty, and their inter-annual variability?
- (2) What patterns arise in overall spatially explicit densities of each groundfish?

- (3) Are there changes in the center of gravity and effective area occupied throughout our time series when combining US and Russian portions of the Bering Sea?
- (4) What is the availability (or proportion of total groundfish biomass) within the eastern Bering Sea AFSC survey, which is the survey that has been conducted most regularly over time?

We use these questions to organize sections of the Results.

Study region and survey extents

Data used span the full extent of the Bering Sea shelf (Fig. 1). We consider three sub-regions in the Bering Sea shelf: the EBS, the NBS, and the WBS. The EBS is the portion of the Bering Sea east of the international maritime boundary in the US territorial waters, and the survey in this region extends from Bristol Bay north to north of Nunivak and St. Matthew islands and west to the 200 m depth contour at the shelf break (Fig. 1; Armistead and Nichol, 1993). The NBS as defined here also occurs in the US territorial waters, and survey data collection ranges from north of St. Matthew and Nunivak islands to the Bering Strait, including Norton Sound (Fig. 1). The WBS is defined as west of the international maritime boundary between the US and the Russian Federation, with data collection extending from the Bering Strait along the shelf down the Russian coastline to Bering Island.

All data in the eastern and northern Bering Sea are from fishery-independent bottom trawl surveys conducted by the AFSC. The majority of data in the western Bering Sea shelf are from fisheries-independent bottom trawl surveys conducted by the TINRO.

Fisheries-independent survey data description

The EBS survey data were all collected during daylight hours from 1982 to 2019. This annual survey occurs from May to early August over a fixed set of stations sampled from a stratified, centric-systematic grid. The maximum depth is 200 m, and the minimum grid resolution is 37.04 km². The survey starts in the southeastern corner of the EBS and proceeds west using two vessels under the same protocol. The tow duration is 30 min at a speed of 1.54 m/s. A standard survey bottom trawl is used (83–112 eastern otter trawl, or 25.3 m/34.1 m with a 10 cm mesh; Stauffer, 2004) on a total of 12 unique chartered fishing vessels over the entire survey time period. Survey effort is determined by the area-swept (e.g. Alverson and Pereyra, 1969), a product of the duration of net bottom contact (measured using a bottom contact sensor) and net width (measured using acoustic spread sensor).

The NBS survey data collection matches the EBS survey in terms of vessels, gear, and sampling strategy, but primarily occurs from August to mid-September. The timing and spatial extent of the NBS survey have occurred irregularly, with portions of the NBS survey area sampled during 1982, 1985, 1988, 1991, 1994, 2001, 2005, 2006, and 2018, and all of the NBS survey area sampled during 2010, 2017, and 2019 (Fig. 1). See Supplementary Materials Section A for additional data details.

The WBS survey sampled from 1982 to 2017 throughout all months of the year, but primarily from May to August. Tow duration was primarily 30 min at a speed of 1.65 m/s. Thirty-two unique vessels were used throughout the survey period, and there was no maximum defined depth for the sur-



Figure 1. (top) Bering Sea shelf region with the location of knots, Conventional Line indicated by solid black line, and total spatial extent of model-based density estimates indicated by blue dots; and (bottom) spatiotemporal map of survey data used in spatiotemporal models, where purple represents the extent of the Alaska Fisheries Science Center eastern Bering Sea (AFSC EBS) survey each year, green represents the extent of the Alaska Fisheries Science Center's northern Bering Sea (AFSC NBS) survey each year, and yellow represents the extent of the Pacific Branch of the Russian Federal Research Institute of Fisheries and Oceanography western Bering Sea (TINRO WBS) survey each year. The TINRO WBS survey overlaps with the AFSC EBS survey in the EBS during 1982–1991.

vey. The timing and spatial extent of the survey have occurred irregularly, as the survey does not follow a probabilistic survey design (Fig. 1). TINRO collected data on the EBS shelf that overlapped with the EBS survey during 1982–1991. These data were included in the sampling efficiency ratio calculation (Volvenko *et al.*, 2018; Fig. 1).

