

**The relative influence of temperature and ontogeny on groundfish
distribution varies across life stages**

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A short running title:

Distributional changes of groundfish

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Distributional changes for fish populations may be difficult to interpret since temperature responses are often confounded with ontogenetic shifts. However, the relative importance of these two types of fish movement (temperature responses and ontogenetic shifts) to population distribution remains largely unstudied. This study presents the first attempt to compare the two types of movement in depth, latitude, and longitude for ten abundant groundfish species across size class and subregion. We utilized large, quality-controlled datasets from random depth-stratified, bottom trawl surveys consistently conducted during the summer along NE Pacific shelf from 1996 to 2015. We show that the size structure of each species varied across years and subregions with dramatically strong or poor recruitments for some species in 2015 during a marine heatwave. Principal Component Analysis (PCA) demonstrated that ontogenetic shifts in depth represented the primary movement pattern while temperature responses in latitude and longitude constituted a major, but a secondary pattern. Re-run by size class, PCA results further showed that the influence of temperature and ontogeny on population distribution varied by size classes with greater ontogenetic shifts in smaller fish and elevated temperature responses in larger fish. We further show substantial ontogeny-induced movements by depth, latitude, and longitude with high variability among species and subregions. Our analyses suggest that failing to account for size structure can lead to serious misinterpretation of population distributional changes in all three dimensions: depth, latitude, and longitude for populations with or without episodic recruitments.

Keywords: climate change, deepening, distribution, Heincke's law, marine heatwave, ontogenetic shifts, thermal tolerance

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Introduction

Species distributional changes (often reported as movements in the scientific literature; hereafter movements) have been increasingly documented in response to changing temperatures globally in the oceans (Cheung et al., 2013; Fredston, Pinsky et al., 2021; Perry et al., 2005; Pinsky et al., 2013) and terrestrial environments (Chen et al., 2011; VanDerWal et al., 2013). Future spatial distributions have been projected for the next several decades assuming the same distributional changes of fish in poleward and downward movements across space and time (Kleisner et al., 2017; Morley et al., 2018; Rooper et al., 2021; Rutterford et al., 2015). As species distribution models have been increasingly used, some recent studies developed new approaches (Barnet et al., 2021; Hazen et al., 2018) and some examined model uncertainties (Brodie et al., 2022; Commander et al., 2022; Santini et al., 2021). There has also been a growing body of literature to highlight spatial scales. A few recent studies have noted that subregional dynamics play a key role in the movement of temperature responses in large marine ecosystems (Kleisner et al., 2016; Li et al., 2019; Marshall et al., 2016) while some studies stressed fine-scale spatial distribution (English et al., 2021; Oldfather et al., 2020).

Irrespective of responding to climate change trends in temperature, fish species normally change their distribution as they age and grow. These well-studied ontogenetic movements typically follow Heincke's Law (Heincke 1913) where fish occupy deeper depths with increasing size, such as flatfish (Gibson et al., 2002; Methratta & Link 2007) and coral reef fishes (Gratwicke et al., 2006). A large-scale study in the northeast Pacific shelf discovered that ontogenetic shifts of ten commercially important groundfish were more complicated than deepening: some species exhibited shoaling; some species demonstrated major ontogenetic shifts in latitude and/or longitude while keeping small ranges of depth (Li et al., 2022).

However, the degree to which ontogenetic shifts contribute to the reported temperature responses of a population has rarely been investigated. The fish movements in responses to temperature (hereafter temperature responses) and ontogeny (hereafter ontogenetic shifts) can be confounded and difficult to disentangle. This is concerning particularly for fish that demonstrate episodic recruitments with a single year class dominating the entire population. This year class dominates the observed change in distribution for the whole population while it responds to the variable temperatures. Most climate change studies attribute fish movements to temperature responses without considering the ontogenetic shifts. A few recent climate change studies have started to account for the size structure of the population in assessing their temperature responses (Barbeaux & Hollowed 2018; Li et al., 2019; Yang et al., 2019). Additionally, Thorson et al. (2017) developed a spatio-temporal model to quantify the contributions of size structure and temperature to the overall movements of individual species. However, to date, the relative importance of ontogenetic shifts and temperature responses in the population distribution remains largely unknown for many species globally.

