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Ontogeny matters: Climate variability and effects on fish distribution in the eastern Bering Sea

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Abstract

Analyses of climate effects often ignore differences in life history for individual species. We analyzed a 34-year time series of eastern Bering Sea fish surveys to evaluate changes in distribution by length and between cold and warm shelf-wide average water temperatures for 20 species over inhabited depth, temperature, and location. All species showed evidence of ontogenetic migration. Differences in distribution between years with warm and years with cold shelf-wide water temperatures varied among species and within species at different lengths. For species where shelf-wide temperature effects were detected, the mid-sized fish were most active in changing spatial distribution. For aquatic organisms ontogenetic migration occurs because life history stages have different environmental requirements. This study illustrates the need to consider species responses to climate change over different life history stages, and that studies on ecosystem responses should take ontogenetic differences into consideration when assessing impacts.

KEYWORDS
Bering Sea, climate change, ecosystem, fish distribution, fisheries, ontogenetic migration

1 | INTRODUCTION

Human-induced climate change is affecting ecosystems planet-wide (Walther et al., 2002; Root et al., 2003). The effects of climate change on marine ecosystems have been widely reported (Doney et al., 2012) from the North Sea (Perry, Low, Ellis, & Reynolds, 2005; Dulvy et al., 2008) to South-eastern Australia (Last et al., 2011), and regions in between (Murawski, 1993; Hughes et al., 2003; Hsieh, Kim, Watson, Di Lorenzo, & Orgesugihara, 2009). Evidence of climate impacts on shifts in the spatial distribution of marine organisms has been observed in several regions of the globe with associated implications for transboundary stock fisheries management (Astthorsson, Valdimarsson, Gudmundsdottir, & Óskarsson, 2012; Dulvy et al., 2008; Lehodey, Senina, Nicol, & Hampton, 2015; Nye, Link, Hare, & Overholtz, 2009; Pinsky et al., 2013).

The ecosystem-wide impacts of climate variability on the eastern Bering Sea shelf have previously been described (Overland & Stabeno, 2004; Grebmeier et al., 2006; Mueter & Litzow, 2008), as well as impacts on the distribution (Spencer, 2008; Kotwicki & Lauth, 2013; Spencer et al., 2016; Stevenson & Lauth, 2012), and recruitment of individual populations (Wilderbuer et al., 2002; Wilderbuer, Stockhausen, & Bond, 2013; Mueter, Bond, Ianelli, & Hollowed, 2011). However, these studies have focused on climate effects at the population or ecosystem level.

The biotic and abiotic requirements for marine organisms change over subsequent life stages (Dahlgren & Eggleston, 2000) and ontogenetic migration of marine species is common (Wilbur, 1980; Gibson, Robb, Wennhage, & Burrows, 2002; Kotwicki, Buckley, Honkalehto, & Walters, 2005; Hoff, 2008). Therefore, diverse life histories within marine ecosystems present multiple avenues for climate to impact individual species as they grow and mature (Rijnsdorp et al., 2009; Petitgas et al., 2013). Evaluating effects of climate variability across multiple species with divergent life history strategies at different life stages could help identify which species are sensitive to changes in the environment and whether consistent chokepoints exist for species with similar strategies.

The Alaska Fisheries Science Center (AFSC) has conducted annual bottom trawl surveys of the south-eastern Bering Sea shelf since 1982 (Lauth & Conner, 2014). Length data on fish species commonly encountered were collected during these surveys, providing a 34-year time series of species distributions by size. Changes in fish distribution from juvenile post-settlement stages through maturity are available for 20 eastern Bering Sea fish species based on bottom temperature data collected during the annual surveys. The goals of this study were to use these data to: (i) identify ontogenetic distributional patterns, (ii) distinguish how species with similar life history strategies utilize habitat throughout their lifetime, and (iii) assess trends in spatial distribution by length that may be associated with changes in shelf-wide bottom temperatures.

2 | MATERIALS AND METHODS

All data used in this study were from the 1982 through 2015 AFSC annual south-eastern Bering Sea bottom trawl survey. The AFSC annual south-eastern Bering Sea bottom trawl survey data collection methods have been fully documented by Bakkala (1993), Spencer (2008), and Lauth and Conner (2014). Bottom trawl surveys of the south-eastern Bering Sea shelf have been conducted since the 1940s. However, a change in trawl gear occurred in 1982; thus, only data collected since 1982 were used in this study to ensure consistency. Each annual survey consisted of an average of 407 trawl hauls. In each trawl haul all fauna in a sample were identified to the finest taxonomic category possible (Stevenson & Hoff, 2009), weighed, and individually measured (Lauth, 2010).

The catch/unit effort (CPUE number km^{-2}), weighted mean location (eastings and northings in UTM zone 2), weighted mean depth, and weighted mean bottom temperature were calculated for each species and length category for each year. There were 20 species from six families for which there were sufficient data to conduct this analysis (Table 1). For each species the length data were binned into five percentile length categories: 0%–10%, 10%–30%, 30%–70%, 70%–90%, and 90%–100% of the raw length frequency distribution for the full time series.

For each individual haul, h, and species, s, CPUE was calculated as,

$$\text{CPUE}_{sh} = \frac{K_{sh}}{W_h D_h} \quad (1)$$

where K is the total number of fish of species s in haul h, W is the average net width of haul h in kilometers and D is the tow length of haul h in kilometers. The proportion, p, of fish of species s in length category l in haul h was calculated as,

$$p_{slh} = \frac{n_{slh}}{n_{sh}} \quad (2)$$

where n_{slh} is the number of fish of species s in length category l for haul h, and n_{sh} is the number of fish of species s in haul h. The number of fish of species s in length category l for haul h/km^2, N_{slh}, was calculated as,

$$N_{slh} = p_{slh} \times \text{CPUE}_{sh} \quad (3)$$

The weighted mean latitude, longitude, bottom depth, or bottom temperature for each length category by year, M_{xly}, was calculated as the weighted mean by year, y, as,

$$M_{xly} = \frac{\sum N_{slhy} x_{shy}}{\sum N_{slhy}} \quad (4)$$

where x_{shy} is the location of a haul in latitude, longitude, bottom depth, or bottom temperature.

The mean shelf-wide bottom temperature for each year, $\bar{t}_y$ were calculated following the methods presented in Spencer (2008) as,

$$\bar{t}_y = \sum_{i=1}^{b} \sum_{j=1}^{n_{iy}} \frac{f_i}{m_{iy}} x_{jiy} \quad (5)$$

where f_i is the proportion of the survey area in strata i, m_{iy} is the number of hauls in strata i for year y, x_{ij} is bottom temperature in haul j and strata i and year y, and b is the number of strata. Each year was categorized as warm, cold, or medium (above, below, or within ± 0.5 SD of the overall years shelf mean bottom temperature; $\mu = 2.43°C$, $\sigma = 0.78°C$). For the 1982–2015 time series there were 12 warm years and 12 cold years (warm years 1983, 1987, 1989, 1993, 1996, 1998, 2002–2005, 2014 and 2015; cold years 1986, 1992, 1994, 1995, 1999, 2006–2010, 2012, and 2013), and contrary to other regions and metrics (Levitus, Antonov, Boyer, & Stephens, 2000) no consistent warming trend has been observed.

