

## Three-dimensional ontogenetic shifts of groundfish in the northeast Pacific

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## Abstract

It has been more than 100 years since fish were first described to move to deep waters as size increased, termed “Heincke’s Law”. However, large-scale studies on ontogenetic shifts are rare compared to increased reports of distributional changes in response to temperature, often confounded with the ontogenetic shifts. We fill this gap by examining the distribution of ten abundant groundfish species in three dimensions, depth, latitude, and longitude, at 10-cm size intervals within nine subregions of NE Pacific. Here we utilized large, quality-controlled datasets from random depth-stratified, bottom trawl surveys consistently conducted during the summer along the NE Pacific shelf from 1996 to 2015. Groundfish demonstrated complex ontogenetic movements in three dimensions across species, size class, and subregion. In addition to the expected ontogenetic deepening, shoaling also occurred and some species demonstrated major ontogenetic shifts in longitude and/or latitude with limited changes in depth. Based on standardized ontogenetic shifts in three dimensions, our analyses show that there were significant differences in aggregate fish ontogenetic shifts between small ( $\leq 30$  cm) and large ( $> 30$  cm) size groups. Small fish exhibited substantially larger ontogenetic shifts in depth than the large size group while both groups showed relatively small shifts in latitude and longitude. Our analyses strongly suggest that size structure and ontogenetic shifts should be included in the population distribution.

Keywords: climate change, demographic, distribution, Heincke’s law, population, size structure

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## Introduction

Fish species commonly change their distribution as they age and grow. The general tendency for fish to occupy deeper depths with increasing size was termed Heincke's Law (Heincke, 1913) more than 100 years ago. Ontogenetic shifts of groundfish have been sparsely quantified across juvenile and adult stages in areas such as the Gulf of Alaska (Yang et al. 2019), eastern Bering Sea (Barbeaux & Hollowed, 2018; Yang et al., 2019), and Rockall Trough, northeast Atlantic ocean (Mindel et al., 2016). However, comprehensive large-scale studies are rare, and many ecological questions remain unanswered, e.g., how the ontogenetic shifts of a species differ across size classes and areas. Furthermore, based on local bathymetry, a shift in depth along the plane of the seafloor for groundfish may also correspond to a simultaneous change in longitude, latitude, or both. To date, no studies compared the ontogenetic shifts across these dimensions.

Understanding ontogenetic shifts within the context of climate change is important because these movement responses can be confounded. If groundfishes exhibit episodic recruitment events where a few year classes dominate the population and strong ontogenetic deepening occurs, then the ontogenetic shift due to strong recruitment can be confounded with thermally induced movements. Although species distributional responses to changing temperatures have been increasingly described (Kleisner et al., 2017; Morley et al., 2018; Rutterford et al., 2015), efforts to account for the size and age structure of the population are more recent (Barbeaux & Hollowed, 2018; Li et al., 2019; Yang et al., 2019). There is a strong need to study natural ontogenetic shifts to provide insights for climate change studies.

In this study, we fill this gap by quantifying groundfish ontogenetic shifts in depth, latitude, and longitude across species and subregions in the northeast Pacific shelf using quality-controlled long-term survey data. We also used the same subregional areas described in Li et al.

(2019): 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 U.S. classified into northern (NWUS), central (CWUS), and southern (SWUS) (Fig. 1). Our current study has two goals focusing on the same ten groundfish species across subregions as in Li et al. (2019): 1) estimate ontogenetic shifts along three-dimensions; 2) examine which factors influenced the ontogenetic shifts including size class, species and subregion. Our analyses confirm the need to consider size structure and spatial scale for future climate change studies.

## **Materials and Methods**

### **Survey data and quality control**

We use depth-stratified, random bottom trawl survey data that were originally quality-controlled by Li et al. (2019). The surveys included the Gulf of Alaska (GOA) and the west coasts of Canada and the U.S. from 1996 to 2015. Since each regional survey extended for several months, seasonal conditions could vary markedly over the sample periods. Consequently, each survey was divided into three subregions based on survey characteristics, geographic and oceanographic conditions, and management areas. Each resulting subregion had a constricted sampling period of about one month (Fig. 1). 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 were

excluded with 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 class**

We studied the same ten commercially important species (Table S1) as in Li et al. (2019), which were the abundant species within each subregion. 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).

Due to the low survey selectivity for small size classes of fish and the low number of large fish, small and large size classes often had fewer samples than others. The threshold for low sample size was defined as fish within a species, size class and subregion being present in at least 50% of the survey years and the minimum number of fish as 2.5 times of the number of survey years. The smallest size class with low sample size was excluded, and the largest size class with low sample size was merged with the second largest (or even with the third largest when necessary). We decided not to merge the small size classes because unlike the largest size classes, there may be large ontogenetic shifts between sequential small size classes.

Consequently, some smallest size classes of fish, which contributed 0.02% to the whole sample, were excluded in the analyses.

## Centroids of groundfish distribution

We computed catch-per-unit-effort- (CPUE) and stratum area-weighted centroids for groundfish distributions (also called center of gravity) by species, size class (at 10 cm intervals), and subregion. The annual centroids of fish distribution,  $MF_{jsy}$  for species  $j$ , size class  $s$ , in year  $y$  in each subregion (Li et al., 2019) were calculated as:

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

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<sup>2</sup>) 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, depth, longitude, or latitude) of haul  $h$ , in stratum  $i$ , in year  $y$ ; and  $k$  is the number of strata in each subregion.

## Habitat and ontogenetic shifts

We defined ontogenetic shifts (OS) as the differential habitat between a given size class and that of the next larger size class. Habitat was estimated as the overall mean of annual centroids of the species distribution for a size class ( $MF_{jsy}$ ) across all survey years for each subregion. The habitat  $HA_{js}$  and ontogenetic shifts  $OS_{js}$ , for species  $j$ , size class  $s$ , in each subregion were estimated as follows:

$$HA_{js} = \frac{\sum_{y=1}^m MF_{jsy}}{m} \quad (2)$$

$$OS_{js} = HA_{j(s+1)} - HA_{js} \quad (3)$$

Where  $MF_{jsy}$  is computed as in Equation 1 and  $m$  represents the total number of survey years in each subregion. Habitat for each size class, species and subregion was described in four dimensions: temperature, bottom depth, latitude, and longitude. As ontogenetic shifts refer to fish movements, temperature was dropped, and the rest of three dimensions were applied. The largest size classes were excluded in ontogenetic shifts because the next size class,  $s+1$ , was absent.

Ontogenetic shifts were further standardized to be comparable across dimensions, species and subregions. The same standardization process as in Li et al. (2019) was applied: the original ontogenetic shifts,  $OS_{js}$  (Equation 3), were divided by the standard deviation of the annual centroids  $MF_{jsy}$  (Equation 1) across all survey years.