In this study, we fill this gap by comparing groundfish ontogenetic shifts and temperature responses by size class, species, and subregion. Li et al. (2019) computed temperature responses in depth, latitude, and longitude by 10-cm interval size class and subregion for ten commercially important groundfish along the northeast Pacific; Li et al. (2022) estimated ontogenetic shifts in the three dimensions for the same groundfish species also at 10-cm intervals in the same subregions using the same quality-controlled bottom trawl survey data. Here we first examine how the size structure of each groundfish species changed over time and space. We then compare ontogenetic shifts in Li et al. (2022) and temperature responses in Li et al. (2019) to determine the relative importance of three-dimensional temperature responses and ontogenetic shifts in

groundfish distribution. Lastly, we compute ontogeny-induced movement along the three dimensions and discuss how different the interpretation of groundfish movements would be with and without considering the population's size structure.

Materials and Methods

Survey data and quality control

We use the depth-stratified, random bottom trawl survey data that were quality-controlled in Li et al. (2019). Three regional surveys along the northeast Pacific shelf were included: the Gulf of Alaska, the west coast of Canada, and the west coast of the USA from 1996 to 2015. Since each regional survey required about three months to complete, seasonal conditions could vary markedly over the extended sampling periods. Consequently, each survey was divided into three subregions based on survey characteristics, geographic and oceanographic conditions, and management areas. The Gulf of Alaska divided into western (WGOA), central (CGOA), and eastern (EGOA); the Canadian west coast split into Hecate Strait (HS), Queen Charlotte Sound (QCS), and west coast of Vancouver Island (WCVI); and the west coast of USA classified into northern (NWUS), central (CWUS), and southern (SWUS). Each resulting subregion had a constricted sampling period of about one month.

Survey data were further quality controlled and bias-minimized in five steps: 1) the GOA datasets were constrained to the period since 1996 when digital temperature sensors replaced manual sensors; 2) a stratum depth range was set with deep strata excluded; 3) invalid hauls were excluded based on standard operating procedures; 4) hauls were excluded when conducted at depth outside their designated stratum range; 5) Biased years, such as 2004 from WCVI and 2005

and 2007 from CWUS, were excluded because of an uneven or anomalous distribution in depth, latitude or longitude. See more details about subregion classification and quality control in Li et al. (2019).

Fish species and size structure

We studied the same ten commercially important species examined in Li et al. (2022, 2019), which were the abundant species within each subregion (Table S1). The ten species include arrowtooth flounder (*Atheresthes stomias*, Pleuronectidae), Dover sole (*Microstomus pacificus*, Pleuronectidae), northern rock sole (*Lepidopsetta polyxystra*, Pleuronectidae), southern rock sole (*L. bilineata*, Pleuronectidae), Pacific cod (*Gadus macrocephalus*, Gadidae), Pacific hake (*Merluccius productus*, Merlucciidae), Pacific ocean perch (*Sebastes alutus*, Sebastidae), petrale sole (*Eopsetta jordani*, Pleuronectidae), sablefish (*Anoplopoma fimbria*, Anoplopomatidae), and walleye pollock (*Gadus chalcogrammus*, Gadidae). We applied the same criteria for low sample size as in Li et al. (2022): presence in 50% of the survey years and a minimum number of fish defined as 2.5 times the number of survey years. The size structure of each species was estimated as the proportion of each size class (in 10-cm intervals) to the whole population for each year in each subregion. As the survey in each subregion extends about one month consistently over years, we believe that the chance of fish growing from one size class to the next is minimal within year and subregion.

Temperature responses and ontogenetic shifts

Both Temperature Responses (TR) and Ontogenetic Shifts (OS) were based on annual centroids of fish distribution, catch-per-unit-effort (CPUE) and stratum area-weighted centroids for

groundfish distributions by species, size class, and subregion (Li et al., 2019). The mean annual centroids of fish distribution, MF_{jsy} for species j , size class s , in year y in each subregion were calculated as (Li et al., 2019):

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

where $CPUE_{jshiy}$ represents CPUE of species j and size class s in haul h , stratum i , and year y ; 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} represents environmental variables {e.g., temperature ($^{\circ}\text{C}$), depth (m), longitude ($^{\circ}$), or latitude ($^{\circ}$)} of haul h , in stratum i , in year y ; and k is the number of strata in each subregion.

Temperature responses were then estimated as differential centroids between cold and warm years for a given size class of species in each subregion (Li et al., 2019). Temperature responses in each dimension, TR_{js} , for species j , size class s , in each sub-region were computed as:

$$TR_{js} = \frac{\sum_{y=1}^w MF_{jsy}}{w} - \frac{\sum_{y=1}^c MF_{jsy}}{c} \quad (2)$$

where w is the number of warm years and c is the number of cold years. Warm or cold years were defined as the annual bottom temperature above or below the 0.66 standard deviation from the overall mean across all survey years for each sub-region (see details in Li et al., 2019).

