


Subregional differences in groundfish distributional responses to anomalous ocean bottom temperatures in the northeast Pacific

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Abstract

Although climate-induced shifts in fish distribution have been widely reported at the population level, studies that account for ontogenetic shifts and subregional differences when assessing responses are rare. In this study, groundfish distributional changes in depth, latitude, and longitude were assessed at different size classes by species within nine subregions. We examined large, quality-controlled datasets of depth-stratified-random bottom trawl surveys conducted during summer in three large regions—the Gulf of Alaska and the west coasts of Canada and the United States—over the period 1996–2015, a time period punctuated by a marine “heat wave.” Temporal biases in bottom temperature were minimized by subdividing each region into three subregions, each with short-duration surveys. Near-bottom temperatures, weighted by stratum area, were unsynchronized across subregions and exhibited varying subregional interannual variability. The weighted mean bottom depths in the subregions also vary largely among subregions. The centroids (centers of gravity) of groundfish distribution were weighted with catch per unit effort and stratum area for 10 commercially important groundfish species by size class and subregion. Our multivariate analyses showed that there were significant differences in aggregate fish movement responses to warm temperatures across subregions but not among species or sizes. Groundfish demonstrated poleward responses to warming temperatures only in a few subregions and moved shallower or deeper to seek colder waters. The temperature responses of groundfish depended on where they were. Under global warming, groundfish may form geographically distinct thermal ecoregions along the northeast Pacific shelf. Shallow-depth species exhibited greatly different distributional responses to temperature changes across subregions while deep-depth species of different subregions tend to have relatively similar temperature responses. Future climate studies would benefit by considering fish distributions on small subregional scales.

KEYWORDS

centroids, climate change, depth, global warming, marine heat wave, poleward, subregion, survey variability, the center of gravity, thermal ecoregion

1 | INTRODUCTION

Distributional responses of marine organisms to warming temperatures have been well documented in the North Sea (Marshall et al., 2016; Perry, Low, Ellis, & Reynolds, 2005), Gulf of Maine (Kleisner et al., 2016; Nye, Link, Hare, & Overholtz, 2009), and elsewhere worldwide (Cheung, Watson, & Pauly, 2013; Pinsky, Worm, Fogarty, Sarmiento, & Levin, 2013). Several factors, including species, size, and subregional dynamics influence distributional responses to temperature changes, but the significance of each factor in shaping fish movements remains unknown. Differences in species-specific rates and direction of distributional responses to increasing temperatures have been recognized (Morley et al., 2018; Pinsky et al., 2013; Poloczanska et al., 2013). Some studies differentiated the responses to warm temperatures between deep-water species and shallow-water species (Hsieh, Kim, Watson, Lorenzo, & Sugihara, 2009; Kleisner et al., 2016) while others related differences in species responses to the traits and life history characteristics (Hollowed, Planque, & Loeng, 2013; Perry et al., 2005; Sunday et al., 2015). Yang et al. (2019) and Barbeaux and Hollowed (2018) detected that only some size classes responded to temperature changes. Moreover, recent studies suggest that the local geographic and oceanographic dynamics that operate on a subregional scale play a key role in shaping fish movements in northeast US shelf waters (Kleisner et al., 2016) and the North Sea (Marshall et al., 2016). Although distinct subregions have been identified based on physical and biological processes in the Gulf of Alaska (GOA; Mueter & Norcross, 2002) and the US west coast (King et al., 2011), previous studies examined fish distributions within large marine ecosystems (GOA and US west coast) rather than by subregions. To date, no studies have compared temperature responses of groundfish in space by species, size class, and subregion.

In this study, we assembled data of three long-term bottom trawl surveys along the northeast Pacific shelf and addressed two questions: (a) How does the ocean bottom temperature change across the northeast Pacific shelf, and (b) Are the groundfish distributional responses to anomalous ocean temperatures influenced by subregion, species, or size? These survey data are unique and valuable in that they provide coincident measurements of bottom temperature and groundfish population at each trawl site over a large geographic area. Because each regional survey required a few months to complete, the measurements were not simultaneous. This introduced biases owing to the Earth's annual solar cycle. These biases were reduced by subdividing each regional survey into three subregions, each requiring about 1 month to complete. We present the first attempt to quality control the data and as well as investigate the survey's inherent variations in depth, latitude, and longitude. Additionally, we dealt with two confounding factors. First, because many fish species showed strong ontogenetic shifts in addition to responses to warm temperatures (Barbeaux & Hollowed, 2018; Yang et al., 2019), we focused on distributional responses to warm temperatures for different size classes by species within subregion. Second, we compared fish multidirectional movements and identified the primary

movement due to temperature responses. As groundfish live on the sea floor with its complicated topography, their movement can be in three simultaneous directions: depth, longitude, and latitude. To analyze the multidirectional groundfish movement by subregion, species, and size class, we applied multivariate analyses, which are widely used in studying the community structure of fish (e.g., Baker & Hollowed, 2014) and zooplankton (e.g., Li et al., 2013) to the field of fish movement.

2 | MATERIALS AND METHODS

2.1 | Survey data and quality control

Time series data from three fishery-independent summer bottom trawl surveys conducted by NOAA's Alaska Fisheries Science Center (AFSC), Fisheries and Oceans Canada, and NOAA's Northwest Fisheries Science Center (NWFSC) from 1996 to 2015 were analyzed. These surveys span an area along the northeast Pacific shelf: the GOA, Canadian west coast, and US west coast (Figure 1). These three surveys are comparable in that they have a stratified random design based primarily upon depth and topography and measure: (a) the concentration of fish at each station (e.g., number per km²), (b) the ambient bottom temperature, and (c) the sizes (total or fork length to the nearest centimeter) of commercially important fish at each station. Each survey is consistently conducted in the same time of year from late May to late July or early August. We excluded US west coast survey data from mid-August to October (referred as survey pass 2) due to asynchronous timing relative to the GOA and Canadian west coast summer (May–early August) surveys. We also excluded earlier triennial bottom trawl surveys (conducted by NWFSC in 2004 and AFSC 1977–2001) along the US west coast due to inconsistency in survey design, gear, period, depths, and protocols. Description of the surveys utilized here, including stratum depth, can be found in the Supplement with more details in von Szalay, Raring, Shaw, Wilkins, and Martin (2016), Nottingham, Williams, Wyeth, and Olsen (2017, 2018a, 2018b) and Keller, Wallace, and Methot (2017).

Each survey was subdivided into three subregions based on survey characteristics, geographic and oceanographic conditions, and management areas (Figure 1). The surveys were from west to east in the GOA and north to south on the Canadian and US west coasts. As a spring-to-summer survey progresses, the observed sea bottom temperature usually tends to increase due to seasonality. This temporal trend was addressed by partitioning the surveys by subregion where samples were collected at similar months of the year within about a 1-month period. In general, the strata boundaries were selected to account for topography (e.g., canyons and troughs), oceanographic features (e.g., currents and temperatures), and known shifts in biodiversity and species composition. As our surveys are of depth-stratified-random design (see Supplement), we selected subregional boundaries that coincided with survey strata boundaries that were consistent with historical fishery management areas (Evans, 1998, Figure 1). We separated the GOA into

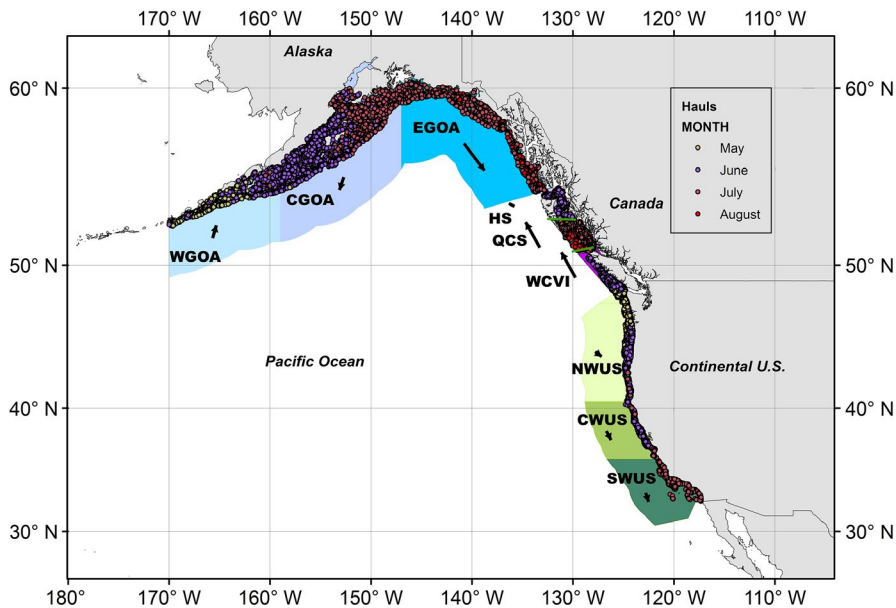


FIGURE 1 The study area (Mercator Projection) of the northeast Pacific including bottom trawl hauls (filled circles) in three surveys, which were divided into nine subregions. The polygons of subregions in the GOA and US west coast are consistent with fishery management areas and Canadian subregions are consistent with survey areas (boundaries in green). See a fine-scale map for the Canadian west coast in Figure 10. Arrows are scaled to the average standardized temperature responses in latitude and longitude for each subregion (Figure 5), indicating that these groundfish tended to form three thermal ecoregions, W-CGOA, EGOA-HS-QCS-WCVI, and US west coast. Such behavior may persist under global warming