Extremes of standardized  $OS_{js}$  were defined the same as the outliers for each dimension in the box-and-whisker plot, which are values that lie more than one and a half times the "interquartile range" (the length of the box from either end of the box).

### **Key factors influencing three-dimensional ontogenetic shifts**

Analyses of Similarity (ANOSIM) with R-statistic were conducted to test the significance of factors, including species, subregion, and size class, that might influence ontogenetic shifts in bottom depth, latitude, and longitude. The three factors have well been documented influencing fish distributional responses to temperature, and Li et al. (2019) discovered that temperature responses of assembled groundfish with size structure significantly differed from subregion.



Here we carried out the same procedures to identify the significant factor(s) influencing ontogenetic shifts. Euclidean distance was computed based on the three standardized ontogenetic shifts variables. R-statistics were then computed to compare rank dissimilarities within and between clusters of samples. R-statistics closer to 1 indicate greater dissimilarity between groups and values closer to 0 indicate less dissimilarity (higher similarity) between groups. We conducted 99,999 permutations to generate significance levels in ANOSIM. Significance was set as R-statistic  $> 0.1$  and  $P < 5\%$  (Li et al., 2019). The ANOSIM was completed using PRIMER (Clarke, 1993).

## **Results**

### **Habitat and ontogenetic shifts in depth and temperature**

We found that most species shifted to cooler, deeper bottom habitat with occasional shoaling movements as they grew (Fig. 2, Table S2). Generally, the largest ontogenetic shifts in distribution occurred in the small size classes before reaching their length at 50% maturity (L50, Table 1), and smaller shifts (sometimes even shoaling to shallow water) occurred as fish approached maximum size across all groundfish species and subregions (Fig. 2). L50 of groundfish tended to decrease in more southern regions. Most fish had L50s within the 31-40 cm size class except Pacific cod and sablefish with L50s in the 51-60 cm size class (Table 1). Deep-water species such as Dover sole and sablefish exhibited greater ontogenetic deepening than others. In particular, sablefish ranged over 300 m in depth as it transitioned through different life stages in most subregions. In the WGOA, 31-40 cm sablefish moved 175 m deeper when growing 10-cm larger. Shoaling movements to shallow water occurred in all species from the

second largest size class to the largest at least in one subregion. However, species with a restricted range in shallow-depths such as southern rock sole, exhibited shoaling between the two largest size classes as their largest shift across all life stages. A few species of semi-pelagic fish that are classified as groundfish, such as walleye pollock and Pacific hake, showed different patterns. They demonstrated complex deepening and shoaling movements along the bottom within some subregions.

Deepening in response to size (ontogenetic change) generally increased from the WGOA southward to the west coast of the U.S. Increasing ontogenetic deepening expanded the depth range of arrowtooth flounder from 35 m in WGOA to more than 200 m off the west coast of U.S. Similarly, Petrale sole demonstrated a depth range of less than 14 m in HS and QCS, their northern leading edge, but substantially larger ranges in the southern subregions, e.g., 45 m in WCVI, 54 m in NWUS, 36 m in CWUS, and 108 m in SWUS. Notably, groundfish of the same size category within a species were found in deeper water in more southerly subregions (Fig. 2). As the greatest temperature difference at the same depth between neighboring areas occurred between the NWUS and CWUS, many groundfish exhibited the greatest deepening between these two subregions. For example, in the CWUS, the 31-40 cm Dover sole size class inhabited depths that were 111 m greater than in NWUS, corresponding to a temperature that was about 0.8 °C cooler in CWUS than at their NWUS depth. HS was an exception in the general geographic deepening trend because it is dominated by depths less than 50 m and lacks opportunities for fish to move to deeper water compared to adjacent QCS and EGOA (Li *et al.*, 2019). These subregional differences in species- and size-specific habitat suggested that they are tolerant of depth changes, thus providing a mechanism to compensate partially for warmer subregional environments.

In general, the temperature-depth habitat which many fish occupied was close to the average characteristics of the region, i.e., fish tended to be found along the average temperature-depth profile (Fig. 2). Notable exceptions were the HS (red lines) and QCS (black lines) subregions, where all species exhibited in warmer waters than the mean at that bottom depth. In particular, the habitat temperatures for Pacific cod in HS were even warmer than those in NWUS, its southern leading edge. These probably suggest hot spots of many species in the warmer areas of HS and QCS. Notably, petrale sole occurred in shallower waters with warmer temperature at those bottom depths everywhere except in the warmest subregion SWUS where they occupied significantly deeper waters at the mean temperature. This may indicate their preference in temperature. Additionally, other factors may also influence groundfish movements and distribution. For example, substratum type can outweigh temperature in habitat choice experiments for some flatfish (Morgan, 2000). WGOA was colder than CGOA in waters shallower than 300 m. However, in each of those subregions, two species – arrowtooth flounder and Dover sole – preferred to occupy the same depth range rather than seek depths in the same temperature range, perhaps suggesting control by substratum type.

### **Habitat and ontogenetic shifts in latitude and longitude**

In addition to the vertical dimension, groundfish also demonstrated substantial horizontal ontogenetic shifts in latitude and longitude (Fig. 3 A-I, Table S2). The magnitude of these shifts appeared associated with the ranges of subregions. For example, ontogenetic shifts in latitude and longitude were generally larger in the enormous subregions of GOA than those in relatively small areas in the west coast of Canada; Ontogenetic shifts in latitude were larger than those in

longitude in the narrow shelf of NWUS where there is large range of latitude with small range of longitude.

Due to large variabilities, it is hard to group all of species, size class, and subregion together (Fig. 3 A-I). As fish grew, most of them moved southward in WGOA (Fig. 3 A) while more fish moved northward at some size classes in CGOA (Fig. 3 B) and EGOA (Fig. 3 C). Also due to complex topography, there were large variabilities of horizontal movements across species and size class in Canada west coast (Fig. 3 D-F). However, in the west coast of the U.S., where deep offshore waters are generally in the west, most fish moved westward in ontogenetic deepening except Petrale sole that consistently moved southeastward in SWUS (Fig. 3 G-I), generally opposite to Dover sole and sablefish, which occupied much deeper water than Petrale sole in this area (Fig. 2). Another exception is Pacific cod in NWUS (Fig. 3 G), which exhibited limited western or eastern movements but large movements in latitude.

The ontogenetic shifts occurred simultaneously in depth, latitude, and longitude, and the major dimension(s) may vary from species, size class, and subregion. Some fish demonstrated changes in latitude and longitude associated ontogenetic shifts in depth probably due to the topography when moving along the seafloor; however, some fish exhibited major shifts in horizontal dimensions only with limited changes in depth. For example, like most fish, arrowtooth flounder moved western from shallow inshore waters to deep offshore waters as they grow in the narrow shelf of NWUS (Figs. 3 G, 4). However, when present in the wider and colder WGOA continental shelves, arrowtooth flounder exhibited large horizontal movements in various directions with small changes in depth, indicating that ontogenetic shifts occur primarily via horizontal movements in those two subregions (Fig. 4). Similarly, southern and northern rock sole, species typically confined to a narrow bottom depth range of <13 m across their life in

shallow waters of WGOA and CGOA (e.g., 61-69 m and 56-66 m in the WGOA respectively, Fig. 2), generally moved southward and westward throughout their life cycle. For example, for each size class of southern rock sole, average depth changes were typically only a few meters while the horizontal movement was up to 54 km in the WGOA and CGOA (Fig. 5, Table S3).