Ontogenetic shifts were defined as the differential centroids across all survey years between a given size class and that of the next larger size class (Li et al., 2022). Ontogenetic shifts OS_{js} , for species j , size class s , in each subregion were estimated as follows:

$$OS_{js} = \frac{\sum_{y=1}^m MF_{j(s+1)y}}{m} - \frac{\sum_{y=1}^m MF_{jsy}}{m} \quad (3)$$

Where MF_{jsy} is computed as in Equation 1 and m represents the total number of survey years in each subregion. The largest size classes were excluded in ontogenetic shifts because the next size class, $s+1$, was absent.

Relative importance of groundfish movements

We used Principal Component Analysis (PCA) to examine the relative importance of fish movement using standardized TR and OS each in depth, latitude, and longitude by species, size class, and subregion. PCA linearly transforms the data into a new coordinate system where most of the variation in the data can be described with fewer dimensions than the initial data. It has been utilized in many ecological studies (Aziz et al., 2021; Claverie & Wainwright 2014; Li et al. 2013). First, we standardized the six movement variables for each size class by species and subregion, TR and OS each in three dimensions, by dividing each variable by the standard deviations of centroids for each size class of fish (MF_{jsy} , Equation 1) across all survey years. For example, both ontogenetic shifts in depth (OS_D) and temperature responses in depth (TR_D)

were divided by the standard deviation of MF_{jSY} in depth across years. Second, Euclidean distance was then computed as a dissimilarity metric for the selected variables. Finally, PCA was conducted aiming for a total of four PCs to explain the variances in fish movements using PRIMER. PCA was first carried out for the aggregated species of all size classes and subregions and then repeated for each size class to examine the differences in the primary movements across life stages.

Ontogeny-induced movement

Ontogeny-induced movement (OM) is fish movement introduced by changes in size structure for species that demonstrate ontogenetic shifts, showing the difference in distribution with or without the size structure. As the bottom temperature featured large interannual variability with cold and warm years instead of steadily increasing temperature (Li et al., 2019), we used anomalies, instead of movement rate such as $m\ year^{-1}$ in depth and $^{\circ}N\ year^{-1}$ poleward, to show the groundfish distributional changes. We first computed anomalies in depth, latitude, and longitude, with and without size structure, respectively. OM was then estimated as the difference between them for each species and subregion.

Anomalies without size structure were computed in two steps. First, annual centroids of fish distribution, MF_{jy} for species j , in year y , in each subregion, were estimated similar to MF_{jSY} in Equation 1 except that no size classes were defined for species:

$$MF_{jy} = \frac{\sum_{i=1}^k \sum_{h=1}^{n_{iy}} \frac{w_i CPUE_{jhiy} E_{hiy}}{n_{iy}}}{\sum_{i=1}^k \sum_{h=1}^{n_{iy}} \frac{w_i CPUE_{jhiy}}{n_{iy}}} \quad (4)$$

where $CPUE_{jhiy}$ represents CPUE of species j , in haul h , stratum i , and year y ; with the rest of parameters (w_i , n_{iy} , E_{hiy} , and k) defined in Equation 1.

The anomalies of species j without size structure in year y , \dot{A}_{jy} , were then estimated as the annual deviation from the overall mean centroids across all survey years (m , the same as in Equation 3) in each subregion:

$$\dot{A}_{jy} = MF_{jy} - \frac{\sum_{y=1}^m MF_{jy}}{m} \quad (5)$$

Anomalies with size structure were also computed in two steps. First, anomalies A_{jsy} for species j , size class s , in year y , was defined as the annual deviation from the overall mean of annual centroids MF_{jsy} (Equation 1) across all survey years (m) in each subregion:

$$A_{jsy} = MF_{jsy} - \frac{\sum_{y=1}^m MF_{jsy}}{m} \quad (6)$$

Second, the anomalies for species j , in year y with size structure, A_{jy} , were estimated as the CPUE-weighted mean of size-specific anomalies in each subregion:

$$A_{jy} = \frac{\sum_{s=1}^z (CPUE_{jsy} A_{jsy})}{\sum_{s=1}^z CPUE_{jsy}} \quad (7)$$

where $CPUE_{jsy}$ represents CPUE of species j and size class s in year y . $CPUE_{jsy}$ differs from $CPUE_{jshiy}$ in Equation 1 in that in a year y , $CPUE_{jshiy}$ was used to weight environmental

variables of each haul for the annual centroids of each size class and $CPUE_{j sy}$ was used to weight anomalies of each size class for the anomalies of a species as a whole.