the western and eastern (EGOA) parts based on geography, oceanography, and biodiversity (Mueter & Norcross, 2002). We further divided the western part by assigning the INPFC Shumagin statistical area to the western GOA (WGOA) and both the Chirikof and Kodiak areas to the central GOA (CGOA), ensuring the duration of each survey was about 1 month. For the Canadian west coast, the surveys in Hecate Strait (HS), Queen Charlotte Sound (QCS), and the west coast of Vancouver Island (WCVI) had different stratum depth ranges and sampling periods (see Supplement), thus becoming three subregions. In contrast, the entire US west coast was subdivided into 13,000 adjacent cells of equal area (1.5 nautical miles [nm] longitude by 2.0 nm latitude, Albers Equal Area projection) with each cell stratified by geographic location and depth. We post-stratified the enormous US west coast into the northern west coast (NWUS, 40.5°–49°N), central west coast (CWUS, 36°–40.5°N), and southern west coast (SWUS, 32.5°–36°N) to best align with oceanographic conditions (King et al., 2011) and previous subregion divisions (Keller et al., 2008).

Within each subregion, survey data were quality controlled. First, the analysis of the GOA bottom trawl survey was constrained to the period since 1996 due to differences in temperature sensors. Second, to have a consistent stratum depth range and to avoid splitting strata, only hauls taken at depths less than or equal to 500 m (in the GOA and Canadian west coast) or 550 m (in the US west coast) were considered (see different stratum depth ranges across surveys in the Supplement). The species selected for analysis were predominantly distributed within this depth range. Third, only valid hauls based on consistency in tow speed, tow duration, and net opening were included as detailed by the standard operating procedures for each survey. Further examination of the data revealed that owing to an incomplete knowledge of the bottom topography when the sampling strata were laid out, some hauls were conducted at depths outside their designated stratum range. Given the importance of depth strata to our analysis, a total of 468 hauls (6.7%) in the GOA, 244

hauls (7.2%) along the Canadian west coast, and 545 hauls (6.8%) along the US west coast were deleted due to these strata assignment errors. Finally, to account for spatial bias in the allocation of survey stations, years with an uneven or anomalous distribution of hauls were excluded. The criterion for classifying sampling biased years is discussed below.

Our previous studies reported that the distribution of demersal fishes was significantly correlated with near-bottom dissolved oxygen levels (DO) both within a known hypoxic area off the central Oregon coast (Keller et al., 2010) and to a more variable extent coastwide from the upper to the lower limit of the oxygen minimum zone and shoreward across the continental shelf (US–Canada to US–Mexico; Keller et al., 2015). Prior analyses revealed an apparent threshold effect at lower oxygen levels, where small changes in oxygen produced large changes in catch for several species (Keller et al., 2015; Keller, Ciannelli, et al., 2017). Since our current study occurred at depths (<550 m) and during months (late May to late July) where and when hypoxia rarely occurred, we excluded near-bottom DO and focused on bottom temperature in the current analysis.

2.2 | Fish species and size classes

The analyses were based on abundant commercial groundfish species in different depth ranges of each subregion of the northeast Pacific shelf: arrowtooth flounder (*Atheresthes stomias*), Pacific cod (*Gadus macrocephalus*), northern rock sole (*Lepidopsetta polyxystra*), southern rock sole (*Lepidopsetta bilineata*), petrale sole (*Eopsetta jordani*), Dover sole (*Microstomus pacificus*), walleye pollock (*Gadus chalcogrammus*), Pacific hake (*Merluccius productus*), Pacific ocean perch (*Sebastes alutus*), and sablefish (*Anoplopoma fimbria*). Only abundant species were included in the analysis due to the large number of nonzero hauls required each survey year for analysis when data were analyzed by subregion and divided into several size classes. Eight species are found in common

within the WGOA and CGOA, three within the EG OA, six in each subregion of the Canadian west coast, seven in NWUS, five in CWUS, and four in SWUS (Table S1). Some fish are widely distributed throughout the northeast Pacific shelf, for example, shallow-depth species such as arrowtooth flounder and Pacific ocean perch, and deep-depth species such as Dover sole and sablefish, allowing us to compare patterns of distributional changes across subregions.

Ten-centimeter size classes were used to examine potential size differences in temperature responses for each species in different subregions. Considering the low survey selectivity for the smallest (mostly 1–10 cm) size class of fish and the low number of large fish, we excluded the smallest size class and merged the two largest size classes for each species.

2.3 | Environmental conditions and fish distribution: weighted mean and variability

To minimize bias introduced by annual variation in station locations and number of hauls in each stratum, we computed stratum area-weighted means for environmental variables in year y , ME_y , for each subregion following Spencer (2008):

$$ME_y = \sum_{i=1}^k \sum_{h=1}^{n_{iy}} \frac{w_i E_{hiy}}{n_{iy}} \quad (1)$$

where w_i is the area (km^2) proportion of stratum i to all surveyed strata (w_i is a fixed ratio as a result of consistent sampling in each stratum in every survey year); n_{iy} is the number of hauls in stratum i in year y ; E_{hiy} is the environmental variable (e.g., temperature, depth, longitude, or latitude) of haul h , in stratum i , in year y ; and k is the number of strata in each subregion.

Warm, medium, or cold years were identified by assessing whether the annual mean bottom temperature (ME_y) was above, within, or below the 0.66 standard deviation (SD) from the overall mean across all survey years. About 50% of survey years lie within the 0.66 SD based on normal distribution, representing a reasonable statistical significance level. The cutoff of 0.66 SD also ensured a sufficient number of cold and warm years in this study.

We used two metrics, catch per unit effort (CPUE) and stratum area, to compute the centroid of the population's distribution (also called center of gravity, COG) in depth and temperature, as well as longitude and latitude for each size class, species, and subregion. We computed annual centroids of fish distribution, MF_{jsy} for species j size class s in year y in each subregion as:

$$MF_{jsy} = \frac{\sum_{i=1}^k \sum_{h=1}^{n_{iy}} \frac{w_i \text{CPUE}_{jshiy} E_{hiy}}{n_{iy}}}{\sum_{i=1}^k \sum_{h=1}^{n_{iy}} \frac{w_i \text{CPUE}_{jshiy}}{n_{iy}}} \quad (2)$$

where CPUE_{jshiy} represents CPUE (number per km^2) of species j and size class s in haul h , stratum i , and year y with n_{iy} , k , w_i , and E_{hiy} defined in Equation (1).

We computed the annual weighted SD of environmental factors or fish distribution, SD_{wy} , in year y based on Cochran (1977):

$$(SD_{wy})^2 = \frac{n}{(n-1) (\sum f_{hy})^2} \left[\sum (f_{hy} E_{hy} - \bar{f}_y M)^2 - 2M \sum (f_{hy} - \bar{f}_y) (f_{hy} E_{hy} - \bar{f}_y M) + M^2 \sum (f_{hy} - \bar{f}_y)^2 \right] \quad (3)$$

where E_{hy} represents the value of the environmental variables (e.g., depth, temperature, longitude and latitude) at haul h in year y ; n is the total number of hauls in year y ; f_{hy} is the weight for ME_y or MF_{jsy} in haul h year y (see Equations 1 and 2) and \bar{f}_y is the average weight in year y ; M represents the annual weighted mean in environment ME_y or in fish distribution MF_{jsy} .

We define the distributional responses to anomalous temperatures as differential distribution in depth, latitude, and longitude between cold and warm years and estimated the temperature responses in each direction, TR_{js} , for species j , size class s , in each subregion as:

$$TR_{js} = \frac{\sum_{y=1}^w MF_{jsy}}{w} - \frac{\sum_{y=1}^c MF_{jsy}}{c} \quad (4)$$

where MF_{jsy} represents centroids of fish distribution for species j and size class s in year y in each subregion based on Equation (2); w is the number of warm years and c is the number of cold years defined for each subregion based on Equation (1). The estimated temperature responses can result from actual movements to preferred water temperatures or by apparent movements due to some populations perishing in parts of their range while others persist or thrive. We standardized the temperature responses, TR_{js} , in depth, latitude, and longitude for multivariate analyses by dividing them by the SD of the annual mean MF_{jsy} across all survey years.