### **Extreme standardized ontogenetic shifts**

To compare across species, size class, dimension, and subregions, we standardized ontogenetic shifts in depth, latitude, and longitude and noted that extreme standardized ontogenetic shifts occurred mainly at smaller size classes before reaching their L50 (Tables 1 and 2). The largest extreme in depth occurred to 1-10 cm of Pacific cod in HS (9.9, deepening); the largest extreme in latitude occurred to 31-40 cm of sablefish in the WGOA (-7.1, southern movement); the largest extreme in longitude occurred to 41-50 cm of Pacific ocean perch in the QCS (-3.8, western movement). Eight of ten species demonstrated extreme standardized shifts in some subregions. Deep water species, Dover sole and sablefish, each exhibited large shifts in five subregions. Dover sole had extremes in a wide range of size classes (11-60 cm), smaller or larger than its L50 of 31-40 cm size class, while all sablefish extremes occurred before its L50 of 51-60 cm size class. In particular, 31-40 cm of sablefish in the WGOA was the only one that exhibited extreme shifts in three dimensions simultaneously, migrating from shallow nearshore to settle in deep offshore waters as larger fish (Fig. 1, S1).

Extreme standardized shifts occurred in all subregions except SWUS and WCVI (Table 2). In HS, the shallowest and warmest area among the subregions (*Li et al., 2019*) (Fig. 1), four species, including arrowtooth flounder (11-20 and 61-70 cm), Petrale sole (11-20 cm), Pacific cod (11-20 cm), and sablefish (31-40 cm), exhibited dramatic ontogenetic shifts in depth, latitude,

and/or longitude, respectively. Unlike multi-dimensional shifts in most subregions, extremes occurring in NWUS were mostly in longitude showing western movement to deep offshore waters.

### **Factors influencing three-dimensional ontogenetic shifts**

Based on standardized ontogenetic shifts for the aggregated species of all size classes and subregions, Analyses of Similarity (ANOSIM) results (R-statistic = 0.16, P-value = 0.001%) show that size group, small ( $\leq 30$  cm) vs large ( $>30$  cm), was the significant factor influencing ontogenetic shift patterns in three dimensions. There were exceedingly small global differences (R-statistic  $< 0.05$ ) among all size classes, species, and subregion. ANOSIM was further repeated with different subgroups. A subdivision between  $\leq 30$  and  $>30$  cm generated the largest R-statistic after trying all possible subgroups at 10-cm intervals. This was consistent with the maturity status that all species had L50s larger than 30 cm. Generally, the small size group had dramatically larger ontogenetic shifts in depth than the large size group while both size groups demonstrated small ontogenetic shifts in longitude with minor ontogenetic shifts in latitude (Fig. 6).

## **Discussion**

### **Three-dimensional ontogenetic shifts**

While there is great variability among species in the magnitude of ontogenetic movement across life stages, most species do move to deeper waters as they grow. This is consistent with laboratory studies of Atlantic cod (*Gadus morhua*, Gadidae) that showed their optimal temperature decreased with increasing fish size (Pörtner et al., 2008), suggesting that ontogenetic

deepening matches this life history change. The ontogenetic deepening, also observed in flatfishes in the Gulf of Maine-Georges Bank region, was distinct from seasonal migration (Methratta & Link, 2007). Although seasonal migratory behavior (spawning or feeding) is also an important driver of species' distribution, this study focused on groundfish ontogenetic shifts in spatial distributions during summer seasons only without addressing migratory movements.

Our analyses expand Heincke's law to ontogenetic shifts in three dimensions of depth, latitude, and longitude and reveal comprehensive simultaneous ontogenetic shifts in all dimensions. Some ontogenetic deepening accompanied large shifts in latitude and longitude (e.g., WGOA sablefish in Fig. 1 and Table 2). Similarly, many reef-dwelling fishes use the shallow lagoons as juveniles then move onto deeper reefs as adults (Gratwicke et al., 2006). However, it is also important to note other patterns in the ontogenetic shifts. For example, some species demonstrated key ontogenetic shifts in longitude and/or latitude with limited changes in depth in some subregions (Figs. 5 and 6); some fish also showed shoaling movement at some size classes and subregions (Fig. 2). Our results were consistent with the observation in the eastern Bering Sea (Barbeaux & Hollowed, 2018) that groundfish appeared to optimize their habitat by moving in depth, upward and downward, as well as in latitude and longitude simultaneously.

Environmental characteristics, the local topography, and habitat availability can add substantial complexity to the spatial distribution of the population at different life stages in each subregion.

Our findings of complex ontogenetic shifts suggest ontogenetic shifts as evolutionary or ecological behavioral responses to the environment. The ecological drivers may include feeding habitat (Garrison, 2000; Link et al. 2015), optimization of growth and reproduction (Macpherson & Duarte, 1991; Whitlock et al., 2015), and competition and predator avoidance (Cushing, 1975; Linehan et al., 2001; Pecl et al., 2017) at different life stages. Our results provide insights on the

optimization of growth and reproduction in that smaller fish prior to L50 generally had larger ontogenetic shifts than larger fish. Similarly, Pan et al. (2021) reported based on nine commercially important species in the North Sea that fish larger than L50 tend to distribute less heterogeneously and thus reduce the variability of population distribution. Dover sole was an exception demonstrating large ontogenetic shifts over their lifetime. This finding is consistent with a previous study in central California (Hunter et al., 1990) which showed: Juveniles moved from inshore to deep water on the continental shelf and then continued to move down the slope even after the maturation. Large mature Dover sole occupied a depth range of 640-1006 m with a marked increase in body water content and a consequent decrease in caloric density per gram wet weight, indicating an adaption to the deep oxygen-minimum zone. By contrast, one modeling study of a heavily exploited species Atlantic cod in the eastern Scotian Shelf suggests that ontogenetic deepening was driven by fishing exploitation (Frank et al., 2018). However, analysis of empirical bottom trawl survey data indicated that declining fishing mortality for eight commercial stocks in the NE Atlantic did not result in a rebound of larger fish to shallow water (Baudron et al., 2019).