Finally, OM was defined as the deviation of anomalies of fish distribution without size structure from those with size structure. OM for species j in year y , OM_{jy} , was estimated for each subregion:

$$OM_{jy} = \dot{A}_{jy} - A_{jy} \quad (8)$$

Since OM was computed on a yearly basis, it reflected the annual speed of ontogeny-induced movement for each species and subregion in depth (m year^{-1}), latitude ($^{\circ} \text{year}^{-1}$), and longitude ($^{\circ} \text{year}^{-1}$). The mean of absolute OM and standard deviation of OM were further calculated across all survey years to compare among species and subregion.

Results

Changes in size structure

Most groundfish species had different size ranges across subregions and their maximum size classes tended to be smaller in more southerly waters (Fig. 1, 2, S1 a-e). For example, the maximum size class of sablefish reduced from 81-90 cm in the CGOA to 61-70 cm in the CWUS and SWUS (Fig. 1); the maximum size class of Dover sole decreased from 61-70 cm in CGOA and EGOA to 41-50 cm in CWUS and SWUS (Fig. 2). Additionally, there were considerable subregional differences in the smallest size class within region where the same fishing gear was used. For example, the smallest Dover sole was one size class larger in the WGOA than in

CGOA and EGOA and also one size class larger in QCS than in HS and WCVI (Fig. 2). The within region differences may be related to the local densities of small fish.

The species-specific size structure demonstrated large differences between subregions. For example, in the west coast of Canada (subregions HS, QCS, and WCVI), distributions of Dover sole sizes appeared similar with the same size class dominant over the years. By contrast, the interannual variability in that distribution was much larger in the GOA and the west coast of USA, and dominant size classes were inconsistent across years in most of these subregions (Fig. 2). Additionally, all species demonstrated substantially larger changes in size structure across years in the subregions at the leading-edge of their distributional ranges relative to other subregions, e.g., NWUS as the southern edge of Pacific cod (Figure S1 b) and HS as the northern edge of Petrale sole (Figure S1 d). The temperatures in these leading-edge areas are likely close to their species-specific temperature tolerances.

There was substantial interannual variability in size structure for each species within each subregion (Figs. 1, 2, S1 a-e). Some species exhibited variability in the dominant size classes across years within each subregion including sablefish, arrowtooth flounder, Pacific cod, pollock, and Pacific Hake (Figs 1 and S1 a, b, and e). By contrast, Dover sole, Pacific ocean perch, Petrale sole, and northern and southern rock sole showed substantially lower interannual variability in size structure, most with the same dominant size class in each subregion (Figs. 2, S1 c d e). However, none of the ten species demonstrated a constant size structure across years within any subregion (Figs. 1, 2, S1 a-e). Additionally, the edge subregions exhibited larger interannual variability and incomplete size classes compared to the rest of subregions, e.g., Petrale sole in HS, Pacific ocean perch and Pacific cod in NWUS, and arrowtooth flounder in CWUS.

Groundfish also demonstrated variable responses in recruitment during the 2015 marine heat wave. 2015 was an extremely warm year in the GOA only and moderately warm or even neutral year in the rest of subregions (see temperature anomalies in Li et al., 2019).

Consequently, sablefish recruitment exhibited considerable variation across subregions. It was strongest across the entire GOA (Fig. 1) in 2015 as shown by the highest proportion of small sablefish (≤ 40 cm). The proportion ranged from medium to high levels in HS, CWUS, and SWUS, where 2015 was a moderately warm year. By contrast, some fish exhibited low recruitment during the heat wave, e.g., arrowtooth flounder in the entire GOA (Figs S1 a) and Pacific cod in the CGOA (Fig S1 b). The remaining species demonstrated no obvious recruitment responses to the marine heat wave, probably suggesting that they are less sensitive to changes in temperature.

Relative importance of groundfish movements

Using the two types of standardized movements in depth, latitude, and longitude for the aggregated species of all size classes and subregions, a Principal Component Analysis (PCA) showed that ontogenetic shifts in depth were the largest observed component of variance in the spatial distributional changes of groundfish (Fig. 3). PC1, accounting for 39.9 % of the overall variance, was dominated by the ontogenetic shifts in depth (loading 0.99) with the least contribution from temperature responses in depth. PC2, accounting for 17.9% of the total variance, was dominated by temperature responses in latitude and longitude (loadings 0.62 and -0.72, respectively) with small contribution from the rest of movements.