2.4 | Survey sampling variability

The mean SD_{wy} across all years (SD_W) shows the average within-year survey variability and the SD of annual mean ME_y across all years represents among-year survey variability (SD_A) in depth, longitude, and latitude. With regard to survey sampling, within-year variability in depth, latitude, and longitude reflects the natural differences in sampling locations, which were randomly selected within each stratum; among-year variability shows the variability in annual mean representing the consistency of our surveys in depth, longitude, and latitude. We then defined the combined SD (SD_C) as square-rooted sum of the squared SD_W and SD_A to represent the average total survey variability.

Three-year subregion blocks were excluded based on unusual sampling distributions: 2004 from WCVI and 2005 and 2007 from CWUS, that had a larger deviation than 1.5 SD_C from the overall mean. The 2004 survey in WCVI sampled substantially more stations in the south and east (Figure S1), and the 2007 survey in CWUS sampled remarkably more stations in the north and west (Figure S2). In contrast, the 2005 survey in CWUS was

considerably shallower than other years (Figure S2) due to a large fraction of hauls in the shallowest stratum, only one haul in the medium stratum and no hauls in the deep stratum. By removing those biased survey years, we reduced biases in our bottom temperatures and as well as in fish distributions. We reran the analyses using the reduced subset of years and found no additional years with deviation from the overall mean greater than the re-estimated SD_C (Table 1) and the remaining years were used for further analyses.

2.5 | Key factors influencing fish movements

We conducted multivariate analyses, including nonmetric multidimensional scaling (NMDS) and analysis of similarities (ANOSIM), using standardized temperature responses in depth, longitude, and latitude for each size class by species in each subregion. Since our variables of temperature responses represented spatial movements, we chose the Euclidean distance method to compute dissimilarities between samples for all multivariate analyses, instead of the Bray–Curtis similarity method, which is more appropriate for community abundance data (Clarke, 1993). All multivariate analyses were completed using PRIMER (Clarke, 1993).

We conducted NMDS analyses to examine clustering factors influencing groundfish movement. NMDS does not require an assumption of linearity; NMDS ranks similarities (similarity = 1 – dissimilarity) between each pair of samples, where a shorter distance between samples signifies higher similarity (Clarke, 1993). Consequently, this method aids detection of clusters by subregion, species, and size class. We used two-dimensional NMDS and constrained our results with stress less than 0.2 where the samples precisely represent the distance among the samples.

We applied ANOSIM as a significance test for clustering factors that may influence fish movements. ANOSIM is analogous to an ANOVA for univariate data and contrasts fish movements

within and between clusters of samples by comparing their rank similarities (Clarke & Green, 1988). An R -statistic is computed as:

$$R = \frac{r_B - r_W}{n(n-1)/2} \quad (5)$$

where r_B is the average of rank similarities of pairs of samples (or replicates) originating from different clusters, r_W is the average of rank similarity of pairs within cluster, and n is the number of samples. The R -statistic is constrained between -1 and $+1$. The closer R is to 1, the more differences there are among clusters. We conducted 999,999 permutations to generate significant levels in ANOSIM. We defined significance as $R > 0.1$ and $p < 5\%$. After we detected the most influential single factor, we conducted additional nested analyses to examine differences in the rest of factors within the key factor for fish distribution.

3 | RESULTS

3.1 | Survey variability

The within-year, among-year, and combined variability of survey depth, longitude, and latitude varied among subregions (Table 1). Generally, the within-year variability was greater than the among-year variability (Table 1) which means that span of depths and trawl locations in a given stratum were little affected by random changes in the trawl locations each year. This indicates the consistency in survey design and execution over time. With regard to depth, the surveys in GOA and west coast of Canada showed lower variation with SD_C less than 9 m while the survey in the US west coast exhibited substantially larger variation with SD_C ranging 13–23 m. The smaller scale HS and QCS surveys had the smallest horizontal variation. The large zonal surveys in the GOA had the largest variability in longitude in WGOA and EGOA (0.3–0.4°W), and the large meridional surveys in NWUS and CWUS had the largest variability in latitude (0.24–0.26°N).

TABLE 1 Standard deviation (SD) of survey depth, longitude, and latitude in each subregion: (a) within-year SD (SD_W), which was estimated as the mean of annual stratum area-weighted standard deviation SD_{wy} (Equation 3); (b) among-year SD (SD_A), which was estimated as the SD of annual mean ME_y (Equation 1); and (c) combined SD (SD_C , *italic*), the square-rooted sum of the squared SD_W and squared SD_A

Survey	Subregion	Depth (m)			Longitude (°)			Latitude (°)		
		SD_W	SD_A	SD_C	SD_W	SD_A	SD_C	SD_W	SD_A	SD_C
GOA	WGOA	5.5	1.9	5.8	0.25	0.16	0.30	0.06	0.03	0.07
	CGOA	4.5	2.3	5.1	0.19	0.05	0.20	0.09	0.03	0.09
	EGOA	7.4	1.7	7.5	0.42	0.14	0.44	0.16	0.07	0.17
Canadian west coast	HS	8.1	2.8	8.6	0.06	0.03	0.07	0.05	0.04	0.06
	QCS	6.9	1.6	7.1	0.06	0.05	0.08	0.04	0.04	0.06
	WCVI	6.4	1.5	6.6	0.07	0.08	0.11	0.05	0.04	0.06
US west coast	NWUS	11.8	4.4	12.5	0.03	0.02	0.04	0.21	0.12	0.24
	CWUS	21.6	4.1	22.0	0.11	0.12	0.16	0.18	0.19	0.26
	SWUS	21.2	7.3	22.5	0.17	0.14	0.22	0.11	0.09	0.14

3.2 | Environmental conditions in the northeast Pacific shelf

Overall mean bottom temperatures generally increased along the northeast Pacific shelf from WGOA eastward to EGOA and then southward to SWUS (Figure 2a) following well-known climatological characteristics of the region. Only HS with its protected waters and shallow depths broke this trend. For summer in the entire northeast Pacific shelf, WGOA was the coldest area with a mean temperature $<5^{\circ}\text{C}$, while HS, and CWUS and SWUS with their southern locales were the warmest areas with a mean of about 8°C during the surveys. Just like the mean bottom temperature, the mean bottom depth generally increased along the northeast Pacific shelf with HS, WCVI, and NWUS shallower than their adjacent subregions (Figure 2b). SWUS was the deepest subregion with average overall depth 312 m. HS and WGOA were the shallowest, at 108 m depth.

Bottom temperature anomalies (the annual weighted mean temperature minus the overall mean for each subregion) tended to decrease along the northeast Pacific shelf from WGOA eastward to EGOA and then southward to SWUS (Figure 3). Anomalies were largest in the coldest region, the GOA, particularly in the WGOA where differences between warm and cold years exceeded 2°C . Farther

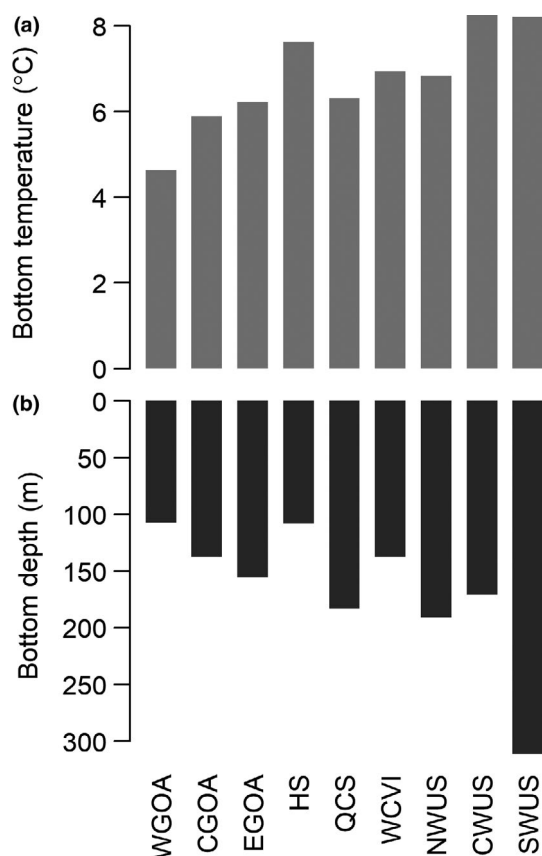


FIGURE 2 Overall mean ocean bottom temperature (a) (See sampling month(s) in Figure 3) and depth (b), the mean of annual stratum area-weighted ME_v , across the survey years, in the Gulf of Alaska (WGOA, CGOA, and EGOA), Canadian west coast (HS, QCS, and WCVI), and US west coast (NWUS, CWUS, and SWUS)

south, bottom temperature anomaly differences between warm and cold years were less than 1°C from Canada to California (Figure 3), suggesting that summer upwelling buffers demersal species from larger temperature fluctuations encountered at the surface along the west coast of North America. Within-year bottom temperature variability was large in HS, CWUS, and SWUS (Figure 3), implying that for a given survey season bottom temperatures were more spatially inconsistent in the three subregions.