Two-tailed permutation testing (Sprent, 1993) was used to evaluate the differences in the weighted mean locations, bottom temperatures, and bottom depths between length categories and whether there were differences in distribution within length categories between years with warmer and colder than average shelf-wide water temperatures. All data extraction, manipulation, and analysis was conducted using R (R Core Team 2015). For each permutation test, 10,000 resamplings of the shuffled data were performed. Tests were deemed significant when the absolute observed differences were greater than 95% of the absolute permuted differences ($\alpha = 0.05$).

3 | RESULTS

3.1 | Ontogenetic distributional shifts

The species evaluated in this analysis exhibited a diverse array of distributional differences over their life histories. Every species displayed some differentiation in location (Figure 1), depth (Figure 2), or temperature (Figure 2) at different lengths. Most demonstrated differentiation across more than one of these environmental axes. All species but Arctic cod (*Boreogadus saida*) exhibited changes in northings (latitude) between at least one pair of length categories (Figure 3) and all species except yellow Irish lord (*Hemilepidotus jordani*) displayed a change in eastings (longitude) for at least one pair of length categories (Figure 3). Except for Kamchatka flounder

TABLE 1 AFSC eastern Bering Sea summer bottom trawl survey catch per unit effort (number kg^{-2}) overall weighted mean bottom temperature (°C), overall weighted mean bottom depth (m), direction of ontogenetic depth migration, and difference in weighted means from colder to warmer than average years for 20 eastern Bering Sea species from the 1982–2015 Alaska Fisheries Science Center summer bottom trawl surveys. Length categories are the length ranges used in the analysis, Δ is the change from cold to warm years for the weighted mean bottom depths (Δ depth), bottom temperatures (Δ temp.), northings UTM (Δ northings), and eastings UTM (Δ eastings)

Species	Mean temp. (°C)	Mean depth (m)	Ontogenetic depth migration	Length categories		Δ depth (m)	Δ temp. (°C)	Δ northings (km)	Δ eastings (km)
Shelf-wide means	2.43	81.6				−0.1	−1.7	−0.7	−1.6
Family: *Cottidae*									
Great sculpin *Myoxocephalus polyacanthocephalus*	2.36	76.1	Descending	1	0–33 cm	−6.0	−1.5**	−24.0	135.4
				2	34–42 cm	3.3	−2.3**	21.0	−40.8
				3	43–54 cm	−7.0	−1.9**	0.0	23.3
				4	55–66 cm	−1.6	−1.9**	30.8	−74.2*
				5	67–94 cm	−3.2	−1.6**	−22.7	−30.5
Yellow Irish lord *Hemilepidotus jordani*	3.12	73	Ascending	1	0–24 cm	2.6	−2.2**	−36.1	3.0
				2	25–31 cm	3.1	−2.0**	−17.8	−57.9
				3	32–38 cm	−3.2	−2.2**	−18.2*	−7.5
				4	39–42 cm	−6.3**	−2.6**	−8.0	−3.9
				5	43–51 cm	−7.6**	−2.4**	−18.9	−10.2
Family: *Gadidae*									
Arctic cod *Boreogadus saida*	−0.6	64.1	Descending	1	0–9 cm	−11.7	0.2	−84.9**	100.3
				2	10–11 cm	−13.5	−0.2	−89.6	102.8
				3	12–15 cm	0.6	−0.8	−74.3*	39.0
				4	16–18 cm	−8.1	−0.6	14.3	41.9
				5	19–30 cm	−5.1	−0.3	−28.5	46.7
Pacific cod *Gadus macrocephalus*	2.5	67.5	Descending	1	0–20 cm	1.8	−2.2**	−14.7	10.3
				2	21–34 cm	5.7	−1.9**	−69.3**	0.3
				3	35–55 cm	9.7*	−1.8**	−43.8**	−24.6
				4	56–69 cm	7.2	−1.4**	−27.1	−5.1
				5	70–117 cm	−0.4	−1.2**	−9.0	7.6
Walleye pollock *Gadus chalcogrammus*	2.4	97.4	Mixed	1	0–15 cm	1.8	−1.4**	−35.5*	2.4
				2	16–39 cm	7.1	−1.5**	−1.1	−47.9
				3	40–54 cm	9.1*	−1.1**	−6.4	−39.9
				4	55–63 cm	9.2**	−1.3**	−29.3	−69.3*
				5	64–95 cm	9.1**	−1.8**	−72.8**	−7.3
Family: *Pleuronectidae*									
Alaska plaice *Pleuronectes quadrituberculatus*	1.94	56.5	Descending	1	0–24 cm	−0.8	−1.7**	6.8	−9.3
				2	25–30 cm	−1.8	−2.0**	3.4	11.9
				3	31–38 cm	−2.4*	−1.9**	4.5	14.0
				4	39–45 cm	−1.4	−2.2**	−4.5	6.4
				5	46–72 cm	−3.8*	−2.2**	3.9	9.6
Arrowtooth flounder *Atheresthes stomias*	3.53	111.5	Descending	1	0–19 cm	5.7	−1.0**	−10.4	−29.4
				2	20–28 cm	13.0**	−1.0**	−22.5	−16.7
				3	29–41 cm	9.3**	−1.0**	−7.3	−34.0
				4	42–52 cm	2.9	−0.8**	−32.7	20.5
				5	53–98 cm	3.7	−0.8**	−33.2	29.6

(Continues)

TABLE 1 (Continued)

Species	Mean temp. (°C)	Mean depth (m)	Ontogenetic depth migration	Length categories		Δ depth (m)	Δ temp. (°C)	Δ northings (km)	Δ eastings (km)
Bering flounder	0.19	83.1	Mixed	1	0–14 cm	−2.9	−1.3**	−19.5	30.0
Hippoglossoides robustus				2	15–19 cm	3.9	−1.2**	−40.1**	1.7
				3	20–29 cm	7.2**	−1.2**	−22.2*	−13.3
				4	30–35 cm	9.6**	−1.2**	−27.3**	−25.5*
				5	36–51 cm	7.8**	−1.3**	−52.1**	−12.2
Flathead sole	2.9	108.1	Ascending	1	0–15 cm	8.1	−0.6**	−15.7	−7.2
Hippoglossoides elassodon				2	16–23 cm	2.4	−0.8**	−10.8	4.8
				3	24–33 cm	−0.3	−1.1**	−1.4	−9.5
				4	34–39 cm	−0.1	−1.4**	1.9	−17.1
				5	40–66 cm	−2.8	−1.6**	−25.9	9.3
Greenland turbot	1.47	117	Descending	1	0–14 cm	−7.2	−1.2**	−98.6**	89.0
Reinhardtius hippoglossiodes				2	15–26 cm	−0.3	−0.9**	−28.5	17.9
				3	27–46 cm	5.7*	−1.0**	4.2	−23.4*
				4	47–75 cm	12.5*	−0.6**	25.4	−56.1*
				5	76–109 cm	10.8**	−0.9**	15.1	−43.6
Kamchatka flounder	3.15	119.6	None	1	0–18 cm	2.0	−1.0**	−65.1	100.9
Atheresthes evermanni				2	19–27 cm	0.9	−1.0**	−73.3*	137.5
				3	28–39 cm	5.5*	−1.1**	7.6	−26.2
				4	40–48 cm	4.2	−1.0**	10.5	−33.1
				5	49–96 cm	7.2	−1.0**	7.3	−30.3
Northern rock sole	3.07	52.1	Descending	1	0–15 cm	−0.6	−2.0**	−11.3	39.9
Lepidopsetta polyxystra				2	16–22 cm	0.6	−2.4**	2.2	14.0
				3	23–30 cm	2.2	−2.5**	−34.1**	20.2
				4	31–35 cm	2.5	−2.4**	−49.0**	−0.5
				5	36–65 cm	−0.1	−2.2**	−35.4*	2.2
Pacific halibut	3.53	60.6	Descending	1	0–32 cm	5.6	−2.3**	−5.7	43.3
Hippoglossus stenolepis				2	33–43 cm	9.1*	−2.9**	−44.9**	22.6
				3	44–63 cm	5.1*	−2.4**	−37.5	19.3*
				4	64–81 cm	−1.0	−1.7**	−21.7	42.9
				5	82–198 cm	1.4	−1.7**	−0.6	−3.2
Rex sole	3.76	126.7	Ascending	1	0–23 cm	5.9	−0.8**	1.7	−50.0
Glyptocephalus zachirus				2	24–30 cm	−3.7	−0.5**	6.6	3.6
				3	31–39 cm	−2.3	−0.7**	10.1	−20.4
				4	40–45 cm	0.7	−0.9**	−15.6	−5.7
				5	46–75 cm	0.6	−0.9**	−14.6	−8.5
Starry flounder	3.95	38.9	Descending	1	0–34 cm	6.1	−3.1**	−49.0**	73.4**
Platichthys stellatus				2	35–40 cm	3.5	−2.5**	−43.9**	60.6**
				3	41–49 cm	1.7	−2.3**	−28.9	57.7**
				4	50–55 cm	−0.6	−2.2**	3.0	8.4
				5	56–78 cm	3.9	−2.1**	−37.1*	15.5
Yellowfin sole	3.1	47.7	Descending	1	0–17 cm	0.0	−1.6**	−6.5	29.1
Limanda aspera				2	18–23 cm	0.3	−2.1**	−0.2	1.9
				3	24–30 cm	−1.9	−1.9**	2.2	13.3
				4	31–34 cm	−2.8	−1.8**	6.3	7.8
				5	35–73 cm	−3.6*	−1.7**	6.1	10.4