Data from all three regions included both presence and absence of catch for the species of interest for each tow, and, where groundfish were found, the total biomass. Survey station data were compiled to a catch rate in weight of fish per hectare, which is the catch divided by the "area-swept" for each survey trawl (Alverson and Pereyra, 1969).

Oceanographic Conditions: Cold pool extent index (CPI)

The cold pool extent, here defined as the bottom temperature layer $< 2^{\circ}$ C, is related to the winter sea ice areal extent, with more extensive cold pools observed during years with high sea ice coverage and late sea ice retreat (Stabeno and Bell, 2019). The cold pool extent is known to influence stratification, the timing of warming, and nutrient availability. The presence of sea ice and associated ice algae or phytoplankton in spring can provide an early food source for lipid-rich zooplankton and euphausiids, important prey for fish in the Bering Sea (Hunt *et al.*, 2011). The cold pool also can act as a cross-shelf barrier that prevents subarctic fish from migrating to northern waters (Kotwicki *et al.*, 2005; Stabeno *et al.*, 2012). Therefore, the cold pool extent can be indicative of important bottom–up ecosystem drivers and can directly impact movement and distribution of fish in the Bering Sea.

The cold pool extent index (CPI) is an annual index from 1982 to 2019 of the measured spatial extent in km² of bottom temperatures 2°C or colder. This index was included in the analysis as a spatially explicit annual zero-centered covariate to predict changes in density across space and time to represent oceanographic conditions. In other words, the cold pool extent was the same value across space within a year but varied among years, and it was modeled to impact densities via a log-linear response of local density to regional cold pool extent. The cold pool extent was included as an environmental covariate to potentially maximize model accuracy and performance, based on its known role as a driver of interannual variability in the EBS and the NBS (Wyllie-Echeverria and Wooster, 1998; Kotwicki and Lauth, 2013; Thorson, 2019a; Brodie et al., 2020). While the influence of the cold pool on the WBS is less clear (but see Eisner et al., 2020), preliminary investigations using Empirical Orthogonal Function (EOF) analysis suggest that the cold pool is an important driver of groundfish distribution at a shelf-wide scale that includes the WBS (Supplementary Materials Section B).

Model description

Annual biomass was estimated using a spatiotemporal model with and without cold pool effects for the entire Bering Sea shelf region using data from the EBS, NBS, and WBS surveys. We used the vector autoregressive spatiotemporal (VAST) model v3.5.0 (Thorson and Barnett, 2017) implemented in R-4.0.3 (R Core Team, 2020), an extension of the deltageneralized linear mixed model framework. The multiplesurvey data were analyzed using a Poisson-link delta model with a gamma distribution for the positive catch rate observation error distribution. See Supplementary Materials Section C for additional model details.

The sampling variation was decomposed further in a subset of models to include a habitat covariate, the CPI, as predictors of encounter probability (p) and positive catch rate (r) to estimate the impact of a habitat covariate on local density. As a habitat covariate, density estimates are conditioned upon the CPI when predicting population density.

We also included a catchability covariate $O_i(k)$ in the model to account for the use of three survey data sources, so differences in catchability between surveys were controlled for. We estimated two separate temporally and spatially invariant catchability parameters per species $Q_1(k)$ for the first linear predictor and $Q_2(k)$ for the second linear predictor where k = 1, as the EBS and NBS were used as the "base" or reference value when defining contrasts. In other words, estimates of $Q_i(k)$ were only estimated for the WBS survey because this approach effectively estimates a catchability ratio. We also specified random variation in surveys due to vessel effects to distinguish potential vessel targeting of fish and differences in gear operation between vessels from covariation in species densities. We include a fixed effect (catchability) for survey and random-effects for vessels to account for both differences between the AFSC and TINRO surveys in their fishing power as well as the overdispersion in the data. See Supplementary Materials Section C for additional model description details.