Subregions did not share the same warm and cold years even within a survey (Figure 3). An extreme year in one subregion may not correspond to an extreme year at another location. For example, 2015—the year of the recent marine heat wave at the sea surface of the entire northeast Pacific (Cavole et al., 2016)—was an extremely warm year only in the GOA (>1 SD), while resulting in moderately warm conditions in HS, CWUS, and SWUS (0.66–0.8 SD) and neutral conditions elsewhere (QCS and NWUS) in bottom temperature during our survey time.

At each bottom depth level, the average bottom temperature generally increased along the northeast Pacific shelf from WGOA to SWUS and decreased with depth in all subregions except in the WGOA (Figure 4). In WGOA, temperature increased with depth in the cold mid-water (75–250 m) layer but decreased with depth below. The bottom temperature differences across subregions generally decreased with depth and became stable below 300 m. There were deep stations in all subregions except in HS (Figure 4).

3.3 | Significant subregional differences in temperature responses of groundfish

We detected significant subregional differences in temperature responses of groundfish using ANOSIM (Table 2) and NMDS (Figure S3). The R -statistic was 0.17 ($p < 0.001\%$) for subregions and very small for species and size classes (Table 2). The largest R -statistic for paired subregions was 0.50 ($p < 0.01\%$) between EGOA and QCS, followed by 0.46 ($p < 0.01\%$) between EGOA and WGOA. An example of arrowtooth flounder (Figures S4 and S5) shows how temperature responses of a species varied from subregion to subregion with no consistent size classes responding to temperature changes.

Groundfish demonstrated substantially different responses to warm temperatures across subregional depth, latitude, and longitude gradients (Figures 1 and 5). The average subregional movements were based on all size classes of all species and not driven by any species. In warm versus cold years, the temperature responses of groundfish in depth was positive toward deeper water which corresponds to colder temperatures (Figure 4). The exception was in the WGOA where fish seemed to be shallower in warm years, probably because temperature increased with depth in the mid-water layer (Figure 4). Therefore, in all subregions of substantial vertical responses, fish tended toward colder water in warm years. Horizontally, groundfish in EGOA, QCS, and WCVI exhibited the largest responses in latitude and longitude for warm

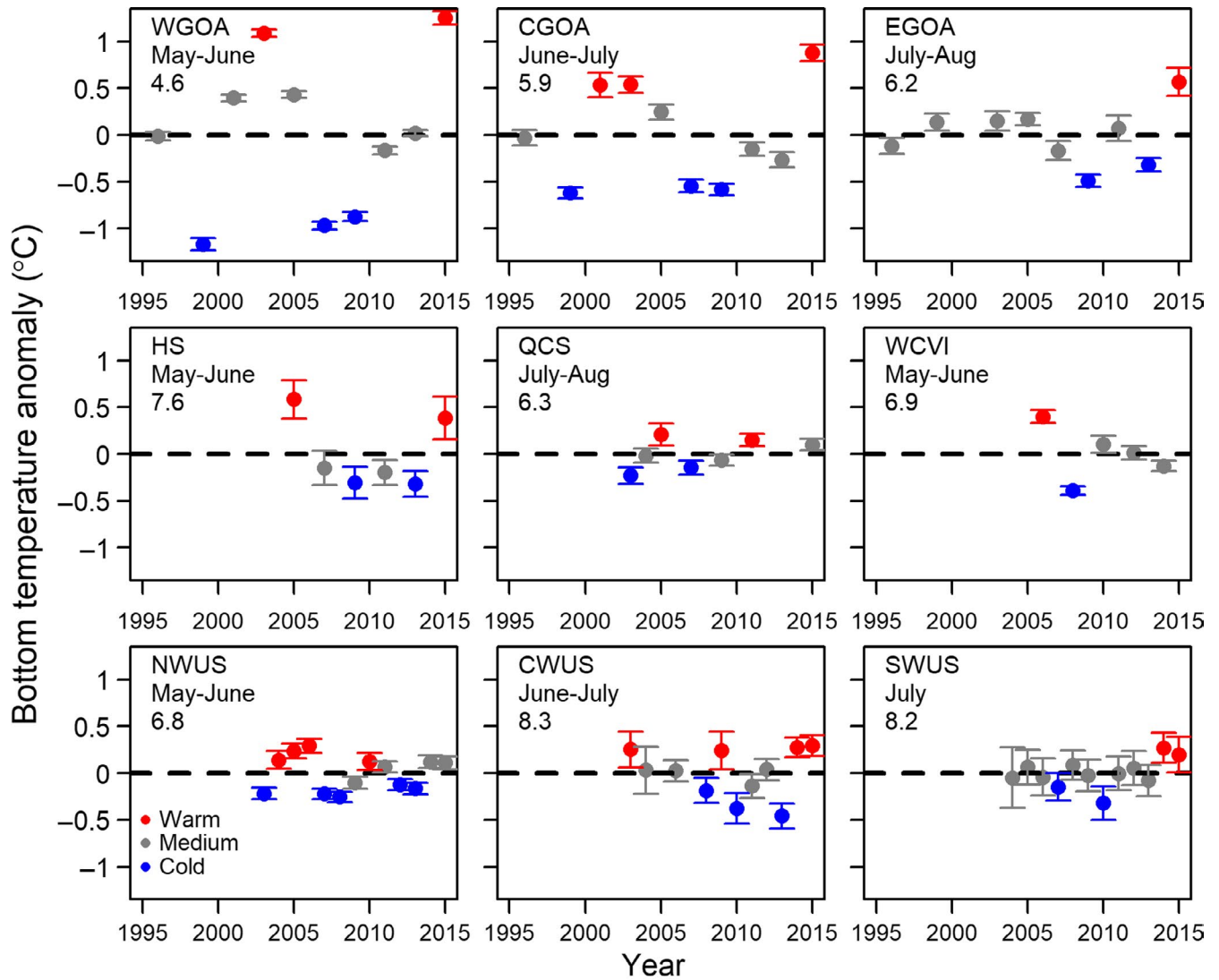


FIGURE 3 Bottom temperature anomalies with stratum area-weighted standard deviation (SD_{wy} , Equation 3) during the sampling month(s) in each subregion. Cold (blue) and warm (red) years are defined as the annual stratum area-weighted temperature (ME_y , Equation 1) below or above 0.66 standard deviations from the overall mean, and medium years (gray) are in-between. Dashed lines represent the overall mean across survey years with the value shown in each panel. There was no survey in 2001 in the EGOA or 2013 in the SWUS

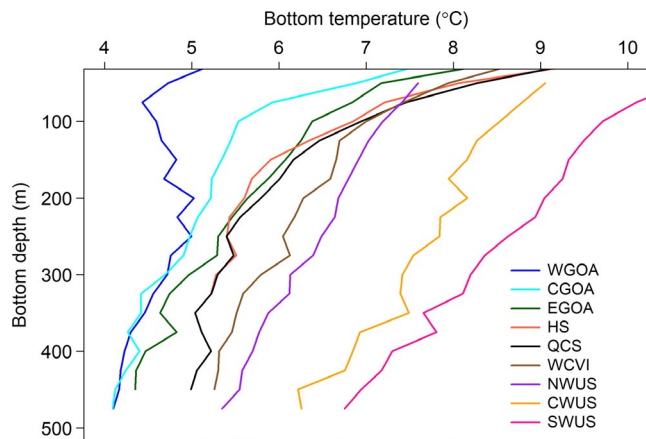


FIGURE 4 Average bottom temperature in 25-m depth intervals across all survey years for each subregion. Note maximum sampling depth of 330 m in Hecate Strait (HS)

over cold years but in opposite directions. Consideration of vertical and horizontal responses shows that subregional responses to warm temperatures differed in direction and strength. For example, EGOA and WCVI had strong responses in all three directions with opposite horizontal directions, that is, SE versus NW. Bordering EGOA to the west, the CGOA had small responses in all three directions with the same direction in depth and latitude and opposite direction in longitude while HS bordering EGOA to the south had relatively large responses in depth and medium responses in longitude but small in latitude. Adjacent WCVI and QCS had strong and similar responses in latitude and longitude but not in depth while NWUS, CWUS, and SWUS had small responses in latitude and longitude and minor responses in depth except for a large depth response in SWUS. The relatively weaker movements in US west coast might be associated with relatively smaller changes in temperatures (Figure 3).