(Continues)

TABLE 1 (Continued)

Species	Mean temp. (°C)	Mean depth (m)	Ontogenetic depth migration	Length categories		Δ depth (m)	Δ temp. (°C)	Δ northings (km)	Δ eastings (km)
Family: *Rajidae*									
Alaska skate	2.26	78.2	Mixed	1	0–37 cm	2.7	−1.4**	−29.3	11.5
Bathyraja parmifera				2	38–54 cm	6.8**	−2.1**	−15.6	−26.1
				3	55–84 cm	5.6*	−2.0**	−20.4*	−24.2
				4	85–98 cm	−2.6	−1.6**	−12.4	−0.5
				5	99–162 cm	−6.1	−1.4**	4.1	13.1
Bering skate	3.34	130.4	Ascending	1	0–38 cm	3.0	−0.8**	−22.1	23.0
Bathyraja interrupta				2	39–56 cm	3.9	−1.0**	−17.4	31.0
				3	57–72 cm	3.0	−0.8**	−48.8	60.6
				4	73–76 cm	−4.7	−1.2**	−0.5	13.9
				5	77–162 cm	−4.5	−1.2**	−13.2	14.1
Family: *Scorpeniformes*									
Bigmouth sculpin	2.56	110.1	Ascending	1	0–36 cm	9.4	−1.1**	26.6	−85.5
Hemitripterus bolini				2	37–50 cm	3.6	−0.7**	−20.7	3.9
				3	51–63 cm	11.4**	−1.2**	16.6	−56.8*
				4	64–68 cm	2.2	−1.5*	−29.6	3.3
				5	69–79 cm	8.8	−1.3**	−6.1	−39.2
Family: *Sebastidae*									
Pacific ocean perch	3.48	151.6	Descending	1	0–19 cm	−14.8*	−0.5	30.7	−108.5
Sebastes alutus				2	20–25 cm	−27.3	−0.4	−1.5	−70.9
				3	26–36 cm	−20.3	−0.7*	−104.7*	40.5*
				4	37–40 cm	−11.9	−0.8*	−79.9	30.6
				5	41–66 cm	−18.1	−0.9*	−107.9	43.0*

**indicates p values ≤0.01 and *indicates p values >0.01 and ≤0.05 from the two-tailed permutation test.

(*Atheresthes evermanni*) all species exhibited changes in depth between at least one pair of length categories (Figure 4). Only Arctic cod, yellow Irish lord, and Pacific ocean perch (*Sebastes alutus*) failed to exhibit detectable changes in temperature between at least one pair of length categories (Figure 4).

Each of the environmental factors investigated were confounded to some extent in the survey area (e.g., temperature with northings and depth with eastings). However, for some species, changes in one axis did not correlate with changes in the other factors. All but three species which did not exhibit significant differences in mean temperature between at least one pair of length categories showed a combination of changes in depth and location to maintain a static temperature. This suggests a strong temperature preference throughout post-settlement life stages in these species.