When PCA was applied to each size class, the relative importance of temperature responses and ontogenetic shifts varied from size classes (Fig. 4). Ontogenetic shifts in depth

dominated PC1 in the four smallest size classes 1 - 40 cm and contribution to the overall movements decreased greatly in the larger size classes. Ontogenetic shifts in depth had a major contribution to PC2 in size classes 41-60 cm and small contribution to PC1 for fish larger than 60 cm. Ontogenetic shifts in latitude and longitude were the largest for the medium size classes (31-50 cm) where ontogenetic shifts in all three dimensions dominated both PC1 and PC2. Temperature responses demonstrated opposite trends. Temperature responses in latitude and longitude contribute greatly to PC2 and temperature responses in depth tended to remain small for small fish. However, for larger mature fish (> 50 cm), the temperature responses in all three dimensions were greater than ontogenetic shifts and became dominant to both PC1 and PC2. Generally, ontogenetic shifts (first in depth and then in latitude and longitude as well) dominated overall movements until fish reached their medium size classes, after which the population distribution responded more to temperature than to ontogeny in three dimensions.

The variance explained by PC1 and PC2 varied greatly across size classes (Figure 4). PC1 was the highest for 1-10 cm of fish, explaining 73.3% of total variance and was second highest for the largest size of fish (>70 cm), explaining 53.8% of overall variance. The variance explained by PC1 ranged from 27.6 % to 42.9% in the remainder of size classes of fish with the smallest percentage (<30%) in 41-70cm size classes. PC2 explained 20% - 27% of overall movement variance across all size classes. The sum of PC1 and PC2 explained more than 60% of movement variance except 41-70cm size classes, showing greatest diversity in the population movement of medium-large fish. As there are fewer species in fewer subregions with the smallest and largest size classes, caution is suggested for interpreting the general patterns here. For example, there were five species in the 1-10 cm group including arrowtooth flounder (WGOA), Pacific ocean perch (WGOA, CGOA, and EGOA), Pacific cod (HS), Pacific hake

(SWUS) and walleye pollock (WGOA and CGOA). The group of fish larger than 70cm consisted of three species only, arrowtooth flounder (WGOA and CGOA), Pacific cod (CGOA, HS), and sablefish (CGOA, WCVI, and NWUS).

Ontogeny-induced movements

The proportion of a population at critical life stages (e.g., migration or settlement) can greatly confound interpretations of a population's spatial distribution for groundfish that exhibit episodic recruitments such as sablefish. Small sablefish occupied shallow inshore waters until reaching a size of 40 cm and then moved south-west-ward to deep offshore waters in the WGOA to settle for the later life stages (Li et al., 2022). The ontogenetic shifts between 31-40 cm size class and 41-50 cm size class were dramatic in depth, latitude, and longitude, leading to a significant migration in their lifetime. This species is also known for their episodic recruitments. In 2014, there was an exceptionally large cohort of sablefish in the WGOA (Hanselman et al., 2018). This resulted in a large proportion (>60%) of small sablefish ($\leq 40\text{cm}$) in the survey catches in 2015 marine heat wave and the entire population appeared to move northward to shallower water if size structure was not considered (Equation 4; Fig. 5). By contrast, in a cold year of 1999, fewer small sablefish were caught, and the population appeared to move southward to deeper habitats (Fig. 5). However, the interpretation was not supported when examined by size class (Equation 1): no deepening was observed for any size classes in 1999 and no shoaling movements in any individual size class in 2015 (Fig. 6). Particularly, there was a clear deepening of large sablefish (>50 cm) in 2015 while the smaller sizes classes continued to remain at the same mean depth.

Considering all life stages instead of focusing on a specific stage as in the example above, our estimation of ontogeny-induced movement (OM, Equations 4-8) showed that ontogeny

introduced significant population distributional changes in depth, latitude, and longitude across all species and subregions (Fig. 7). Although the primary fish movements were ontogenetic shifts in depth (Fig. 3), OMs were also considerable in latitude and longitude (Fig. 7), suggesting that the influence of ontogeny on population movements occurs in all three dimensions. Additionally, the trends were similar between absolute and variability of OMs (Fig. 7). Large absolute OMs synchronized with the large variability of OMs.