Estimation, evaluation, and model comparison

Parameters in the VAST model were estimated by maximizing the marginal log-likelihood of fixed effects given the data using Template Model Builder (Kristensen *et al.*, 2016). Using a gradient-based non-linear minimizer, we confirmed that all absolute gradients of the marginal log-likelihoods with respect to each fixed effect were < 0.001. We report epsilon biascorrected (Thorson and Kristensen, 2016) biomass to account for retransformation bias when calculating total biomass and center of gravity for each survey region.

To compare between VAST models that included cold pool effects and those that didn't, we evaluated goodness-of-fit using the marginal Akaike information criterion (mAIC; Greven and Kneib, 2010), an approach that identifies the models that best fit the available data based on the Akaike weight (Akaike, 1974). mAIC is reported as delta mAIC or the difference in mAIC for each model relative to the lowest mAIC value. We also estimated the % of residual spatial and spatiotemporal variance explained by the regional CPI covariate (Thorson, 2019a; Supplementary Materials C).

To evaluate individual model fits, we considered the unexplained variation in log-density, the coefficients of variation for the estimates for the log-index of biomass abundance, and simulation-based probability-integral-transform (PIT) residuals (Smith, 1985; Warton *et al.*, 2017) via Q-Q plots. We used the DHARMa package in R (v0.4.0; Hartig, 2021) to simulate data sets from the predictive distribution of the data conditioned on estimated fixed and random effects, and calculated the PIT residuals from the observed and simulated values to create diagnostic objects for the simulation-based quantile residuals from a delta-model.

Table 1. The delta-mAIC (Δ mAIC), or difference in each model's mAIC from lowest mAIC value, and the % variance explained for the spatiotemporal residual variance for the models without Cold Pool Extent Index (CPI) covariate effects (σ_{e0}^2) and with CPI covariate effects (σ_{e0}^2) for all species models.

Species	ΔmAICwith CPI covariate	∆mAICwithout CPI covariate	σ_{ϵ}^2 with CPI covariate	$\sigma_{\epsilon 0}^2$ without CPI covariate	Percent variance explained with CPI covariate
Pollock	0	22.7	1.02	1.12	8.6%
Cod	0	95.4	0.83	0.94	11.9%
Plaice	0	10.6	0.8	0.82	2.4%

Measures of population shifts: Availability, center of gravity, and effective area occupied

We considered the proportion of stock biomass within the spatial extent of the WBS and NBS surveys relative to within the spatial extent of the total combined (EBS + NBS + WBS) surveys to understand the availability of groundfish to the EBS survey each year. The standard deviation of availability was calculated by drawing 100 samples from the joint distribution of the model's random and fixed effects to approximate the predictive distribution of biomass estimates by species and location. We then calculated the proportion of stock biomass within the WBS and NBS relative to the entire shelf (EBS + WBS + NBS) for each sample and calculated the standard deviation among these values.

The centers of gravity of the population distribution (as a whole and for subregions) Z(t, l) for time *t* consider the area a(s, l) for region *l* at each knot location *s*, the location in eastings and northings of each knot z(s, l), and the predicted population density d(s, t)

$$Z(t,l) = \sum_{x=1}^{n_x} \frac{z(s,l) \ a(s,1) \ d(s,t)}{I(t,1)},$$
(1)

when region l = 1, representing the mean population location weighted by population density.

The effective area occupied A(t, l), or the area that contains the total index given the average density for each year t and region l, is the ratio of the biomass over the average density (Eqn. 1) for each region l

$$A(t,l) = \frac{I(t,l)}{D(t,l)}.$$
(2)

with a different denominator (mean-density) for each region *l*. Further details on all derived quantities can be found in Thorson (2019b).

Results

Question #1: Effect of oceanographic variability

The most parsimonious model based on mAIC (i.e., that which explained the most spatiotemporal variance) for all three groundfish species was the spatiotemporal model that included the spatial covariate effects of the CPI. All models showed no evidence of non-convergence. The % variance explained by the combined linear effects for the spatial oceano-graphic covariate (CPI) was 8.6%, 11.9%, and 2.4% for pollock, cod, and plaice, respectively (Table 1).