In general, smaller fish resided in nursery areas which presented environmental conditions (temperature, depth, and location) different from the mean shelf conditions. Fish typically expanded across the shelf into a broader range of temperatures and depths as they grew. Their mean distribution therefore tended to move from specific nursery conditions at smaller sizes towards the mean shelf conditions at larger sizes. Three distinct depth migration strategies can be discerned from these data; descending, ascending, and mixed ontogenetic migration. A descending strategy in which larger fish were found in deeper waters was most common, being observed in eleven species (Table 1). Five species exhibited an ascending strategy with larger fish found in shallower waters. How each species ascends or descends depended on where they initially settled. For example, Bering skates (*Bathyraja interrupta*), which have nurseries near the shelf edge (Hoff, 2008), ascended and spread to the northwest, bigmouth sculpin (*Hemitripterus bolini*) ascended to the southeast, yellow Irish lord (*H. jordani*) did not change depth substantially, while flathead sole (*Hippoglossoides elassodon*) and rex sole (*Glyptocephalus zachirus*) both ascended and spread easterly. All of the descending species, except arrowtooth flounder (*Atheresthes stomias*) and Arctic cod, descended either south or southwest. Arrowtooth flounder, a deeper water species, descended and spread to the northwest at larger lengths, while the center of abundance of Arctic cod shifted westward for the three largest length categories. The three species with mixed ontogenetic migration were walleye pollock (*Gadus chalcogrammus*), Bering flounder (*Hippoglossoides robustus*), and Alaska skate (*Bathyraja parmifera*). Small walleye pollock were widespread throughout the shelf area, mid-length walleye pollock were
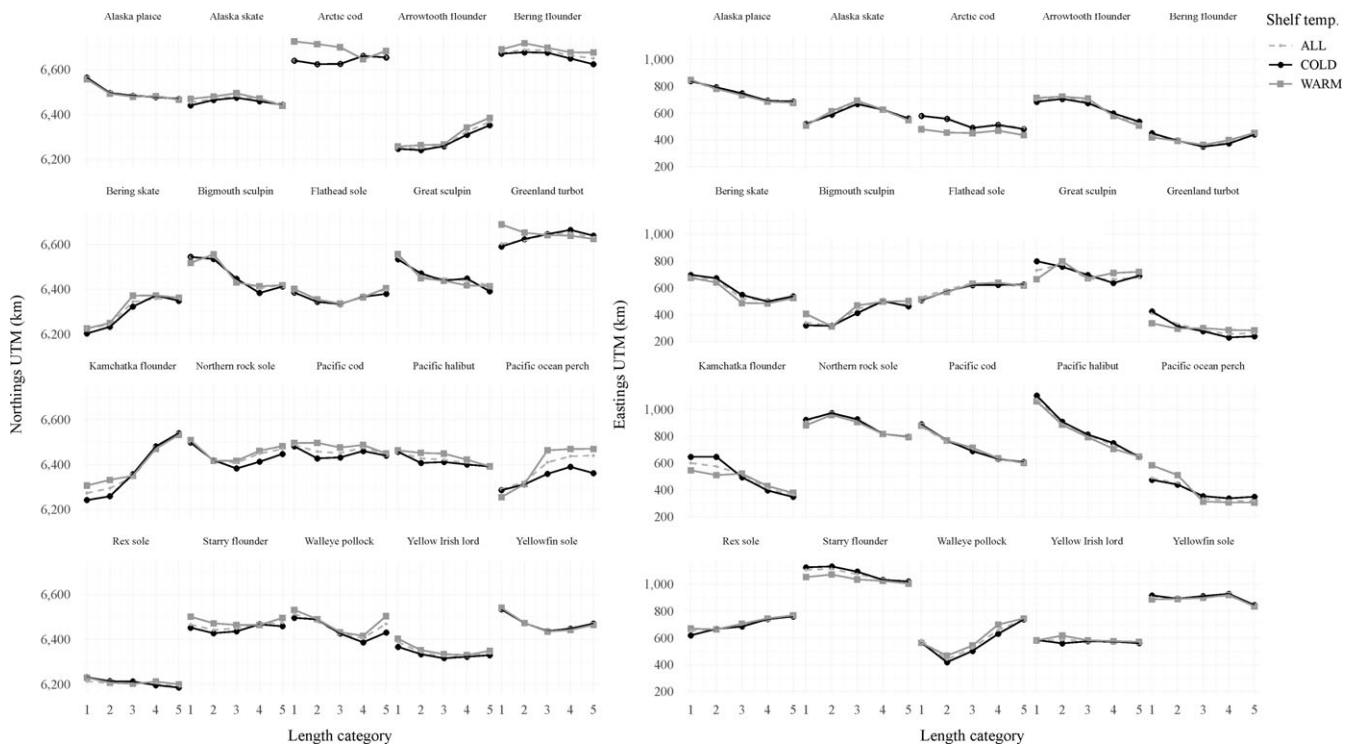
FIGURE 1 Weighted mean eastings and northings in kilometers for UTM zone 2 for warm and cold years for 20 eastern Bering Sea species from the 1982–2015 Alaska Fisheries Science Center summer bottom trawl surveys. Dashed line is the mean for all years for each length category
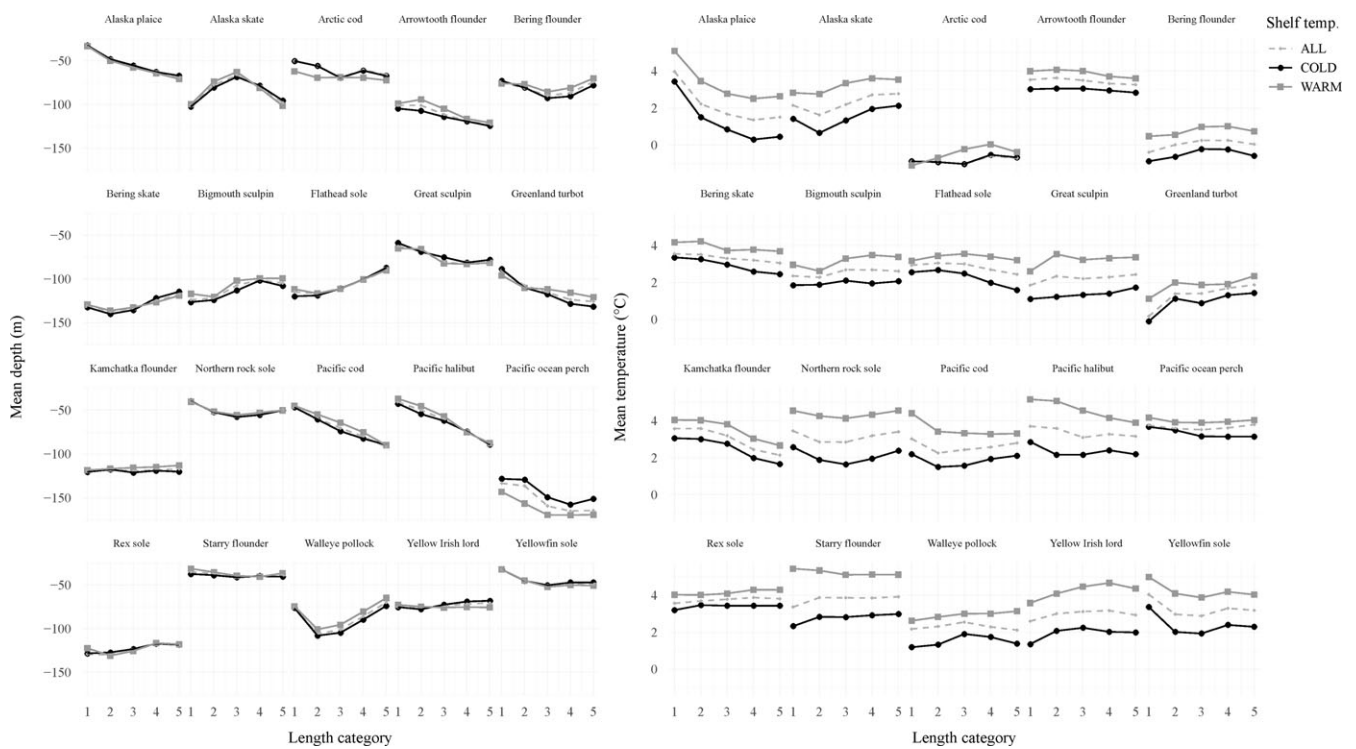
FIGURE 2 Weighted mean depth (m) and temperature (°C) for warm and cold years for 20 eastern Bering Sea species from the 1982–2015 Alaska Fisheries Science Center summer bottom trawl surveys. Dashed line is the mean for all years for each length category

farther west in deeper, colder waters, and the largest walleye pollock were farther to the east in shallow, warmer waters. Small Bering flounder were centered in cold northern waters then spread westerly

to deeper warmer waters as they grow. The largest and smallest length categories of Bering flounder were observed at the same depths; however, the largest category appear to have a more

southern center of abundance. Alaska skate also presented a mixed strategy with the smallest and largest specimens found in deeper waters than the mid-sized specimens. Small Alaska skates, although found at the same mean depth as the larger Alaska skates, were distributed farther north in colder waters.

Only Kamchatka flounder displayed no discernable change in mean depth as they grew larger. Although their center of distribution changed to colder waters farther to the northwest as they grew, their mean depth remained between 117 and 119-m for all length categories. The lack of movement was likely due to the survey encountering Kamchatka flounder in a small fraction of its depth range (Hoff, 2016). The center of distribution for this species is much deeper than the maximum depth of the AFSC annual southeastern Bering Sea bottom trawl survey used in this study (Hoff, 2016).