Ontogeny-induced movements in depth varied across subregions and species (Fig 7 a d). Generally, most species demonstrated smaller OMs in depth in WCVI and larger OMs in depth in CWUS with larger variation across species and years; the largest ranges of OMs in depth across species occurred in WGOA and CWUS. Sablefish showed the largest OM in depth among species in each subregion and the OM of sablefish in CWUS was the greatest among species and subregions. A few species, including southern and northern rock sole and arrowtooth flounder in WGOA and CGOA, exhibited smaller OMs in depth across all subregions. Additionally, OMs in depth of each species varied across subregion. For example, Dover sole demonstrated the lowest OM in depth in HS and the highest in WGOA. Just like in ontogenetic deepening, OMs in depth of arrowtooth flounder also increased from WGOA southward to CWUS.

The magnitude of groundfish OMs in latitude appeared associated with the ranges of subregions (Fig. 7 b e). Groundfish OMs in latitude were generally small in Canadian west coast subregions of HS, QCS, and WCVI, where ranges in the latitude of these areas were considerably smaller than other subregions; most groundfish had the largest OMs in latitude in NWUS where there is the largest latitude range among all subregions. Sablefish in CWUS showed the largest OM in latitude followed by Pacific ocean perch and sablefish in NWUS. Particularly, Pacific ocean perch and arrowtooth flounder had substantially higher OMs in

latitude in CWUS (0.35° and 0.25° respectively) than other subregions (<0.1°). The smallest variation of OM in latitude across species occurred in WCVI and the greatest in WGOA.

Ontogeny-induced movements in longitude also appeared associated with the spatial ranges of surveys and varied across subregions and species (Fig. 7 c f). Groundfish exhibited larger OMs in longitude in GOA subregions where there are substantially larger longitude ranges than other subregions. HS and WCVI with small longitude ranges had the smallest OMs in longitude with the smallest variation while WGOA had the largest OMs with the largest variation across species and years. Sablefish in WGOA and CGOA had considerably higher OMs in longitude than other species and subregions. Dover sole, Pacific ocean perch, and Pacific cod also demonstrated higher OMs in longitude in the GOA than in other subregions. Dover sole and Pacific hake exhibited the lowest OMs in longitude in NWUS across species and subregions.

The largest OMs of a species along each dimension occurred in different subregions. For example, OMs in depth of arrowtooth flounder were the greatest in CWUS; OMs in latitude of this species peaked in NWUS; the largest OM in longitude occurred in EGOA. Petrale sole had the largest OM in depth in SWUS, the largest OM in latitude in NWUS, and the largest OM in longitude in QCS.

Generally, OMs appeared to be influenced by two factors: ontogenetic shifts and size structure. If there are no changes in either factor, there will be no influence of ontogeny on the population distributional changes. Minor changes in both factors lead to small OMs and large changes in both factors result in dramatic OMs. WGOA Sablefish exhibited large ontogenetic shifts in depth, latitude and longitude (Li et al., 2022) with large changes in size structure (Fig 1). Consequently, this species had the largest OMs in the three dimensions in WGOA (Fig. 7). Generally, Canadian west coast subregions had smaller OMs in three dimensions than GOA and

US west coast subregions (Fig 7) as a result of relatively smaller ontogenetic shifts associated with small geographic areas. With given changes in size structure for a species and subregion, different magnitude of ontogenetic shifts led to different OMs in three dimensions. For example, northern and southern rock sole, shallow-water species demonstrated minor ontogenetic shifts in depth but large ontogenetic shifts in latitude and longitude (Li et al., 2022), corresponding to minor OMs in depth and large OMs in latitude and longitude (Fig. 7). However, the high variability of OMs across species, subregion, and dimension makes it difficult to correct once species distributional shifts are estimated without accounting for size structure.

Discussion

Changes in size structure

The varying size structure of groundfish supports the common pattern known as the “temperature-size rule”. The rule suggests that body size increases with latitude (Atkinson & Sibly 1997). Furthermore, recent studies have reported that body size of various organisms have declined within territorial and aquatic ecosystems (Sheridan & Bickford 2011; Gardner et al., 2011) including many fish species (Audzijonyte et al., 2020; Baudron et al., 2014; McQueen & Marshall 2017; Oke et al., 2020) under global warming. In addition, fishing can also lead to declining fish size (Hollins et al., 2018; Link & Watson 2019; West et al., 2020), contributing to the varying size structure observed in this study.