There is a strong estimated spatial effect of the annual CPI on the distributions of pollock and cod, where densities decrease in the typical area of the cold pool and increase outside of it, as expected given behavioral avoidance of cold nearbottom waters for these species (Fig. 2). The effect of CPI on the distribution of plaice is much smaller (Fig. 2). The aggregated spatial effect of the CPI (i.e. $exp(Xi_1 + Xi_2)$) (± standard error) for pollock, cod, and plaice are $-0.08 (\pm 0.08)$, $-0.15 (\pm 0.11)$, and $0.02 (\pm 0.02)$, respectively. The CPI effect on positive catch rate $exp(Xi_2)$ is estimated as $-0.10 (\pm 0.37)$, $-0.11 (\pm 0.40)$, and $-0.008 (\pm 0.14)$ for pollock, cod, and plaice, respectively.

Question #2: Patterns in spatio-temporal densities

The changes in density distributions over the time series, after accounting for catchability (Table S2), portray how the distribution of these groundfish species span the entire Bering Sea shelf (Fig. 3). Often, the "hot spots" or areas of high density spanned the US–Russia Conventional Line (Fig. 1), particularly during warmer years when the CPI is lower than the long-term average (e.g. in 2003, 2019). Cod, in particular, exhibited estimated hotspots emerging in the NBS, north of St. Lawrence Island that span the Conventional Line. All three groundfish species expanded across the Bering Sea during the final four years (2016–2019) (Fig. S4). Estimated pollock and cod densities from 2016 to 2019 were high across the EBS and WBS, but all three species were noticeably more abundant and spread their distribution north of St. Lawrence Island towards the Bering Strait.

Question #3: Changes in center of gravity and effective area occupied

Examining the average latitude of survey samples each year illustrates that all three groundfish species are shifting northward, though at varying degrees of magnitude (Fig. 4). Cod shifted the furthest north of the three groundfish. Examination of the average longitude reveals that the eastings center of gravity for cod and pollock fluctuates across the Conventional line, while the longitude component of the center of gravity for plaice is consistently west of the Conventional line (Figs. 1, 4). All three groundfish species were shifting northward from around 2000, and continued this overall trend during 2016–2019.

The effective areas occupied by pollock and plaice are steadily increasing over the entire time series but with high interannual variation (Fig. 5). The effective area occupied by cod steadily declined from 1982 to 2000 but then increased again up to levels that match the early 1980s. The effective area occupied by cod is also highly variable from year to year.

These two pieces of evidence combined—increased effective area occupied and northward-moving center of gravity suggest an expanded range for all three species in the Bering Sea, but not necessarily depletion at the southern edge.



Figure 2. Estimated spatial effect of the annual cold pool extent index (CPI) for pollock, cod, and place in the Bering Sea, and the normalized annual cold pool extent index from 1982 to 2019. A value of 0.1 on the map indicates that the corresponding location is expected to have an approximately 10% increase in density as cold-pool increases from 0 to 1.0.

Question #4: Trends in availability to the eastern Bering Sea survey

The estimated proportion of pollock, cod, and plaice biomass available to the EBS survey from 1982 to 2019 is nearly the same regardless of whether the cold pool is accounted for. The proportion of groundfish available to the EBS survey relative to the total (combined EBS, NBS, and WBS) is highly variable interannually, particularly for pollock and cod (Fig. 6).

The proportion of pollock biomass in the combined WBS + NBS relative to the total Bering Sea (EBS + NBS + WBS), or proportion of pollock unavailable to the EBS survey, was below 0.5 for most years. The availability of pollock in the EBS was below 0.5 for only one out of 38 years (2018). Since 2014, the estimated proportion of pollock in the WBS + NBS increased until 2018, when the majority of pollock (> 50%) were in the combined WBS + NBS. The proportion of pollock in the WBS + NBS relative to the entire Bering Sea was 0.49 during 2017, the last year with groundfish observations in the WBS.