3.2 | Shelf-wide temperature influences

Differences in distribution between years with above and years with below average shelf-wide water temperatures were not found to be consistent among species or within species at different length categories (Table 1 and Figure 5). Not including inhabited temperature differences, all but Bering skate, flathead sole, and rex sole showed significant change in at least one of three axes for some portion of their life history. The three species that did not change were species which settle in deeper than average depths

and have an ascending life history. For species in which a shelf-wide temperature effect was detected, the mid-length fish displayed the most shifts in distribution, with five of 20 species from length category 1 having significant differences in axes other than inhabited temperature, seven of 20 from category 2, 16 of 20 from category 3, seven of 20 from category 4, and nine of 20 from category 5. Detectable latitudinal shifts were observed in 12 of 20 species and 22 of 100 length categories. Latitudinal shifts were always to the north for the warmer than average years. Detectable longitudinal shifts were less common, with changes in eight of 20 species and 13 of 100 length categories. However, the direction of significant change was not consistent; eight were observed eastward and five westward. Changes in depth were common, with 12 species and 24 length categories having discernible change in depth with a change in shelf-wide water temperatures. For species having more than one length category with significant changes in depth, the direction of the shift was always consistent across length categories. The directions of change were not consistent among species, with four species found in deeper waters and eight in shallower waters during warm years. Only two species, Arctic cod and Pacific ocean perch, displayed strong temperature preferences, where changes in inhabited mean water temperature did not change significantly with shelf-wide temperatures. Both species were found deeper and farther to the northwest in warm years. These two species also exhibited strong preferences to specific water temperatures across length categories.
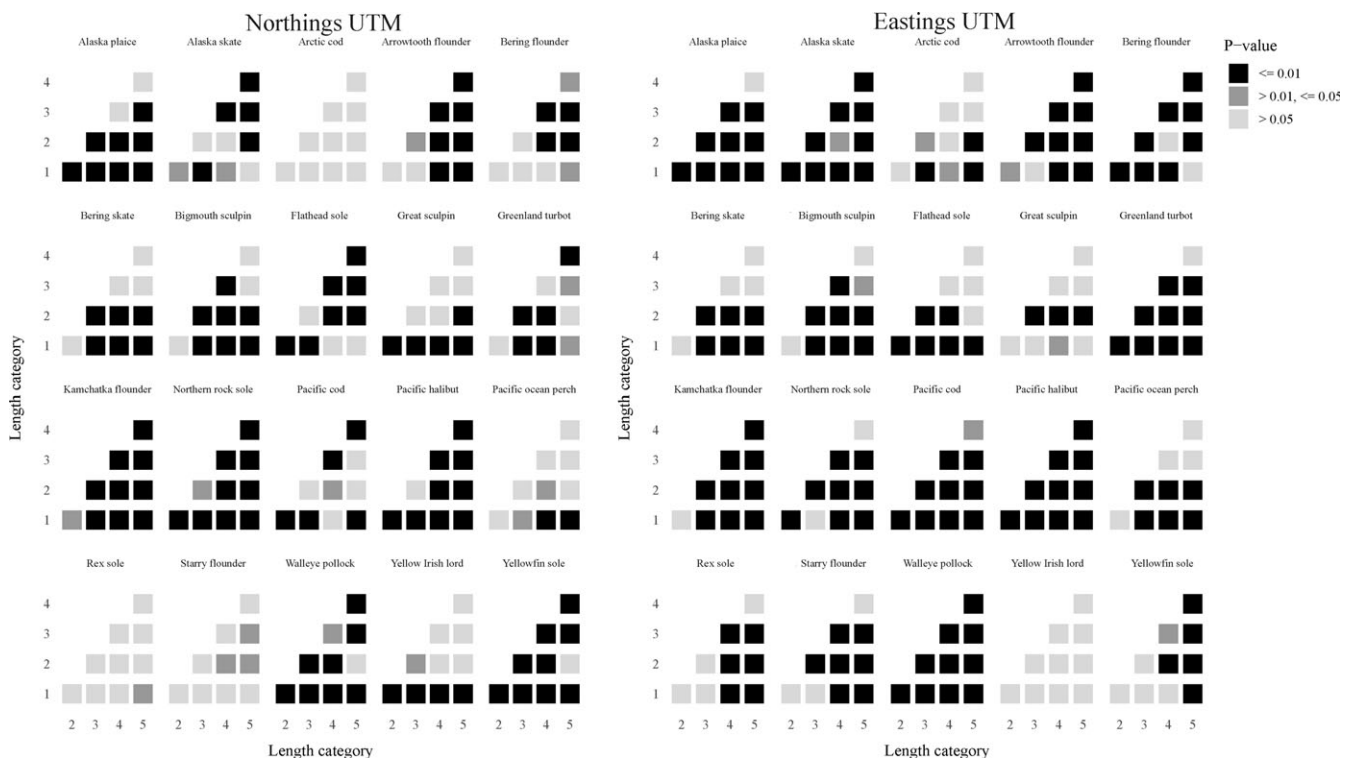
FIGURE 3 Paired length category permutation test result *p* values for mean northings and eastings for 20 eastern Bering Sea species from the 1982–2015 Alaska Fisheries Science Center summer bottom trawl surveys
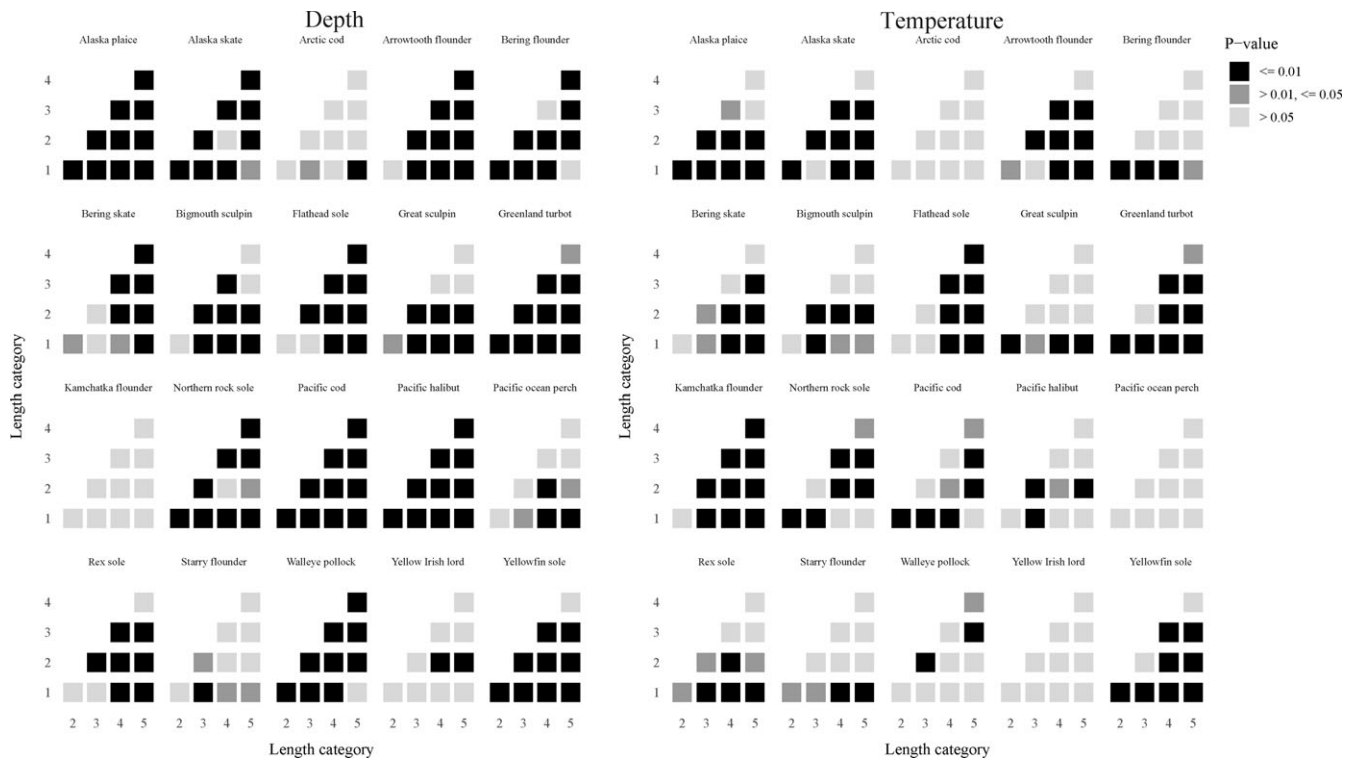
FIGURE 4 Paired length category permutation test result *p* values for mean depth and temperature for 20 eastern Bering Sea species from the 1982–2015 Alaska Fisheries Science Center summer bottom trawl surveys