TABLE 2 Summary of ANOSIM results of *R*-statistic and significance level (*p*-value), including single-factor and nested-factor tests, based on standardized temperature responses in depth, latitude, and longitude of all species and size classes across all subregions

ANOSIM	Factors	<i>R</i>	<i>p</i> (%)
Single factor	Subregion	0.17	<0.001
	Species	0.04	2.5
	Size class	0.01	32.9
Nested species	Subregion	0.23	<0.001
	Species	0.25	<0.001
Nested size	Subregion	0.29	<0.001
	Size class	-0.01	60.6

Note: Significant values are in bold.

Groundfish tended to be constrained in three larger areas in warm years along the northeast Pacific (Figures 1 and 5). Most fish shifted southeastward in the EGOA and northwestward in QCS and WCVI, seeming to stay in this EGOA-HS-QCS-WCVI area in warm years. The WGOA response was toward the northeast while the CGOA response was toward the southwest, seeming to converge within the W-CGOA area. In contrast, on the US west coast, the temperature responses were smaller, but fish tended southwestward or equatorward along the coast and separated from the EGOA-HS-QCS-WCVI area.

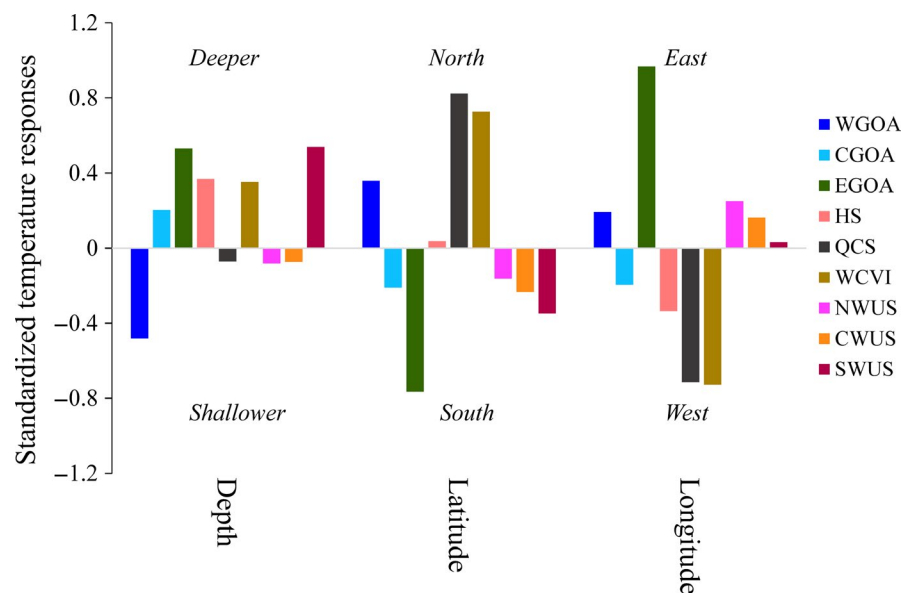
3.4 | Species and size differences in temperature responses of groundfish

The nested ANOSIM tests showed that, within subregion, temperature responses varied among groundfish species ($R = 0.25$, $p < 0.001\%$) rather than from size class ($R = -0.01$, $p = 60.6\%$) (Table 2). For example, in the CGOA, temperature responses of

most species, such as arrowtooth flounder, Pacific cod, POP, and rock sole, were clustered within a species and most species were differentiated from each other (Figure 6). The widely distributed walleye pollock cluster showed the large difference in temperature responses across size classes. In contrast, two deeper species clusters, Dover sole and sablefish, had the largest overlap demonstrating more similar temperature responses across size classes between the two species.

Subsetting the thermal responses of the subsets of data—the six most widely distributed groundfish species of all size classes among subregion, and two size classes across the most species and subregion—demonstrated interesting differences. Differences in the temperature responses were found to be significant across subregions for shallow-depth species ($R \geq 0.31$, $p < 0.2\%$) and insignificant among size classes ($R < 0.1$) or species ($R < 0$; Table 3). For shallow-depth species, including arrowtooth flounder, Pacific cod, petrale sole, and POP, different size classes of each species tended to have similar temperature responses within each subregion, which are significantly different from those in other subregions. The largest differences in paired subregions for arrowtooth flounder occurred between the EGOA and QCS ($R = 0.87$, $p = 0.2\%$) followed by between EGOA and WGOA ($R = 0.81$, $p = 0.2\%$). In contrast, deep-depth species, Dover sole and sablefish ($R = 0.11$, $p = 9.6\%$ and 5.3% , respectively), had relatively similar temperature responses among subregions. There were also significant differences in sablefish between some paired subregions such as NWUS and SWUS ($R = 0.31$, $p = 2.4\%$) but most paired subregions were very similar such as WGOA and CGOA ($R = 0.005$, $p = 42\%$). For each size class (21–30 and 41–50 cm, respectively), all fish demonstrated significantly different distributional responses across subregions ($R = 0.14$ and 0.25 , respectively). Many size and species effects had negative *R*s, which meant between-group similarities were higher than within-group similarities, suggesting unmeaningful groupings.

FIGURE 5 Average standardized temperature responses in depth, latitude, and longitude of all groundfish and all size classes in each subregion. This metric is positive if the fish were found in deeper water, farther north, or farther east in warm years than in cold years. Temperature responses in the three directions are based on Equation (4) and standardized by the standard deviation of annual mean across all years for each species and size class



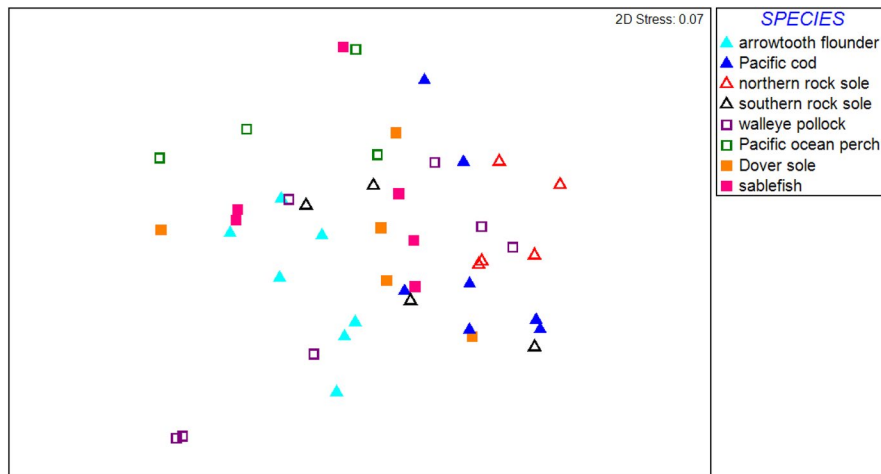


FIGURE 6 NMDS plots by species of all size classes of three-directional movements of temperature responses in the CGOA. The clear clusters by species show that, within this subregion, the same species of all size classes tended to have similar distributional responses to temperature changes

TABLE 3 Summary of ANOSIM results of *R*-statistic and significance level (*p*-value) using different sample subsets of standardized temperature responses in depth, latitude, and longitude. Subsets include widely distributed species of all size classes across all subregions and the two size classes that have the most species across subregions

Single factor	Subsets	<i>R</i>	<i>p</i> (%)
Subregion	Arrowtooth flounder	0.54	<0.001
	Pacific cod	0.53	<0.001
	Petrale sole	0.5	0.1
	POP	0.31	0.2
	Sablefish	0.11	5.3
	Dover sole	0.11	9.6
	21–30 cm	0.14	0.8
	41–50 cm	0.25	0.02
Size class	Arrowtooth flounder	−0.1	99.6
	Pacific cod	0.02	36.3
	Petrale sole	−0.17	92.3
	POP	−0.01	92.9
	Sablefish	0.04	25.9
	Dover sole	0.08	13.1
Species	21–30 cm	−0.03	65.8
	41–50 cm	−0.02	61.9

Note: Significant values are in bold.

4 | DISCUSSION

4.1 | Subregional differences in geographic and oceanographic dynamics

The ocean along the west coast of North America has a heterogeneous response to climate-forcing events, including but not limited to the marine heat wave of 2015. Regional patterns of bottom temperature reflect the spatial variations in the forcing as mediated by local processes.

Anomalies in bottom temperatures were not synchronous across subregions in the NE Pacific shelf over the survey period.