This study explored movements of groundfish within subregions. An extension of this work could be to examine spatial changes within size classes across regions. However, our study covered species widely distributed over large areas. We split each large survey region into three subregions based on survey characteristics and geographic and oceanographic conditions in addition to management areas (Li et al., 2019). The surveys catch fish in each subregion in the same time periods including the fish moving from adjacent subregions and excluding fish migrating out of the current subregion, if cross-subregional movements occurred. Therefore, the ontogenetic shifts in each subregion tended to cover all the fish in each subregion in summer.



Semi-pelagic species – walleye pollock and Pacific hake – may have larger uncertainty in their ontogenetic shifts due to their variable bottom-trawl catchability. Bottom trawls miss the fish above the effective fishing height. As the vertical distribution changes (e.g., caused by dynamic environmental conditions), the proportion of fish available to bottom trawls will also vary in space and time (Monnahan et al., 2021; Kotwicki et al., 2015), introducing variability in ontogenetic shifts. However, there are no such concerns for other groundfish in this study.

### **Implications of this study**

As the first large-scale study on ontogenetic shifts, our findings strongly recommend considering the spatial scale and ontogenetic shifts for future distribution studies and fisheries management. Management units and study areas are usually defined as administrative or political boundaries rather than biological processes (Cardrin 2020; Radon et al., 2018). However, our analyses show that in southern waters, groundfish tended to occupy deeper habitat and have greater ranges in depth across life stages, compensating for the warmer environment. A similar strategy of deepening southward across subregions was previously observed for Atlantic wolffish (*Anarhichas lupus*, Anarhichadidae) that have a maximum depth of 126 m in their northern habitat on the Scotian Shelf (Scott & Scott, 1988) but 240 m in their southern habitat in the Gulf of Maine (Rountree, 2002). Additionally, some fish such as arrowtooth flounder demonstrated substantial differences in ontogenetic shifts across subregions (Fig. 4), further indicating the importance of considering the appropriate spatial scale particularly for a species with a wide range of distribution. However, our analyses are not able to show if they are distinct populations with independent dynamics in each subregion or are the same populations adapted to the local environment. In addition to molecular techniques for genetic differentiation in population

isolation, a recent study by Lindegren et al. (2022) provided an alternative by developing a spatial statistical approach for identifying population structuring. These approaches, together with biological studies such as this one, can help choose the appropriate spatial scales for the management units and study areas. With spatial patterns increasingly recognized as an important factor in understanding the stock population dynamics (Pan et al., 2021; Berger et al., 2017), our study further highlights the importance of considering distributional differences among size classes for the appropriately defined management units and study areas.

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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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Table 1. Length at 50% maturity (L50) for each species and region. Species excluded from a region are denoted by "-". "NA" denotes L50 values that are not assessed or not available in the literature.

Fish species	Region	L50 (cm)	References
Arrowtooth flounder	GOA	46.4	Stark 2008
	West Coast of Canada	38.5	Anderson et al., 2019
	West Coast of U.S.	36.8	Min et al., 2022
Dover sole	GOA	43.9	Abookire & Macewicz 2003
	West Coast of Canada	33.9	Anderson et al., 2019
	West Coast of U.S.	31.1	Hunter et al., 1990
Northern rock sole	GOA	32.8	Stark & Somerton, 2002
	West Coast of Canada	-	
	West Coast of U.S.	-	
Pacific cod	GOA	50.3	Stark 2007
	West Coast of Canada	52.8	Anderson et al., 2019
	West Coast of U.S.	NA	
Pacific hake	GOA	-	
	West Coast of Canada	-	
	West Coast of U.S.	33.4	Melissa Head. NOAA. Personal comm
Pacific ocean perch	GOA	33.4	Conrath & Knoth, 2013
	West Coast of Canada	33.5	Anderson et al., 2019
	West Coast of U.S.	32.1	Wetzel et al., 2017
Petrale sole	GOA	NA	
	West Coast of Canada	37.1	Anderson et al., 2019
	West Coast of U.S.	33	Hannah et al., 2002
Sablefish	GOA	68.9	Howard 2022
	West Coast of Canada	57.9	Anderson et al., 2019
	West Coast of U.S.	54.6	Head et al., 2014
Southern rock sole	GOA	34.7	Stark & Somerton, 2002
	West Coast of Canada	-	
	West Coast of U.S.	-	
Walleye pollock	GOA	42.5	Williams et al., 2016
	West Coast of Canada	37.2	Anderson et al., 2019
	West Coast of U.S.	-	

Table 2. Extremes of standardized ontogenetic shifts (OS). List of critical stages of groundfish that demonstrated extremes of standardized OS (*italicized* and **bold**) from the current size class to the next sequential size class in deepening, northern, and eastern movements. See more details for the top extreme in all three directions, 31-40 cm of WGOA sablefish (**bold**) in Fig. 1 and S1. See Table S2 for the original values of ontogenetic shifts.

Species	Subregion	Size	Standardized OS		
			Deepening	Northern	Eastern
Arrowtooth flounder	CGOA	31-40	0.0	<b><i>1.9</i></b>	<b><i>1.6</i></b>
	HS	11-20	1.1	<b><i>2.6</i></b>	-0.6
	HS	61-70	1.7	-1.6	<b><i>2.4</i></b>
Dover sole	WGOA	21-30	<b><i>5.2</i></b>	-0.2	0.3
	WGOA	41-50	-0.3	<b><i>-1.9</i></b>	<b><i>-2.2</i></b>
	CGOA	21-30	<b><i>4.4</i></b>	-1.1	-0.3
	CGOA	41-50	<b><i>-3.5</i></b>	-0.1	-0.5
	CGOA	51-60	-1.2	<b><i>-2.0</i></b>	<b><i>-1.7</i></b>
	EGOA	11-20	3.1	<b><i>-1.8</i></b>	0.7
	EGOA	31-40	0.4	<b><i>2.8</i></b>	<b><i>-2.3</i></b>
	NWUS	11-20	<b><i>7.9</i></b>	0.3	<b><i>-3.1</i></b>
	NWUS	21-30	2.8	0.0	<b><i>-2.6</i></b>
	CWUS	11-20	<b><i>9.8</i></b>	-0.1	-0.5
Pacific cod	HS	1-10	<b><i>9.9</i></b>	0.1	0.8
	NWUS	21-30	1.0	<b><i>-1.8</i></b>	0.0
Pacific hake	CWUS	21-30	<b><i>6.5</i></b>	0.2	-0.7
Pacific ocean perch	WGOA	21-30	<b><i>7.0</i></b>	-0.2	0.1
	EGOA	31-40	-0.1	<b><i>-1.9</i></b>	<b><i>1.9</i></b>
	QCS	21-30	<b><i>3.7</i></b>	<b><i>-1.8</i></b>	-0.2
	QCS	41-50	-0.7	<b><i>4.8</i></b>	<b><i>-3.8</i></b>
Petrale sole	HS	11-20	-0.2	<b><i>5.4</i></b>	-1.1
	QCS	21-30	<b><i>4.5</i></b>	0.1	0.2