The proportion of cod biomass unavailable to the EBS survey was also < 0.5 from 2014 to 2017 and was trending upward during these years (Fig. 6). The availability of cod in the EBS was below 0.5 for 5 out of the 38 years, including four of the most recent years (2008, 2016–2019). In 2017, the estimated proportion of cod in the combined WBS + NBS was 0.65. The estimated proportion of cod unavailable to the EBS

survey declined again from 2018 to 2019, down to 0.55 during the final year.

The proportion of plaice biomass unavailable to the EBS survey relative to the combined total Bering Sea region biomass remained below 0.5 for most years between 1982 and 2019. The availability of plaice in the EBS was below 0.5 for 6 out of the 38 years (2004, 2008, 2012, 2014, 2015, 2019). In 2017, the estimated proportion of plaice in the combined WBS + NBS was about 0.47. The estimated proportion of plaice in the combined WBS + NBS in the final year 2019 was 0.53.

Discussion

We used a spatiotemporal model with an estimated catchability parameter to combine fishery-independent bottom trawl data from the US and Russia to create the first-ever modelbased index of abundance for groundfishes across the Bering Sea shelf. This developed methodology combines scientific fishery-independent bottom trawl data in a way that is applicable to other regions where commercially important fish span areas managed by multiple countries or areas monitored by multiple scientific surveys. This methodology also establishes a way to incorporate habitat condition information, including oceanographic indices as demonstrated here, into biomass estimates used for management. This approach includes habitat condition as covariates to explain variation in groundfish spatiotemporal density.



Figure 3. Log-density maps (ln(kg/km²)) for (a) pollock, (b) cod, and (c) plaice in the Bering Sea for (top row) averaged over 1982–2019 and (rows 2–7) for six years (1982, 1990, 1999, 2003, 2012, 2019), selected for their anomalous cold pool extent index (CPI). Larger than the long-term average cold pool extent occurred during 1999 and 2012, smaller than average cold pool occurred during 2003–2019, and near-average cold pool extent occurred during 1982–1990.



Figure 4. Estimates of eastward and northward center of gravity for cod (purple), plaice (aqua), and pollock (yellow) in the Bering Sea from 1982 to 2019.



Figure 5. Effective area occupied by each groundfish species throughout the Bering Sea from 1982 to 2019.



Figure 6. Estimated proportion of groundfish biomass ±1 standard error in the western Bering Sea (WBS) and northern Bering Sea (NBS) relative to the total Bering Sea from models with (pink) and without (aqua) cold pool extent index (CPI) effects (1982–2019) to reflect availability of groundfish to the NOAA-AFSC EBS survey.

In the application of these methods to a specific region, we found that for the groundfish species included in this analysis, "hot spots" or areas of high-density span an international boundary (the Conventional Line between the US and Russia), particularly during warmer years when the cold pool extent is lower than the long-term average. We also found that the centers of gravity of groundfish density shifted northward in the Bering Sea region, particularly over 2015–2019, with all three groundfish species expanding their area occupied to varying degrees (Fig. 4).

The consistent spatial distribution of groundfish density across the southern Bering Sea shelf after correcting for differences in fishing power in the two surveys suggests connectivity between groundfish species in the EBS and WBS, particularly pollock and cod. However, while this work provides spatial density estimates across the Bering Sea, more work is needed to connect the groundfish density distribution to the groundfish population structure in the Bering Sea. All three species appear to be expanding into the NBS, north of St. Lawrence Island to the Bering Strait (the most northern location of the observations in this data set). In addition, pollock and cod appear to expand into the region often occupied by the cold pool extent and northward, indicated by increased densities from 2014. These findings contribute to ongoing genetic and tagging work in the region for pollock and cod that suggest northward movement and stock mixing (Spies et al., 2019; Eisner et al., 2020; Thompson et al., 2020). Eisner et al. (2020) noted that pollock populations from the WBS and EBS are mixing in the NBS during warm years, and ongoing cod tagging work suggests that there is seasonal movement between EBS, NBS, WBS, and Gulf of Alaska (J. Nielsen, AFSC, pers comm., 2021). The spatial extent of plaice appears to extend into the NBS for the entire period considered, but estimated plaice densities increased throughout the NBS from the early 2000s to 2019.