4 | DISCUSSION

Environmental delineations within ecosystems can be clinal, and biotic and abiotic requirements for most species change with ontogeny (Snyder & Chesson, 2004). Previous studies have identified spatial structure within the southeastern Bering Sea shelf (Baker & Hollowed, 2014), and some studies revealed the importance of size as an important determinant of spatial distributions (Bartolino, Cianelli, Bacheler, & Chan, 2011). Our study extends previous work to provide an assessment of summer utilization of the Bering Sea shelf landscape across multiple species. We found that every species examined showed some form of ontogenetic shift in distribution associated with location, depth, temperature, or combinations thereof.

Climate change will impact the Bering Sea and effect changes resembling conditions similar to the warm years examined in this paper (Wang, Overland, & Stabeno, 2012). Results show that the effects of this warming on individual species will be variable and likely specific to each life stage. This suggests that there are multiple points at which climate change differentially impacts the distribution, growth, and survival of aquatic fauna. Therefore, it is essential that future climate vulnerability assessments (Hare et al., 2016) evaluate the exposure of marine organisms at different life stages to changing environmental conditions.

The most consistent effect in the eastern Bering Sea to changes in shelf-wide bottom temperatures was a southward shift in distribution during cold years. This was observed in 12 of the 20 species examined, including fishes from a diverse array of life histories. One of these species, juvenile Greenland turbot (0–14 cm), shifted their

center of distribution 98.6 km southward in cold years. Temperature preference was likely not a strong influence on juvenile Greenland turbot distribution as the difference in inhabited temperature (1.2°C) was similar to the difference in overall shelf-wide bottom temperatures (1.7°C) from cold to warm years (Table 1). However, current flow in the Bering Sea in the spring has alternated between strong northwesterly flow during cold years to relatively weak southeasterly flow in warm years (Stabeno et al., 2012). Greenland turbot larvae are reliant on spring currents for transport between winter spawning locations in southeastern canyons to suitable nursery areas on the northwest shelf (Duffy-Anderson et al., 2013) and are therefore more likely to be transported to suitable habitat during cold years. Better survival of Greenland turbot settled juveniles in cold years may be evident in improved recruitment for year classes originating in cold years (Barbeaux, Ianelli, Nichol, & Hoff, 2016).

Small walleye pollock (0–15 cm) show a 35 km shift southward in cold years. Most of this shift in distribution appears to be in direct relation to the cold pool distribution as small walleye pollock distribution appears to expand and contract with the cold pool (Barbeaux, 2017). The strong distributional relationship between small walleye pollock and the cold pool is likely a strategy to avoid larger groundfish predators such as arrowtooth flounder and adult walleye pollock which are more abundant in warmer waters outside the cold pool (Wyllie-Echeverria & Wooster, 1998; Hollowed et al., 2012; Spencer, 2016).

Similar to Greenland turbot and walleye pollock, northern rock sole demonstrated a 34–49 km southward shift in distribution in cold years; however, unlike Greenland turbot and walleye pollock,
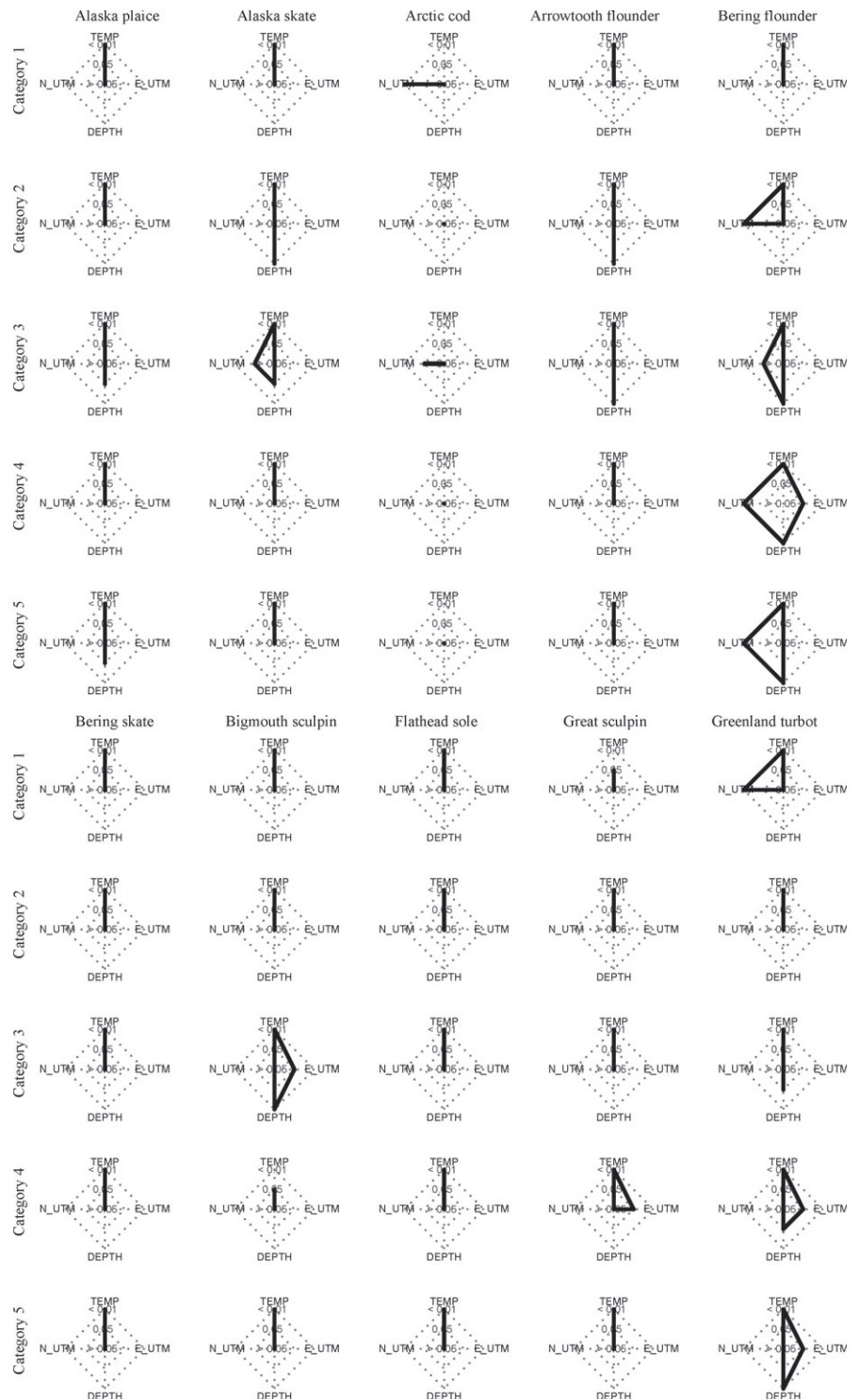
FIGURE 5 p Values from the two-tailed permutation tests for difference in catch/unit effort (number kg^{-2}) weighted mean northings (N_UTM), eastings (E_UTM), bottom depth (DEPTH), and temperature (TEMP) between warmer and colder than average years for 20 eastern Bering Sea species from the 1982–2015 Alaska Fisheries Science Center summer bottom trawl surveys