	NWUS	11-20	3.2	0.6	<i>-2.2</i>
	NWUS	41-50	0.6	1.0	<i>-2.9</i>
<b>Sable fish</b>	<b>WGOA</b>	<b>31-40</b>	<b>6.6</b>	<b>-7.1</b>	<b>-2.8</b>
	CGOA	21-30	2.4	<i>1.9</i>	<i>1.5</i>
	HS	31-40	<i>9.4</i>	0.9	<i>-2.0</i>
	NWUS	31-40	2.1	-0.4	<i>-2.3</i>
	CWUS	21-30	<i>4.4</i>	-0.2	0.0
	CWUS	31-40	2.1	<i>2.0</i>	<i>-2.0</i>
Southern rock sole	WGOA	31-40	0.7	<i>-2.0</i>	-1.0
	WGOA	41-50	-2.3	<i>-1.8</i>	<i>-2.8</i>

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Figure 1. Mean bottom temperature map and WGOA sablefish distribution. (A) Bottom temperature was averaged 1996-2015 and interpolated to a 0.1104 X 0.0833 degree longitude-latitude grid (5 x 5 nmi at 41°N, Mercator projection) across the nine subregions in this study: western (WGOA), central (CGOA) and eastern (EGOA) Gulf of Alaska, Hecate Strait (HS), Queen Charlotte Sound (QCS), west coast Vancouver Island (WCVI), and northern (NWUS), central (CWUS) and southern (SWUS) west coast of U.S. (B) catch per unit effort (CPUE; number per km<sup>2</sup>) of sablefish by size class (color bar on the right) in individual non-zero catch hauls during the bottom trawl survey over the WGOA in 2015 (see other years in Fig. S1). Bathymetric contours are at 50, 100, 200, 500, and 1,000 m depth.

Figure 2. Temperature-depth profiles (dashed lines) of bottom-temperature averaged across all survey years vs bottom-depth for groundfish habitat in the NE Pacific in the color-coded subregions of western (WGOA), central (CGOA), and eastern (EGOA) Gulf of Alaska, Hecate Strait (HS), Queen Charlotte Sound (QCS), west coast of Vancouver Island (WCVI), and northern (NWUS), central (CWUS), and southern (SWUS) west coast of U.S. Separate panels represent different groundfish species. The same subregional temperature profiles are plotted for each groundfish species, but with depth and temperature scales appropriate for the species under study. Numbers connected by solid lines represent the sizes of fish actually caught in 10-cm increments, e.g., 1 represents 11-20 cm, etc. In general, fish of a given species are found deeper in more southern subregions. Fish catches displaced from the average temperature profile represent species whose preferred habitat is warmer or colder than the subregional average temperature.

Figure 3 A. Ontogenetic shifts of groundfish from the current size class to the next sequential one in latitude (top) and longitude (bottom) in the western Gulf of Alaska (WGOA).

Figure 3 B. Ontogenetic shifts of groundfish from the current size class to the next sequential one in latitude (top) and longitude (bottom) in the central Gulf of Alaska (CGOA).

Figure 3 C. Ontogenetic shifts of groundfish from the current size class to the next sequential one in latitude (top) and longitude (bottom) in the eastern Gulf of Alaska (EGOA).

Figure 3 D. Ontogenetic shifts of groundfish from the current size class to the next sequential one in latitude (top) and longitude (bottom) in the Hecate Strait (HS).

Figure 3 E. Ontogenetic shifts of groundfish from the current size class to the next sequential one in latitude (top) and longitude (bottom) in the Queen Charlotte Sound (QCS).

Figure 3 F. Ontogenetic shifts of groundfish from the current size class to the next sequential one in latitude (top) and longitude (bottom) in the west coast of Vancouver Island (WCVI).

Figure 3 G. Ontogenetic shifts of groundfish from the current size class to the next sequential one in latitude (top) and longitude (bottom) in the northwest coast of USA (NWUS).

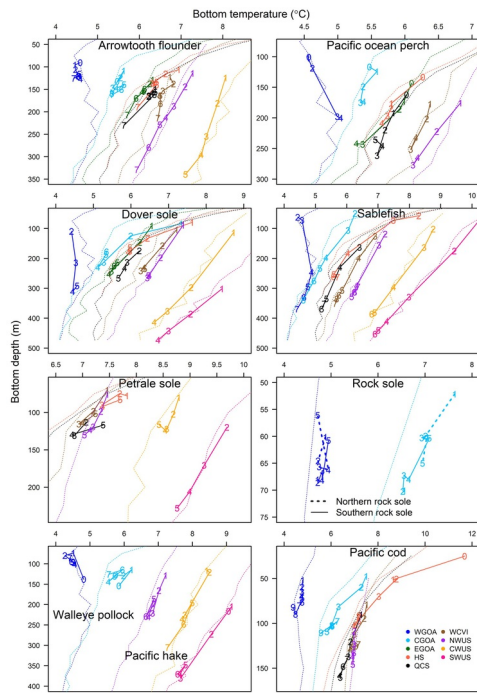
Figure 3 H. Ontogenetic shifts of groundfish from the current size class to the next sequential one in latitude (top) and longitude (bottom) in the central west coast of USA (CWUS).

Figure 3 I. Ontogenetic shifts of groundfish from the current size class to the next sequential one in latitude (top) and longitude (bottom) in the southern west coast of USA (SWUS).