The marine heat wave year of 2015 manifested as an extremely warm year in the sea surface temperature (SST) over the entire northeast Pacific (Cavole et al., 2016). However, it was close to the overall mean bottom temperature in QCS and NWUS (Figure 3) during our survey. SST anomalies represent the upper mixed layer but not necessarily bottom temperatures which have subregional and interannual variations that are not necessarily tightly coupled with near surface conditions. For example, in the GOA where SST data were available, SST-based warm/cold/medium years differed from the bottom temperature-based ones, particularly in the EGOA (Figure 7). This result can be attributed to the EGOA surveys occurring later in the warm season during a period of greater stratification and hence a weaker relationship between SST and bottom temperature. Another example is represented by the shelf-break of the NWUS, where positive temperature anomalies in the 150–300 m depth range became prominent in late 2015 and persisted well into 2017, well after near surface temperatures had moderated. It should be emphasized that even basin-scale fluctuations in the climate forcing are manifested in physical oceanographic conditions that vary geographically and temporally, with resulting differences in biological responses.

Many factors contribute to the observed differences in subregional ocean bottom conditions in the northeast Pacific. Mesoscale variations (e.g., eddies and meanders), tides, and storms (wind mixing) impact physical oceanographic properties sampled during individual trawls. The timing of the survey with respect to the seasonal shift from winter to summer conditions affects perceived spatial patterns. For example, strong stratification can occur in the WGOA in late summer, but the timing of stratification is dependent upon winds and solar radiation. The WGOA survey is conducted in late May to June when the water column is only weakly stratified. Stratification increases toward the east primarily due to warming conditions as the survey progresses but also because of the weaker vertical mixing. Coastal variations in the winds play an important role in determining oceanographic conditions. Winds during the marine heat wave favored anomalous downwelling for the CWUS and SWUS subregions, upwelling for the NWUS, and relatively little in the way of a systematic

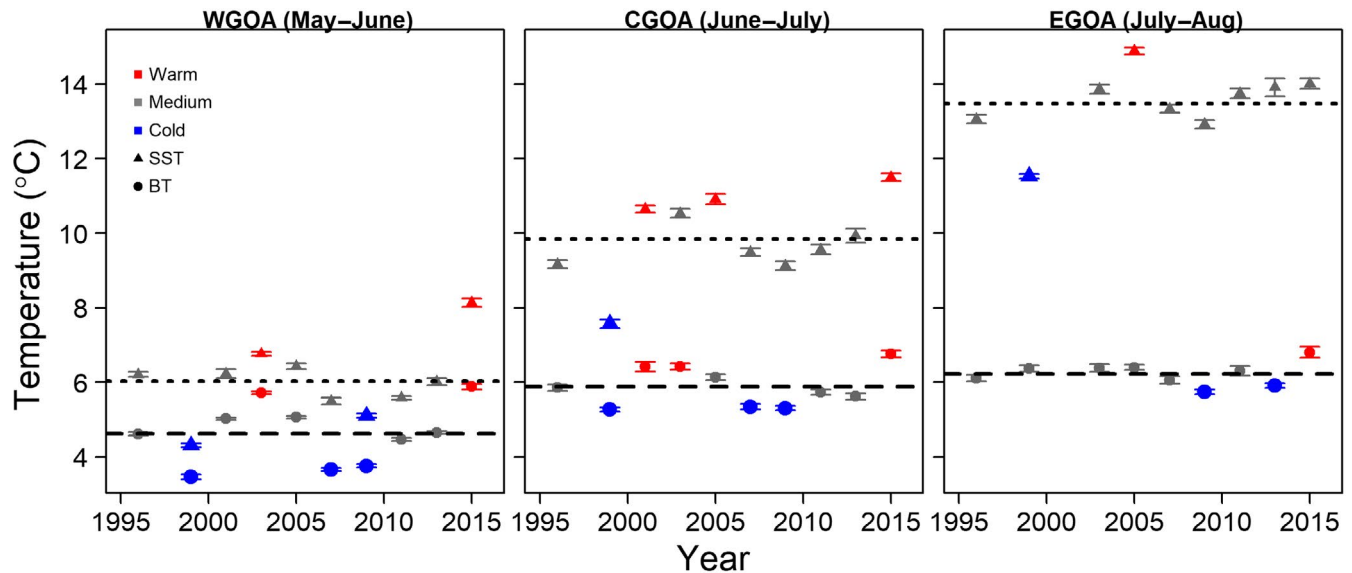


FIGURE 7 Annual stratum area-weighted sea surface temperature (SST, filled triangle) and bottom temperature (BT, filled circles) ($ME_y \pm SD_{wy}$) during sampling months in the subregions of the Gulf of Alaska. Warm/medium/cold years are based on 0.66 standard deviations from the overall mean with the same format as in Figure 3. Lines represent the overall mean SST (dotted) and BT (dashed) across survey years

signal farther north (from upwelling indices provided by NOAA's Pacific Fisheries Environmental Laboratory at <https://www.pfeg.noaa.gov/products/PFEL/modeled/indices/PFELindices.html>). Anomalous downwelling in the south often accompanies El Niño events (e.g., Jacox, Fiechter, Moore, & Edwards, 2015), and indeed moderate El Niño conditions occurred in 2015 that reinforced the effects of an anomalous high-pressure system in the central north Pacific (Bond, Cronin, Freeland, & Mantua, 2015). In addition, wind anomalies are associated with perturbations in wind-induced mixing which affects vertical density stratification. Interannual variations in advection can lead to high between-year temperature variability. In the GOA, currents on the continental shelf (<200 m) are dominated by the Alaska Coastal Current (ACC) and along the slope by the Subarctic Gyre (Alaska Current and the Alaskan Stream, Stabeno et al., 2016). Flow is generally anticlockwise around the gyre. Strong vertical mixing occurs in multiple places on the shelf, particularly in the ACC in Kennedy Entrance (58.7° N, 151.9° W); this well-mixed water is advected southwestward down Shelikof Strait with some water entering the shallow shelf of WGOA thus reducing vertical stratification at times. Due to changing water properties, fish movements in response to temperature are also expected to vary.

4.2 | Subregional differences in temperature responses of groundfish

We discovered that temperature responses of the individual species depend on where they are, regardless of species or size class (Tables 2 and 3, Figures 1 and 5). Recent laboratory experiments for Atlantic cod (Pörtner et al., 2008) show that the upper limit of their

thermal windows and their optimal temperatures decrease poleward in the North Atlantic. These different thermal windows across subregions of Atlantic cod suggest that widely distributed species along the northeast Pacific, that are likely genetically or geographically separated, may have subregion-specific, instead of a uniform, thermal windows over their entire distribution area from the coldest temperatures in the GOA to the warmest temperatures on the US west coast. Therefore, a subregional scale is highly recommended for future studies.

Our analyses suggest that groundfish may be constrained in geographically distinct areas, instead of continuously moving northward along the northeast Pacific shelf in warm years. Groundfish tended to be separated into three areas in warm years: W-CGOA, EGOA-HS-QCS-WCVI, and US west coast (Figures 1 and 5) that may form three thermal ecoregions in the future. This finding differs from some recently published studies that suggest continuous poleward movements when large marine ecosystems are considered on a broad, homogenous scale (Cheung et al., 2009; Hazen et al., 2013; Morley et al., 2018), thus obscuring local or subregional spatial dynamics (Kleisner et al., 2016; Marshall et al., 2016). Here, we extend the concept of ecoregions, defined by Spalding et al. (2007) as “areas of relatively homogenous species composition, clearly distinct from adjacent systems” to include temperature responses of groundfish under global warming. Most ecoregion classifications have been heavily influenced by data from nearshore and intertidal biota (Blanchette et al., 2008; Boschi, 2000). In contrast, our thermal ecoregions may contribute to a better understanding of future deep-water communities along the northeast Pacific shelf. Due to different rates in temperature responses, species' interactions and marine ecosystem functions may be substantially

reorganized (Hazen et al., 2013; Marzloff et al., 2018; Selden, Batt, Saba, & Pinsky, 2017) within the thermal ecoregions.

The groundfish distributional responses to warm temperatures may put them at risk of limitation of local deeper habitat availability during future global warming. In the convergent EGOA-HS-QCS-WCVI area, because HS is shallow (Figures 2 and 4), there may be a local extinction risk when some fish move there from north or south (Figures 1 and 5) and suffer from a lack of available colder deep habitat (Rutterford et al., 2015). There may be a similar risk in the W-CGOA area as this is generally shallower (Figure 2). However, in this region access to the eastern Bering Sea may provide a refuge to the north. Unlike the two bounded thermal ecoregions, along the US west coast groundfish demonstrated continuous southeastward responses, but fish movement in the adjacent Mexican area is needed to define further this thermal ecoregion. Additionally, the substantially stronger movements in the EGOA-HS-QCS-WCVI area may indicate that this thermal ecoregion may form faster than the other two. Future studies are needed to further investigate the formation of the thermal ecoregions.