Temperature can greatly impact recruitments and thus enhances temporal changes in size structure. The extraordinary marine heatwave in the NE Pacific Ocean 2014/2016 caused widespread changes in ichthyoplankton fauna (Nielsen et al., 2020) including recruitment

collapse of Pacific cod in the GOA (Barbeaux et al. 2020; Laurel & Rogers 2020) and the strongest recruitment of WGOA sablefish in the last few decades (Hanselman et al., 2018). With marine heat waves expected more frequently in the future (Oliver et al., 2018) and thermal bottlenecks occurring in spawning adults and embryos stages (Pörtner & Peck 2010; Dahlke et al., 2020), many species may experience larger variation or trends in recruitment patterns. Moreover, combined with other stressors such as acidification, hypoxia, food availability, and predation, the impacts of high temperature on marine organisms were even more profound across life stages (Cominassi et al., 2020; Gobler et al., 2018; Lifavi et al., 2017), leading to larger changes in size structure.

Relative importance of groundfish movements

Both ontogeny and temperature have substantial effects on the distribution of groundfish species with difference in relative importance across life stages from the Gulf of Alaska through the southwest coast of the USA. Our analyses showed that for all size classes combined, ontogenetic shifts in depth were the primary movements and temperature responses in latitude and longitude were secondary (Fig 3). However, ontogeny exhibited larger effects on small fish ($\leq 50\text{cm}$) while temperature had greater effects on large fish ($> 50\text{cm}$) (Fig 4). The cutoff size of 50cm might be associated with maturity since the length at 50% maturity for all these species (except sablefish) ranges from 31 to 52 cm (Li et al., 2022). As some groundfish of early life stages are distributed in critical habitats and oceanographic conditions, such as depth and sediment (Lough et al., 2006; Stuart-Smith et al., 2021), limiting the degree to which they redistribute in responses to climate change (Ciannelli et al., 2022). By applying different approaches to six groundfish species in three different subarctic marine systems, Ciannelli et al. (2022) also discovered that adults are

more likely to respond to temperature changes due to being less constrained in space.

Additionally, fish experience a declining oxygen supply as they grow because the gills can't grow in three dimensions as the bodies do (Pauly 2021). Consequently, the shortage of oxygen for adults can constrain them in low-temperature waters because high temperatures increase metabolism rates demanding more oxygen supply. From the physiological perspective, temperature therefore has larger impacts on distribution of large fish through oxygen supply.

Different temporal scales for 10-cm intervals in size classes may have slightly contributed to the observed patterns in relative influence of temperature responses and ontogenetic shifts on population distribution. We classified fish into size classes to account for ontogeny. However, the 10-cm interval represents different temporal scales for different size classes of a given species within a subregion. For example, warm temperatures may increase fish growth with small fish quickly growing to the next size class and moving to deeper waters, confounding ontogenetic shifts and temperature responses probably within months. By contrast, larger sizes of fish can experience multiple warm and cold years before growing to the next size class, making it easier to detect the temperature responses. Furthermore, life stages within species could vary by subregion due to thermal effects on growth (Conover et al., 2009; McKenzie et al., 2020); life stages also vary across species due to species-specific mean rates of growth as a function of temperature (Leiva et al., 2019; van der Sleen et al., 2022). However, Ciannelli et al. (2022) investigated multiple groundfish distributions by age and reached the similar results of difference in the relative influence of ontogeny and temperature across life stages, indicating the temporal differences in the uniform 10 cm interval might have been minor.

Ontogeny-induced movements

Our analyses show that ontogeny-induced movements to the population distribution can be substantial in three dimensions for all populations. We expected large OMs for fish such as sablefish to show episodic recruitments. However, our analyses revealed that no size structure remained stable for species with or without episodic recruitments and that all species demonstrated substantial OMs in three dimensions. Notably, all fish demonstrated complicated ontogenetic shifts in three dimensions (Li et al., 2022). The combined changes in spatial distribution across life stages and changes in size structure led to considerable changes in ontogeny-induced movements.

Our estimated OMs were strikingly larger than the maximum yearly movements of the whole population in depth and latitude among 56 taxa from the GOA and 42 taxa from the west coast of the USA (Pinsky et al., 2013) (Fig. 7). It is difficult to compare results from our study to similar large-scale studies of shifts in NE Pacific groundfish such as Pinsky et al. (2013) because of differences in the study design as well as the quality control measures and subregional scale applied to our data in addition to size structure of populations. Although scientific survey data have been widely used to track fish movements (e.g., Morley et al., 2018, Pinsky et al., 2013), survey data has rarely been evaluated. Maureaud et al. (2021) discussed survey data availability and survey coverage with emphasis on transboundary fish. Li et al. (2019) conducted comprehensive quality control of long-term survey data to minimize the survey-introduced biases in fish distribution, e.g., accounting for spatial biases in the random allocation of survey stations. Additionally, a few recent studies applied a subregional scale instead of the whole survey area to survey data and found the same species demonstrated different distributional responses to temperature (Kleisner et al., 2016; Li et al., 2019; Marshall et al., 2016; Yang et al.,

2019) and to ontogeny (Li et al., 2022) across subregions. Our analyses further demonstrate that the same groundfish species also vary in size structure across subregions. The combined factors of data quality, spatial scale, and size structure, as ignored in most climate change studies, may confound the true temperature responses of whole populations.