only larger northern rock sole (>23 cm) changed distribution. Northern rock sole is a shallow water species (overall population centered at 52 m) that settles in the inner domain shoreward of the cold pool and migrates westward to deeper water as it grows (Barbeaux, 2017). For this species settlement and growth has been found to be highly dependent on temperature (Laurel, Danley, & Haines, 2014) and distribution was likely influenced by different growth rates between warm and cold years. The change in inhabited temperature between warm and cold years (Table 1) for this species is highly

significant with a greater difference (2.0–2.5°C) than observed on the shelf overall (1.7°C). An apparent southward shift with temperature may be an artifact of different settlement times, growth rates between warm and cold years for this species, and greater ability for larger fish to actively avoid unfavorable conditions. In contrast, although the distribution of small Arctic cod (<15 cm) shifted between 70 and 90 km southward, the difference in inhabited temperature for this species from cold to warm years was not significant (Table 1), suggesting that distribution may be bounded by the
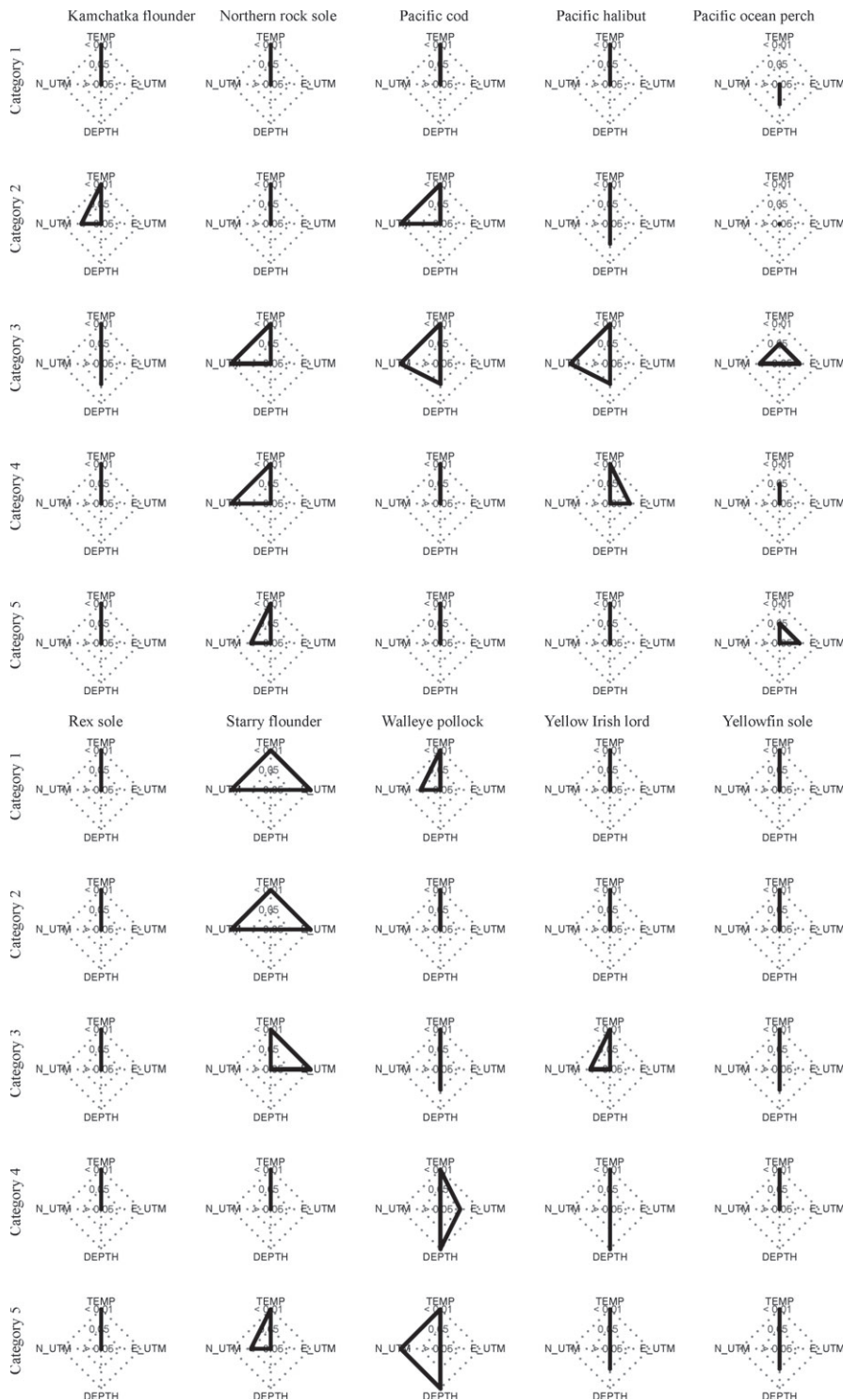
FIGURE 5 Continued

species physiology and temperature range preferences (Laurel, Spencer, Iseri, & Copeman, 2016).

Another common effect, observed in 13 of 20 species examined, was a change in mean bottom depth between warm and cold years. The direction of movement, however, was not consistent among species examined. Of the 13 species examined, nine species shifted to deeper waters and four shifted to shallower waters in cold years in at least one length category. Of those that moved deeper in the cold years, only Greenland turbot (<75 cm), Kamchatka flounder (28–39 cm) and arrowtooth flounder (20–41 cm) did not concurrently change location. Arrowtooth flounder, Kamchatka flounder, and adult Greenland turbot inhabit deeper waters along the continental shelf break and therefore required little movement to reach different bottom depths. Their movement to deeper waters in cold years was likely in response to a shift to deeper waters by walleye pollock, their predominant prey.

Adult walleye pollock prey on euphausiids, copepods, and hyperiids in the summer months (Aydin, Gaichas, Ortiz, Kinzey, & Friday, 2007) which have been at highest abundance in the nutrient rich waters just offshore of the inner front (Hunt et al., 2011, 2016). On the Bering Sea shelf the size of the cold pool defines the location and intensity of the inner front with colder than average years having had a stronger front located deeper and further west (Kachel et al., 2002). In addition, due to differences in timing of the ice melt and subsequent impacts on primary production, large and medium sized copepods and hyperiids have been more abundant in cold years (Hunt, 2011; Coyle et al., 2011; Stabeno, 2012; Eisner, 2014). Stomach content data collected during AFSC summer trawl surveys show copepods and hyperiids as a larger proportion of the walleye pollock summer diet in cold years (NOAA 2008). Variability in the availability of larger zooplankton likely drove the observed shift in adult walleye pollock distribution.

Pacific cod and Pacific halibut followed similar descending ontogenetic migration patterns, spreading as they grow from shallow waters inside Bristol Bay out onto the shelf and deeper waters. Both have shown a southern shift in distribution to deeper waters for mid-sized fish (35–55 cm for Pacific cod and 33–63 cm for Pacific halibut) in cold years. In Pacific cod and Pacific halibut, and over all species in general, changes in distribution with changing shelf conditions were not as common at the smallest or largest length categories. This may suggest that depth and location were in general less elastic for the largest adults and nursery grounds, while mid-sized fish were more mobile, able to move to more favorable feeding grounds and follow temperature range preferences. Alternatively, this may represent a change in growth between warmer and colder years at these mid-ranged-sized fish which would be on the steepest part of their growth curves (Pauly, 1980).