4.3 | Species and size differences in temperature responses of groundfish

Within subregions, we detected substantial differences in temperature responses among species which is consistent with many studies (e.g., Pinsky et al., 2013). Table 4 shows an example of how fish moved in depth by different amounts and direction in the WGOA (see mechanisms in next section). We also showed that species-specific temperature responses varied both horizontally and vertically among subregions (e.g., arrowtooth flounder across subregions; Figures S4 and S5), demonstrating great adaptation to the local environment. Furthermore, we found that deep-depth species of Dover sole and sablefish tended to have similar temperature responses within a subregion (e.g., in the CGOA, Figure 6) and neither of them had large differences in temperature responses across subregions (Table 3), probably due to the relatively consistent temperature in deep waters of all subregions (Figure 4). In contrast, shallow-depth species (e.g., arrowtooth flounder and Pacific cod) tended to have relatively large differences in temperature responses among species within a subregion (e.g., in the CGOA; Figure 6) or for each species across subregions (Table 3), probably due to the more variable environments in shallow-depth waters (Figure 4). Similarly, Hsieh et al. (2009) also observed clear distributional shifts in shallow waters and no pronounced shifts in deep waters using data from the California Cooperative Oceanic Fisheries Investigations. Therefore, the species differences we found in this study seem to result from the environment where they live in each subregion.

We found no detectable consistent size differences in groundfish distributional responses to warm temperatures across species or subregions (Tables 2 and 3). However, our results are consistent

with Barbeaux and Hollowed (2018) who found that only some size classes of fish responded to temperature changes. For a species in a particular subregion (e.g., Table 4 and arrowtooth flounder in Figures S4 and S5), it is still important to understand which size classes had temperature responses and how different the responses were across size classes in future climate studies.

4.4 | Multiple mechanisms of temperature responses

Vertically, temperature generally decreased with bottom depth in all subregions except in the WGOA (Figure 4) which actually provides an excellent example of temperature impacts on groundfish distribution. There, temperature increased with depth in the cold mid-water (75–250 m) but decreased with depth below. In response to this complex water column structure, in warm years, medium sablefish (41–50 and 51–60 cm) and many other species shifted shallower to colder water in mid-water, while in deeper water (>300 m) large sablefish (61–70 and 71–80 cm) moved deeper (Table 4) to colder water. Despite substantial temperature gradients in the remaining eight subregions (Figure 4), groundfish demonstrated strong deepening responses (on average) to temperature changes in CGOA, EGOA, HS, WCVI, and SWUS but not in QCS, NWUS, or CWUS (Figure 5), indicating that the mechanisms underlying the redistribution of fish may be a complex response to local drivers.

Horizontally, the divergence into northward groundfish movements in Canadian west coast waters and southward groundfish movements in the US west coast waters in warm compared to

TABLE 4 The list of size classes of fish species that had larger temperature responses (TR_{js} , Equation 4) in depth than 1.5 times of survey variability ($1.5 SD_C = 8.7$ m) in the WGOA

Species	Size class (cm)	Responses in depth (m)
Pacific cod	11–20	–10
Northern rock sole	41–50	–11
Arrowtooth flounder	41–50	–13
	61–70	–10
Dover sole	31–40	–21
	41–50	–15
Walleye pollock	21–30	–34
	31–40	–53
	41–50	–21
Pacific ocean perch	11–20	–21
	31–40	–30
	41–50	–36
Sablefish	41–50	–27
	51–60	–14
	61–70	35
	71–80	77

Note: Negative values mean upward movements in warm years compared to cold years.

cold years (Figure 1) coincides with that of the West Wind Drift divergence into the northward Alaska Current and the southward California Current (e.g., King et al., 2011). This suggests an ocean transport-based hypothesis whereby pelagic fish (Hollowed, Wilson, Stabeno, & Salo, 2007) and flatfish (De Veen, 1978; Nichol & Somerton, 2009) are advected with currents to favorable oceanic conditions. In warm versus cold years, groundfish moved southeastward in the EGOA opposing the direction of the Alaska Current. They may be responding to high primary production in summer which was observed in the southern EGOA (Brickley & Thomas, 2004) and also simulated by a high-resolution NPZD model (Coyle, Hermann, & Hopcroft, 2019). Similarly, in the northeast US shelf, the northeast and inshore movement of pelagic and groundfish fish seems to correspond with distributional shifts in their prey of copepod populations in addition to warm waters (Friedland, McManus, Morse, &

Link, 2019). This seems to support a prey-pursuit hypothesis (Aoki, Kitagawa, Kiyofuji, Okamoto, & Kawamura, 2017; Hollowed et al., 2012; Kotwicki, Buckley, Honkalehto, & Walters, 2005).

One might expect that in a general sense the bottom temperature would decrease poleward and offshore and that fish would shift poleward and offshore in warm years seeking colder conditions. In the GOA, the overall mean thermal gradient was nearly zero except in the CGOA where the temperature decreased southward and westward toward the subpolar Bering Sea, and fish shifted in that direction. The overall the bottom temperature decreased poleward and offshore (westward) on the Canadian and US west coasts (Figures 8 and 9) with the exception of HS with its outer island boundary (Figure 10). However, only on the QCS and WCVI did the fish shift poleward and westward (Figure 1), while on the US west coast fish shifted southward and eastward on average (Figures 1 and 5). This

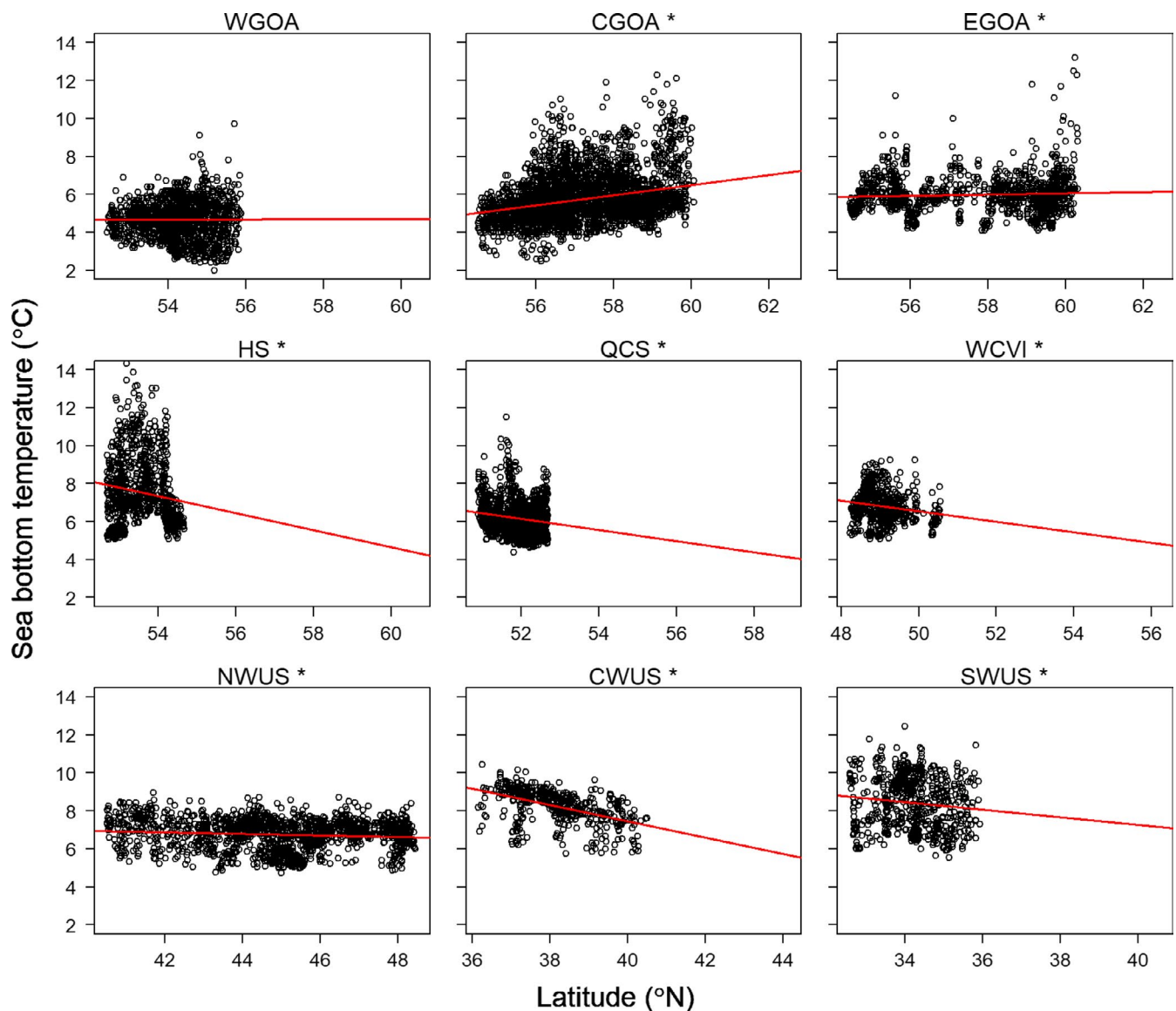


FIGURE 8 Bottom temperature and latitude of each bottom trawl haul across all survey years in each subregion. Red lines show the linear relationship and * represents a significant latitudinal temperature gradient ($p < 0.05$). Each x-axis has the same latitude range of 8° for comparison

indicates the importance of other factors such as depth, currents, and topography relative to poleward or offshore-decreasing temperature.