Implications of this study

Consistent with recent studies, our study suggests that projections of future distribution based on temperature alone are likely to miss a substantial portion of the trends in fish movement. Our analyses agree with Thorson et al. (2017) that ontogeny and temperature explained variations in different components of the population distribution. For example, temperature alone generated a portion of north-south variation while ontogeny explained a portion of east-west movements in pollock distribution in the east Bering Sea (Thorson et al., 2017). Furthermore, Thorson et al. (2017) discovered that most of the variation in pollock distribution in latitude and longitude was unexplained by temperature or ontogeny, highlighting the need to extend similar analyses to other species and regions. In addition to temperature, recent studies have started to include other factors in species distribution such as species interactions (HilleRisLambers et al., 2013; Selden et al., 2018; Urban et al., 2013) and multifactor habitat selection (Cao et al., 2017; Fredston et al., 2021; McHenry et al., 2019). However, as far as temperature is considered, our study recommends that ontogeny should always be accounted for when quantifying distributional changes of a population.

With continuous global warming, groundfish may demonstrate both larger temperature responses and larger ontogenetic shifts. For example, many fish may need to move deeper to locate habitat of the desired low temperature. Furthermore, warmer temperature decreases

dissolved oxygen levels reducing deep habitat availability (Breitburg et al., 2018; Deutsch et al., 2011; Sampaio et al., 2021). Groundfish may have to move more horizontally to establish new long-term suitable habitat as they grow in hypoxic areas. The different combination of temperature and oxygen levels may therefore shape the demersal communities (Clarke et al., 2022). Additionally, fish grow faster and mature earlier at smaller body sizes in warmer conditions (Forster et al., 2012). However, the relative influence of temperature and ontogeny may remain the same that ontogeny has more influences on small fish and temperature has stronger impacts on large fish because of the same constraints in geographic locations for young fish and oxygen supply for adults.

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Data availability: All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. The complete datasets used in this study are available at <https://github.com/Lingbo-fish/NE-Pacific-groundfish>.

CONFLICT OF INTEREST

The authors have no conflict of interest.

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Figure 1. Size proportion of sablefish by year (thick lines for 2015) and subregion

Figure 2. Size proportion of Dover sole by year (thick lines for 2015) and subregion

Figure 3. PC loadings of standardized movement variables including the ontogenetic shift in depth (OS_D), latitude (OS_Lat), and longitude (OS_Lon) and temperature response in depth (TR_D), latitude (TR_Lat), and longitude (TR_Lon). The percentages at x- and y-axes show the variation of fish movements explained by the PCs. All size classes and species of groundfish across subregions were combined. See PCA results by size class in Figure 4

Figure 4. PC loadings of standardized movement variables for each size class (cm) of groundfish. Movement variables and percentages at x- and y-axis are the same as in Figure 3. The two largest size classes were merged into the “> 70” cm group

Figure 5. Time series of sablefish in the WGOA: 1) proportion of small fish (≤ 40 cm) to the entire population (black); 2) distribution centroids of the entire population in depth (red) and latitude (orange) without accounting for size structure

Figure 6. Centroids of sablefish distribution in the WGOA by size class and year. Annual centroids (mean \pm standard deviation) of each size class of sablefish (cm) in the WGOA in warm (red), cold (blue), and medium (dark grey) years based on bottom temperature (See details about warm/cold/medium years in Li et al., 2019). The cold year of 1999 and warm year of 2015 were identified as “99” and “15” respectively

Figure 7. Ontogeny-induced movement (OM) by species and subregion. Mean of absolute annual OM in depth (A), latitude (B), and longitude (C) and standard deviation of annual OM in depth (D), latitude (E), and longitude (F) for each species (by color) across subregion. No points for some species in certain subregions represent being excluded in the analyses due to low abundance or absence in those areas. Dashed lines show the maximum absolute movements

(with a couple of outliers excluded) in depth and latitude in the GOA and the west coast of USA estimated in Pinsky et al. (2013)