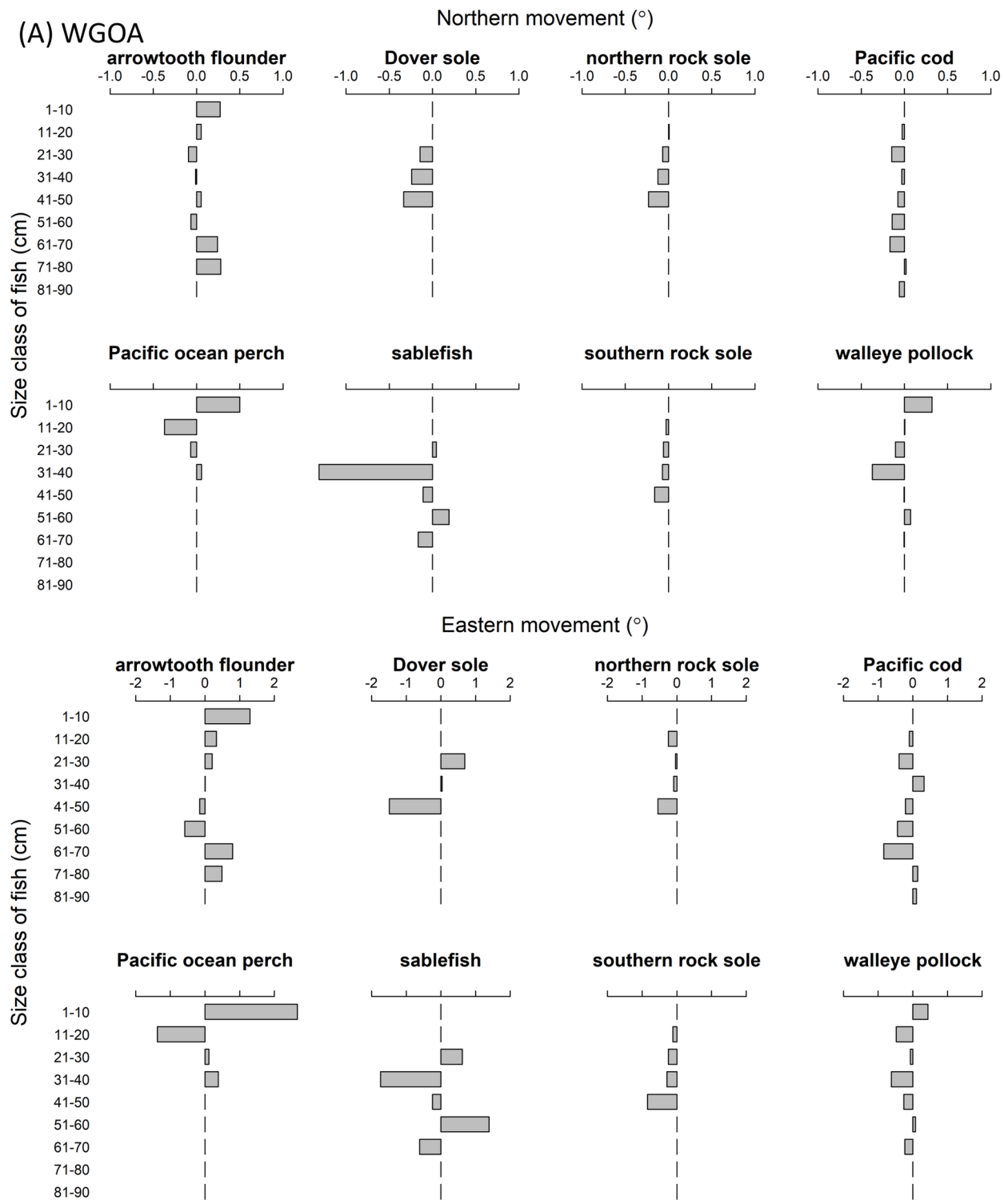
Figure 4. Ontogenetic shifts of arrowtooth flounder from the current size class to the next sequential size class along three dimensions in the WGOA and NWUS.

Figure 5. Ontogenetic shifts of southern rock sole from the current size class to the next sequential size class along three dimensions in the WGOA and CGOA.

Figure 6. Average standardized ontogenetic shifts in depth, latitude, and longitude of all species and subregion by fish size group, small ( $\leq 30$  cm) vs large ( $>30$  cm).