Future work should focus on stock structure as the likelihood of subpopulation mixing increases, particularly as the ocean conditions in the Bering Sea and surrounding regions warm. We advocate expanded efforts to corroborate estimates in areas without consistent sampling data; for example, using upward-facing acoustics as auxiliary information to track movement across the Conventional Line, or nearshore data from the state of Alaska to improve estimates in Norton Sound. Auxiliary information, including acoustic, tagging, genetic, and expanded bottom-trawl coverage data, will be crucial to improve predictions in unsampled areas and as conditions shift (Thorson *et al.*, 2021).

The northward shift of all three groundfish species during the last decade, paired with the estimated covariate effect and spatial trend of the cold pool effect, suggests that these shifts in spatial range and distribution can be attributed in part to changing oceanographic conditions. Further evidence for the hypothesis that the reduction of the cold pool extent allows for northward movement of groundfish is supported by the increase in average estimated effective area occupied as well as the northward shifting center of gravity for pollock, cod, and plaice during 2015–2019 when the cold pool extent was at historic lows. The inverse relationship of both pollock and cod spatial density with the average extent of the cold pool at the location of the cold pool, and the positive relationship outside of the cold pool location, is particularly apparent (Fig. 2). These findings support previous studies that suggest that groundfish densities are moving northward as the cold pool

extent reaches historic lows and that link occupied habitat and distribution with ocean condition variation (Thorson et al., 2017; Thoman and Walsh, 2019; Wilderbuer and Nichol, 2019; Eisner et al., 2020; O'Leary et al., 2020). The increased variance explained with the inclusion of the cold pool extent combined with the small difference in the predicted densities suggests that there are local responses to basin-wide oceanographic conditions for these groundfish species and that there are additional factors or spatially-explicit factors unaccounted for when considering density covariates. This finding, paired with the limited biomass time-series data available from the NBS, highlights the importance of continuing the surveys of this region as conditions in the sub-Arctic region continue to warm. There remains the possibility that there are different modes of variability driving groundfish distribution in the WBS or differences in variability that are age-specific, both of which require additional data-sharing and collaboration to investigate. While preliminary analyses (Supplementary Materials Section B) suggest that the cold pool is an important driver of spatiotemporal patterns in the WBS, there is also substantial variation at the shelf-wide scale that is not explained by cold pool-associated modes of variability (Supplementary Materials Section B). Follow-up work is needed to investigate spatially varying measures of additional oceanographic variables on groundfish density and alternate drivers of variability for the WBS and should continue as more NBS data are collected

Overall, the proportion of groundfish biomass found in the eastern and western sides of the Bering Sea is highly variable, leaving open the potential for stock mixing between Russian and U.S. stocks. The estimated availabilities of all three groundfish to the EBS survey were around 50% or less during the last five available survey years: for pollock from 2017 to 2019, for cod from 2016 to 2019, and for plaice in 2015-2017 and 2019. This is well below the average availability to the EBS survey across the entire period for all three species. which was 74% for pollock, 71% for cod, and 66% for plaice. The proportion of groundfish in the WBS and the total effective area occupied trended upward for all three groundfish species from 2010 to 2019. These distribution and availability trends paired with the CPI covariate effects suggest that there is potentially increased movement of pollock and cod between Russian and US waters as a response to the reduction of sea ice extent and shrinking cold pool. This finding is consistent with Eisner et al. (2020), who also found that pollock had expanded its distribution in the area between St. Lawrence Island and the Bering Strait in US and Russian waters.