Topographic and geographic characteristics may play a role in influencing the vertical and horizontal movements of fish in response to temperature. Thermal depth refuges may be very near to groundfish and their poleward and offshore movements may thus be limited. For example, in those subregions with complex submarine canyons, troughs, and gullies (e.g., around 59° N in the CGOA and 170° W in the WGOA in Figures S6 and S7), some species of fish may not need to move very far in longitude and latitude to seek deeper habitat (Hollowed et al., 2007). The distributional changes in such a fine spatial scale might be any direction and differ from the general trends in Figures 8 and 9, which require long distance movements to achieve the temperature gradients, thus greatly complicating the temperature responses within each subregion. In contrast, colder deeper

water only exists in certain areas in the subregions of the Canadian west coast (Figures S6, S7 and Figure 10). For example, groundfish could find refuges by moving in either northward or southward in HS, probably resulting in no substantial movement in latitude in warm compared to cold years (Figure 10). Similarly, the cold pool on the central continental shelf in the eastern Bering Sea (Kachel et al., 2002) has large impacts on the groundfish distribution (Spencer et al., 2016; Wyllie-Echeverria & Wooster, 1998). As the waters under low temperature vary from subregion to subregion, groundfish may have been adapted to their environments by moving vertically and horizontally to quickly locate those cooler refuges in warm years.

Generally, currents, prey distribution, bottom temperature gradients, topography, and geography may all have contributed to sub-regional differences in temperature responses of groundfish, even though fishing pressure (Engelhard, Righton, & Pinnegar, 2014;

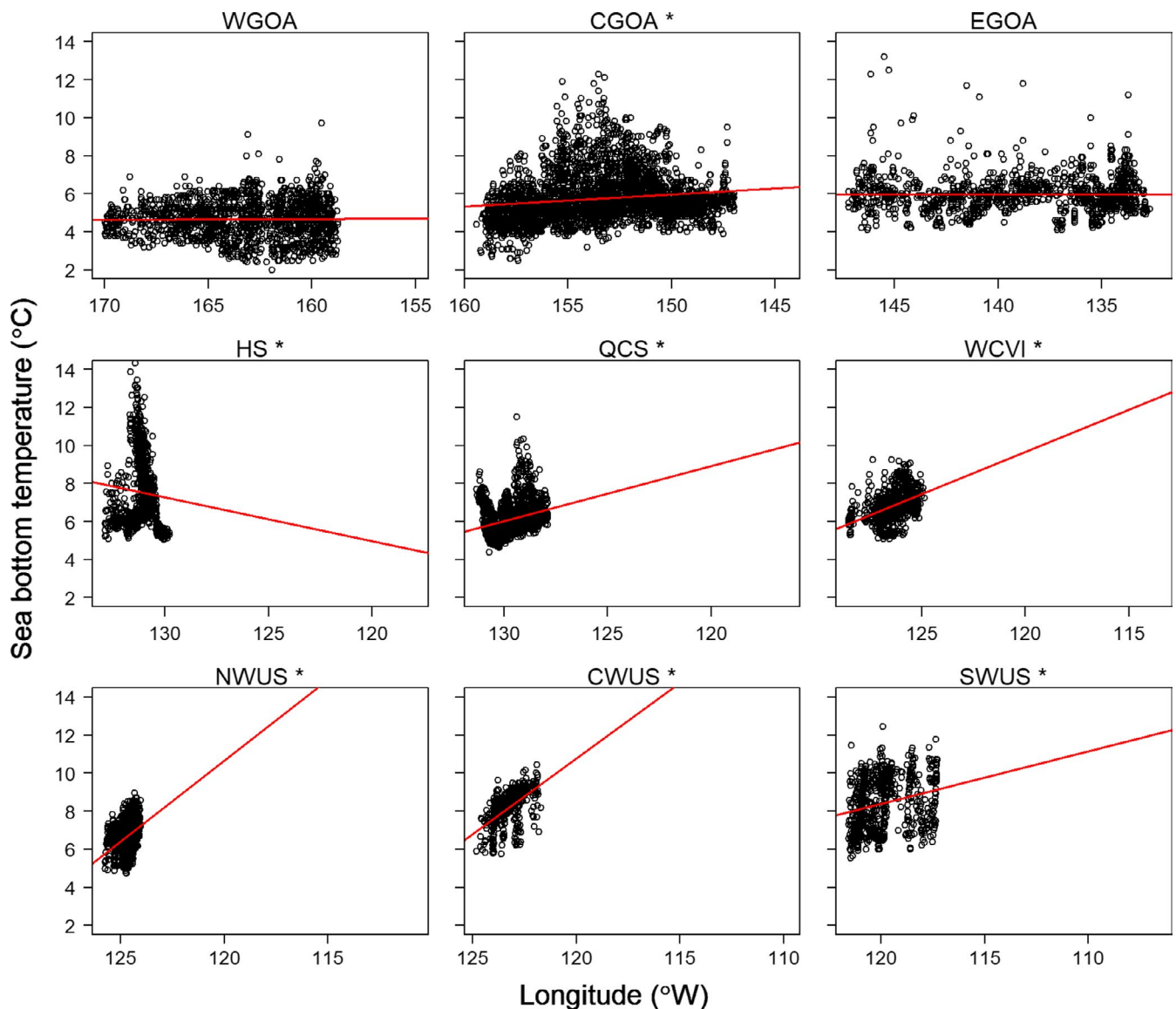


FIGURE 9 Bottom temperature and longitude of each bottom trawl haul across all survey years in each subregion. Red lines show the linear relationship and * represents a significant longitudinal temperature gradient ($p < 0.05$). Each x-axis has the same longitude range of 15° for comparison

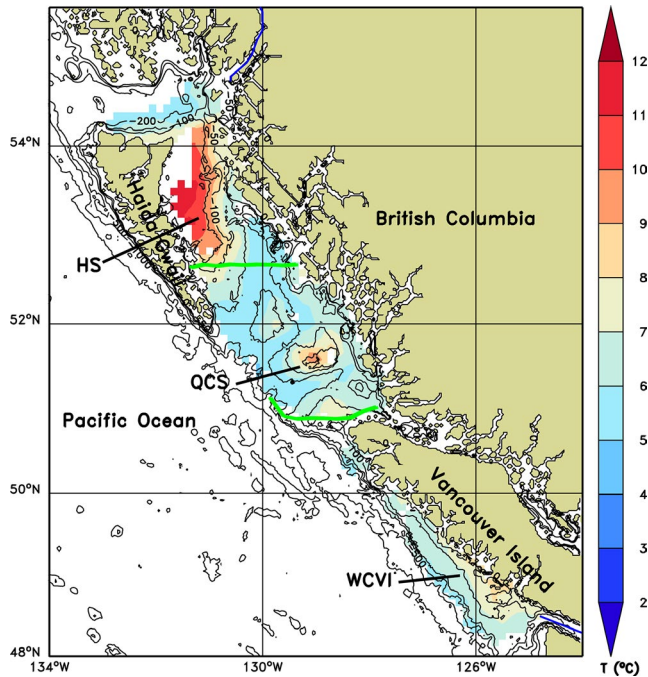


FIGURE 10 Mean bottom temperature ($^{\circ}\text{C}$) interpolated to a 0.1338 by 0.0833 degree longitude–latitude grid across survey years on the west coast of Canada. Bathymetric contours at 30, 50, 100, 200, 500, 1,000, and 2,000 m depth are shown in black. Subregional boundaries are shown in green lines. Deep cold water is only to the west in QCS and WCVI and the northern and southern Hecate Strait (HS)

Jacobson, Brodziak, & Rogers, 2001; Rutterford et al., 2015), fish density (Bartolino, Ciannelli, Bacheler, & Chan, 2011; Spencer, 2008), and predation (Gibson, Robb, Wennhage, & Burrows, 2002) were not considered in this study. No single factors can explain all. Particularly, in the eastern Bering Sea, temperature has been reported to be a less important factor in distribution shifts than temporal (Kotwicki & Lauth, 2013) and unexplained variability (Thorson, Ianelli, & Kotwicki, 2017). We highly recommend considering more factors than temperature in studying fish distributional changes.

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CONFLICT OF INTEREST

The authors have no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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