Four species, Alaska plaice, yellowfin sole, yellow Irish lord, and juvenile Pacific ocean perch (0–19 cm), exhibited a shift in distribution to shallower waters in cold years. The shifts in mean depth were not concurrent with changes in location and, except for Pacific ocean perch, were only observed in the larger length categories. Yellowfin sole and Alaska plaice are shallow water species; however, adult Alaska plaice inhabit lower than average shelf-wide temperatures while adult yellowfin sole inhabit warmer than average shelf-wide temperatures. Adult yellow Irish lord inhabit warmer than shelf-wide average waters primarily concentrated around the Pribilof Islands at depths between 50 m and 100 m. Differences in depths between warm and cold years for Alaska plaice, yellowfin sole, and yellow Irish lord were concurrent with symmetrical changes in distribution that were not detected as changes in mean location. Yellowfin sole exhibited a latitudinal contraction in both the northern and southern extent, yellow Irish lord contracted on a northwest to southeast axis, and Alaska plaice exhibited a longitudinal expansion in their eastern and western extent in cold years (Barbeaux, 2017). For each of these species the spatial changes coincided with a shallower average depth in cold years, but no change in the weighted mean location. For all three of these species the difference in inhabited temperatures between cold and warm years either matched or

exceeded the change in the shelf-wide bottom temperatures (Table 1), suggesting that these species did not have strong temperature preferences and changes in distribution were likely either influenced by prey availability or density (Spencer, 2008; Bartolino et al., 2011; Kotwicki & Lauth, 2013; Baker & Hollowed, 2014). In contrast, a significant change in depth for juvenile Pacific ocean perch between cold and warm years was not concurrent with a significant change in inhabited temperature, suggesting the opposite for this species in the eastern Bering Sea, as documented in other regions (Scott, 1995).

Only three of the species examined in this study failed to exhibit changes in location, or depth distribution between warm and cold years in all length categories. These species, Bering skate, flathead sole, and rex sole, inhabit deeper waters, greater than 100 m, and had ascending life histories. Spawning occurs in shallower waters of the shelf while juveniles migrate or settle in deeper waters on the slope and then migrate back onto the shelf as they grow and mature. Hoff (2010) speculates that for Bering skate this is an adaptation to avoid abundant shelf predators such as Pacific cod. In all three species, although the change in temperature between cold and warm years is statistically significant, the changes were lower for all length categories than the change in shelf-wide mean temperature (Table 1). Bering skates appear to be generalist feeding on whatever species dominates the benthos including tanner crab, shrimp, and fish (Aydin et al., 2007). Although benthic crustacean populations like tanner crab fluctuate with decadal scale temperature changes as recruitment varies, year to year changes in distribution do not track with changes in bottom temperatures (Orensanz, 2004). Rex sole prey on non-pandalid shrimp, polychaetes, and benthic amphipods, and flathead sole on brittle stars (Aydin et al., 2007). For the two flatfish species depth appears to be a more important factor than temperature and likely correlated with the distribution of bottom type and its associated prey (McConnaughey & Smith, 2000), which may change on decadal scales but would not be expected to change substantially between years.

Although other studies have examined the distribution of entire populations, in preparing for climate change impacts, ontogenetic factors should be taken into consideration. Changes in distribution and environmental preferences between life stages can influence projections of likely effects. Kotwicki and Lauth (2013) show distributional changes in many of the bottom fish populations we examined. However, their analysis did not look at ontogenetic factors, and therefore could lead analysts to incorrectly characterize impacts. For example, a change in distribution in both location and depth in walleye pollock was observed between warm and cold years in both Kotwicki and Lauth (2013) and this study. Taking into account ontogenetic differences revealed that these changes were limited to the larger fish. The unexplained variability in their results was likely due in part to changes in year-class strength and differences in ontogenetic distribution. Further, for walleye pollock and many other fish species, bioenergetics studies have shown significant ties between inhabited temperature and growth (Kooka, 2007). The lack of significant movement of the smaller walleye pollock between warm and

cold shelf-wide conditions, coupled with known changes in bioenergetics due to temperature, provides a clearer explanation for the magnitude of the effects on growth, survival, and recruitment to the fishery noted by many between warm and cold conditions in the eastern Bering Sea (e.g., Wespestad, Fritz, Ingraham, & Megrey, 2000; Mueter et al., 2011; Heintz, Siddon, Farley, & Napp, 2013).

Perry et al. (2005), Dulvy (2008), Nye et al. (2009) and Last (2011) describe shifts in distribution in North Sea, western Atlantic shelf and Australian fish species; however, their findings ignore ontogeny. Although these studies identify latitudinal and depth changes for many species, the broad treatment of each species in these studies and others may have masked important effects at finer resolutions across life histories (e.g., Pinsky, 2013). A closer analysis which examines changes at different life stages may reveal many more species with significant shifts in distribution in at least some portion of their life history.

Perry et al. (2005) and Last (2011) also concentrated on unidirectional changes in latitude and depth. We considered observed climate affected changes in depth in both directions, as well as longitudinal shifts. These seemingly contrary shifts make sense in context of the geography and oceanography of the study area. The eastern Bering Sea shelf resembles a slanted rectangular tabletop with shallow water to the east and deeper water to the west. Bottom water temperatures, although somewhat correlated with depth, are greatly influenced by the annual variability in the extent of a cold pool of water that extends and withdraws across the middle part of the shelf from the north to the south (Coachman, 1986). The extent of the cold pool is largely driven by the extent of sea ice during the winter months (Wyllie-Echeverria & Wooster, 1998) and is the driver for annual variability in the mean bottom water temperatures on the shelf measured during the summer bottom trawl surveys (Spencer, 2008). Species that settle on the edge of the shelf in deeper waters to the west of the cold pool are impacted by climate variability differently than species that settle in the shallow waters east of the cold pool.

Ontogenetic shifts in habitat use have been observed in both terrestrial and marine ecosystems. There are numerous evolutionary advantages to spatial shifts in habitat use, especially in species known to exhibit cannibalism (e.g., walleye pollock; Dwyer, Bailey, & Livingston, 1987), or density dependence (e.g., yellowfin sole; Bartolino et al., 2011). In species that exhibit periodic strong year classes that "store" substantial fractions of the population across years ("the storage effect"; Chesson, 1994), ontogenetic shifts in habitat use can be particularly important in mitigating density-dependent stress on a population. When ontogenetic shifts in habitat use and the storage effect are exhibited within a system of interacting species governed by a network of intermittent thermal gateways (Ciannelli & Bailey, 2005), the complex suite of linked factors underlying species co-existence is revealed. These findings suggest that the southeastern Bering Sea ecosystem may be an ideal natural system to explore what Wilson (2011) identifies as three of the most promising explanations for species co-existence: (i) allogenic

disturbance (fishing), (ii) environmental fluctuation and the storage effect, and (iii) ontogenetically mediated alpha niche differentiation.

For aquatic organisms, ontogenetic migration occurs because life history stages have different environmental requirements. This study illustrates the need to consider species responses to climate change over different life history stages, and that studies on ecosystem responses should take ontogenetic differences into consideration when assessing impacts.

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