One shortcoming of this study is that age classes were pooled due to limited availability of individual length and age data. Follow-up work should aim to share age- and lengthspecific information across agencies to investigate age- and length-specific distributions in recent years; many of these species are known ontogenetic migrators, and this level of detail may reveal stronger age-specific spatiotemporal trends with respect to movement between Russian and US waters and responses to the annual cold pool extent. Size-specific data are also necessary to estimate catchability ratios by size class (Ono et al., 2017). Understanding size-specific catchability may provide more accurate estimates of length-specific distributions and biomass, allowing further attribution of length-specific distribution variation to different ontogenetic and environmental factors. We used biomass in the bottom trawl as the response metric, and this is less sensitive to the distribution of young individuals (which are typically smaller, more pelagic, and under sampled by the survey trawl net), but fluctuations in age-structure even among ages 3+ could contribute to the biomass-aggregated patterns seen here (Thorson *et al.*, 2017). There also remains the possibility that the temporally invariant catchability assumption is violated. The catchability term relates the TINRO data to AFSC data, and so any temporal changes in catchability will influence the estimated proportion of stocks in each region, as the covariate used to convert TINRO data to the AFSC scale based on differences in catchability would be different across time.

Spatiotemporal models that reflect species distributions, such as those used here, can be harnessed to combine disparate data to understand large-scale patterns and processes that drive species' habitat use (Brodie et al., 2020; Moriarty et al., 2020). International partnerships are key to tracking fish across international boundaries as their habitat uses change, species shift beyond historical survey areas, and new habitat areas open up (Maureaud et al., 2020). We must collaborate internationally on a global scale, mirroring those efforts already underway in Europe (Moriarty et al., 2020) and between Norway and Russia in the Barents Sea (Michalsen et al., 2011), to calibrate historical data and coordinate future data collection efforts to fully understand and manage changing biomass and shifting distribution of fish species as ocean conditions change. This is particularly crucial and timely in polar regions where warming is occurring at an accelerated rate, causing new regions to open up as sea ice extent is reduced, allowing for fish and fisheries to move into these areas. Future stock assessors should consider incorporating this information into a regional assessment or explore the option of a larger North Pacific wide assessment (Ono et al., 2017). Management decisions will likely depend on considerations such as whether stocks remain behaviourally and genetically distinct as they expand, whether or not stocks split into subpopulations as ranges expand and distributions change, and whether other species are shifting at the same time or new species interactions are introduced. Coordinated efforts through organizations such as the North Pacific Marine Science Organization can serve as platforms to continue data sharing and synthesis and continue to monitor the movement of these groundfish species to determine the permanency of these shifts in a rapidly changing climate and panArctic system.

Supplementary Data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Author's contributions

CAO, JTT, SK, GRH, VVK, JNI, AEP conceived the ideas; CAO, JTT, SK, VVK, JNI, AEP designed methodology; CAO, SK, GRH, VVK collected and/or contributed pre-processed subsets of data; CAO, JTT wrote code and analysed the data; CAO led the writing of the manuscript and all authors contributed critically to the drafts and gave final approval for publication.

Data Availability Statement

NOAA data are available via https://www.fisheries.noa a.gov/alaska/commercial-fishing/alaska-groundfish-bo ttom-trawl-survey-data#northern-bering-sea-shelf. All TINRO data are property of the Russian Federation and should be requested through the Federal Agency for Fishery http://government.ru/en/department/243/and VNIRO http://vniro.ru/en/about-vniro/contacts. Code is available at https://github.com/coleary-noaa/Bering_Sea_shelf_indices_-WBS-EBS-NBS-.

Acknowledgments

We thank the many scientists who have worked long hours to provide additional survey data in the western, eastern, and northern Bering Sea, and in particular B. Lauth and L. Britt for their leadership of the eastern Bering Sea team in the AFSC's Groundfish Assessment Program. We would also like to thank M. Stepanenko for their work in the international surveys and I. Glebov and A. Savin for their leadership in coordinating the Russian survey programs. Finally, we would like to thank L. Eisner, N. Laman, and three anonymous reviewers for their helpful comments on earlier drafts. C. O'Leary and L. De-Filippo were partially supported by North Pacific Research Board grant #1805. The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the author(s) and do not necessarily reflect those of NOAA or the US Department of Commerce.

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Handling Editor: Ernesto Jardim