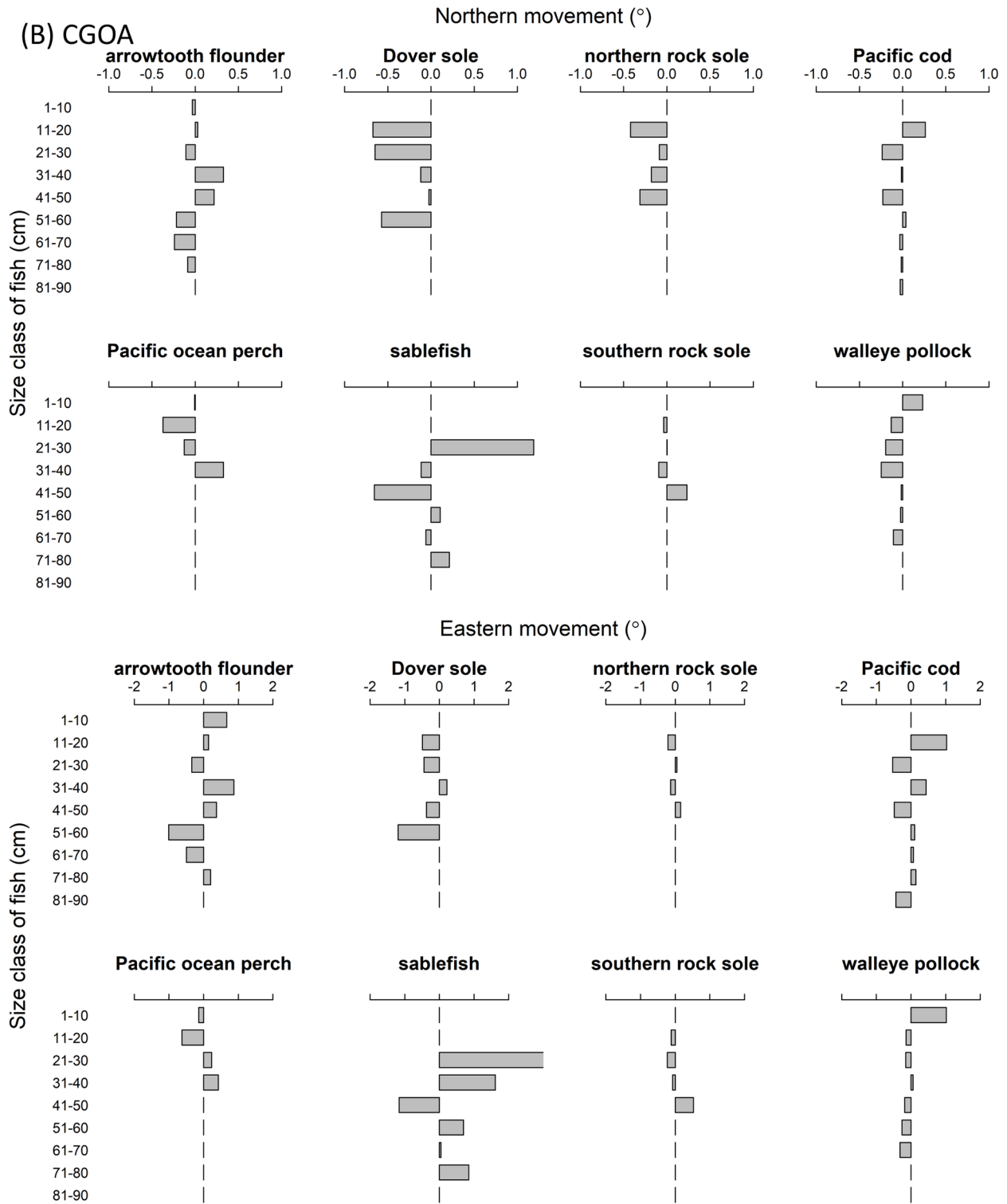


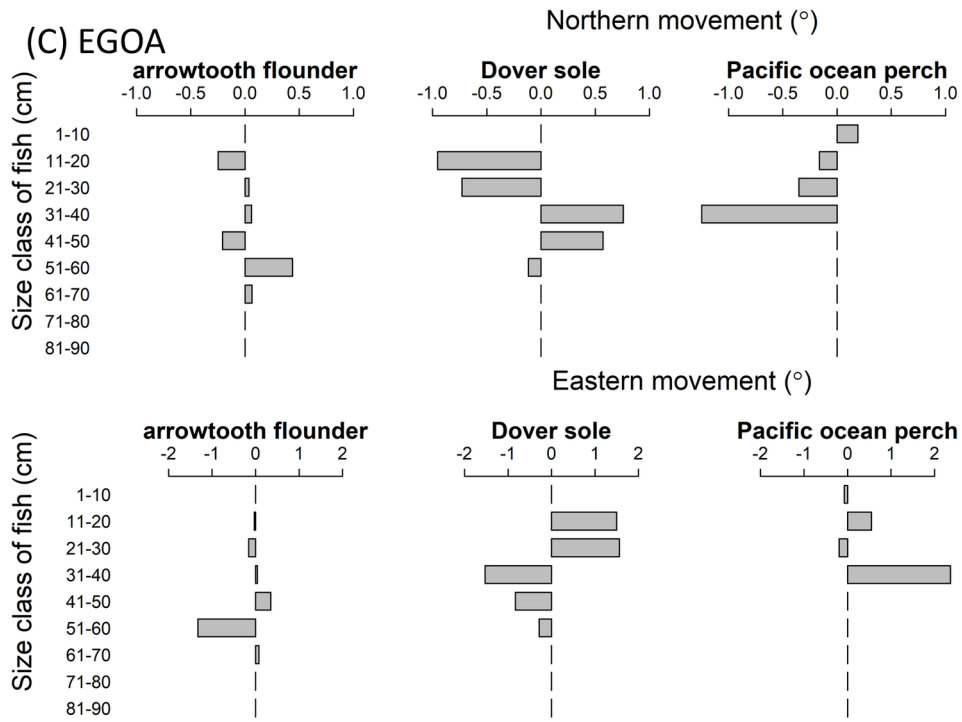
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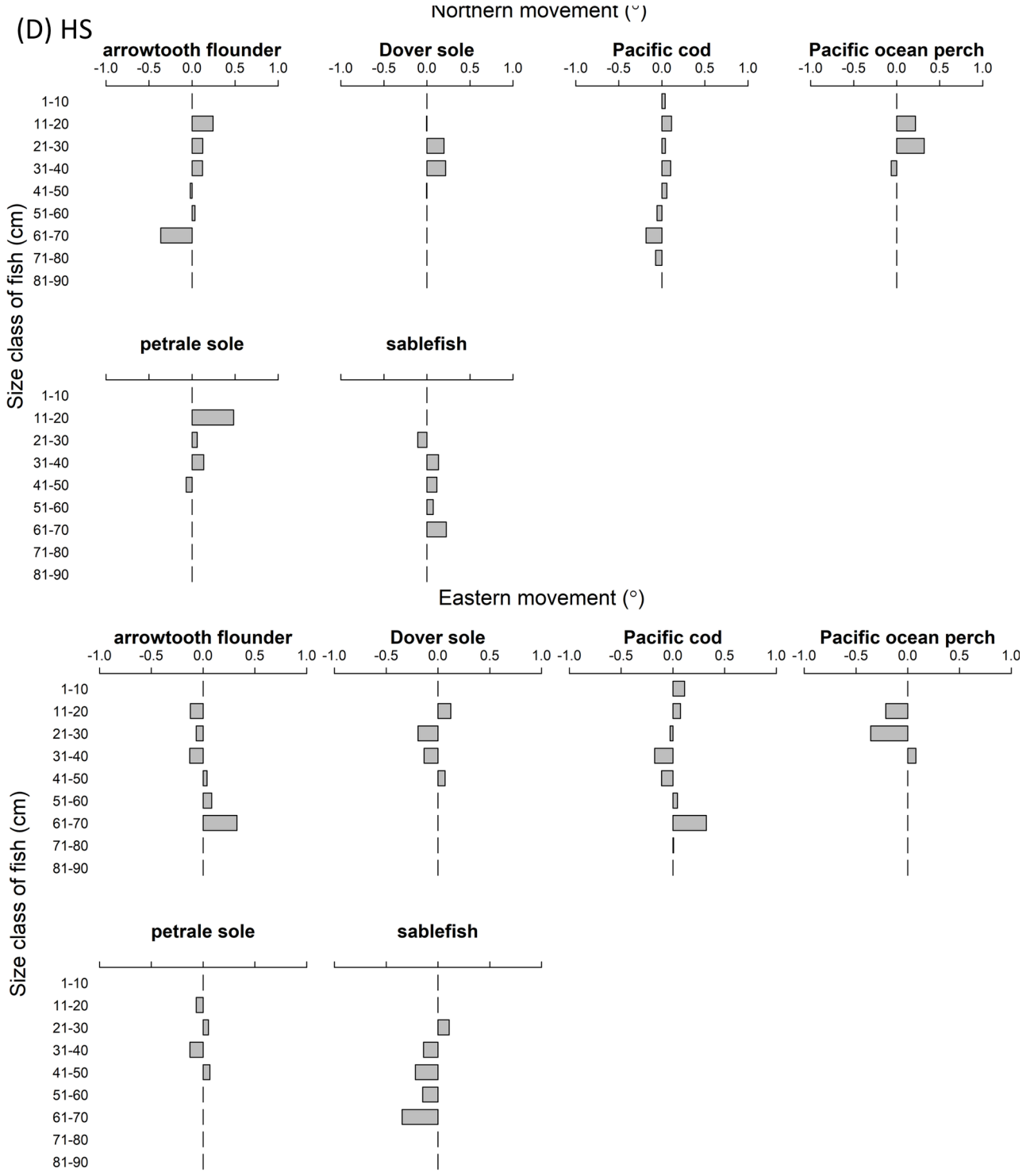


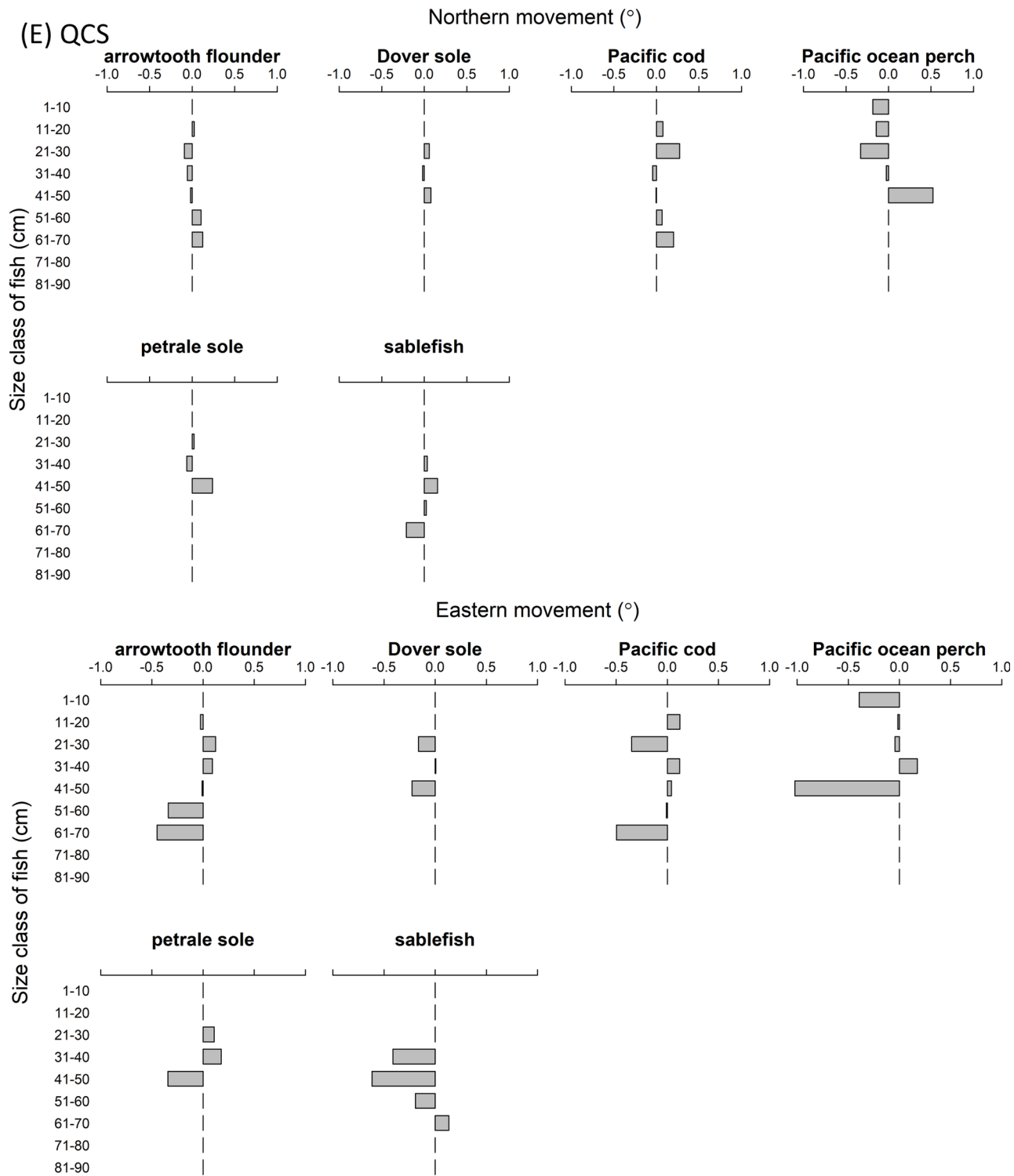
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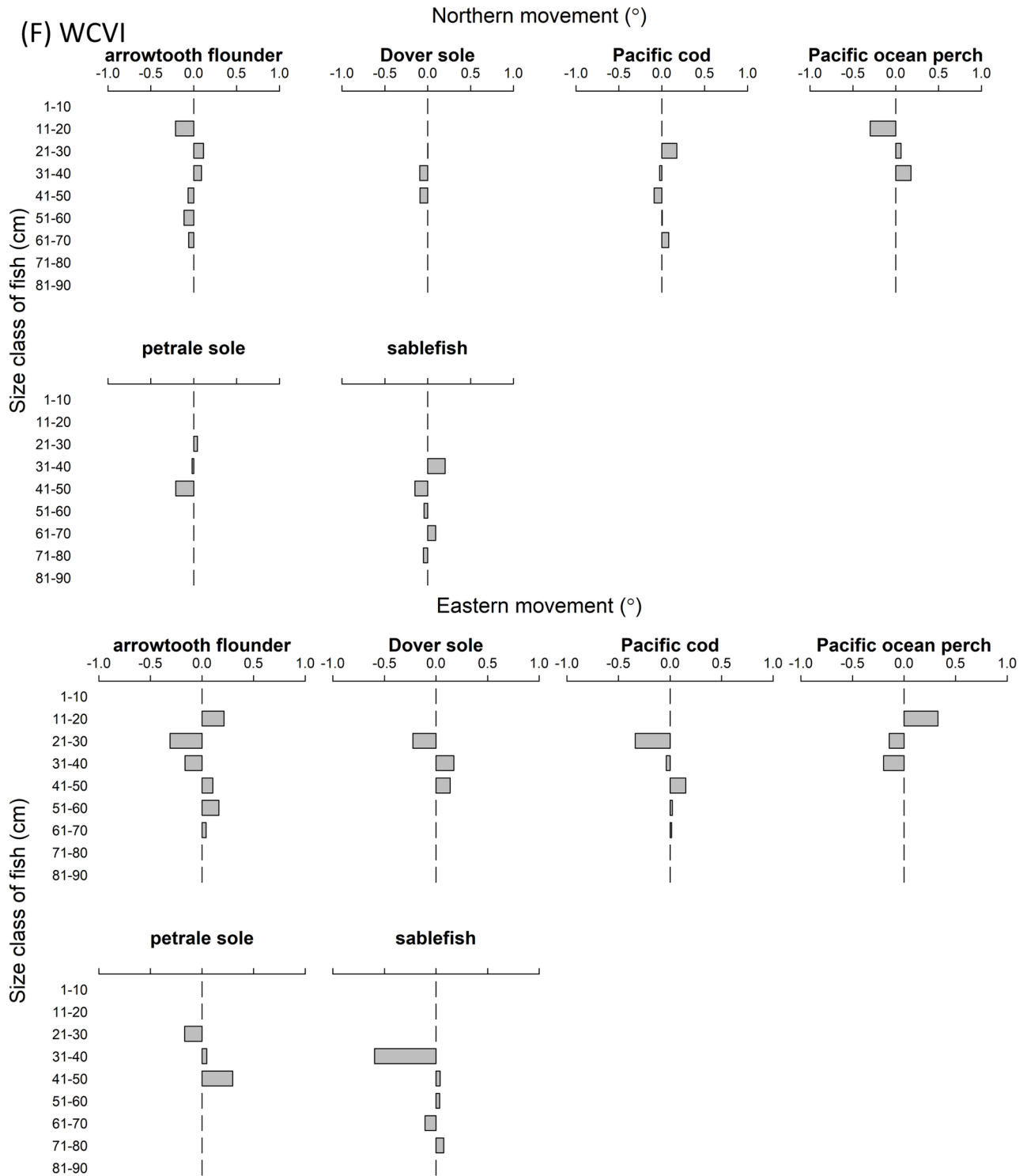


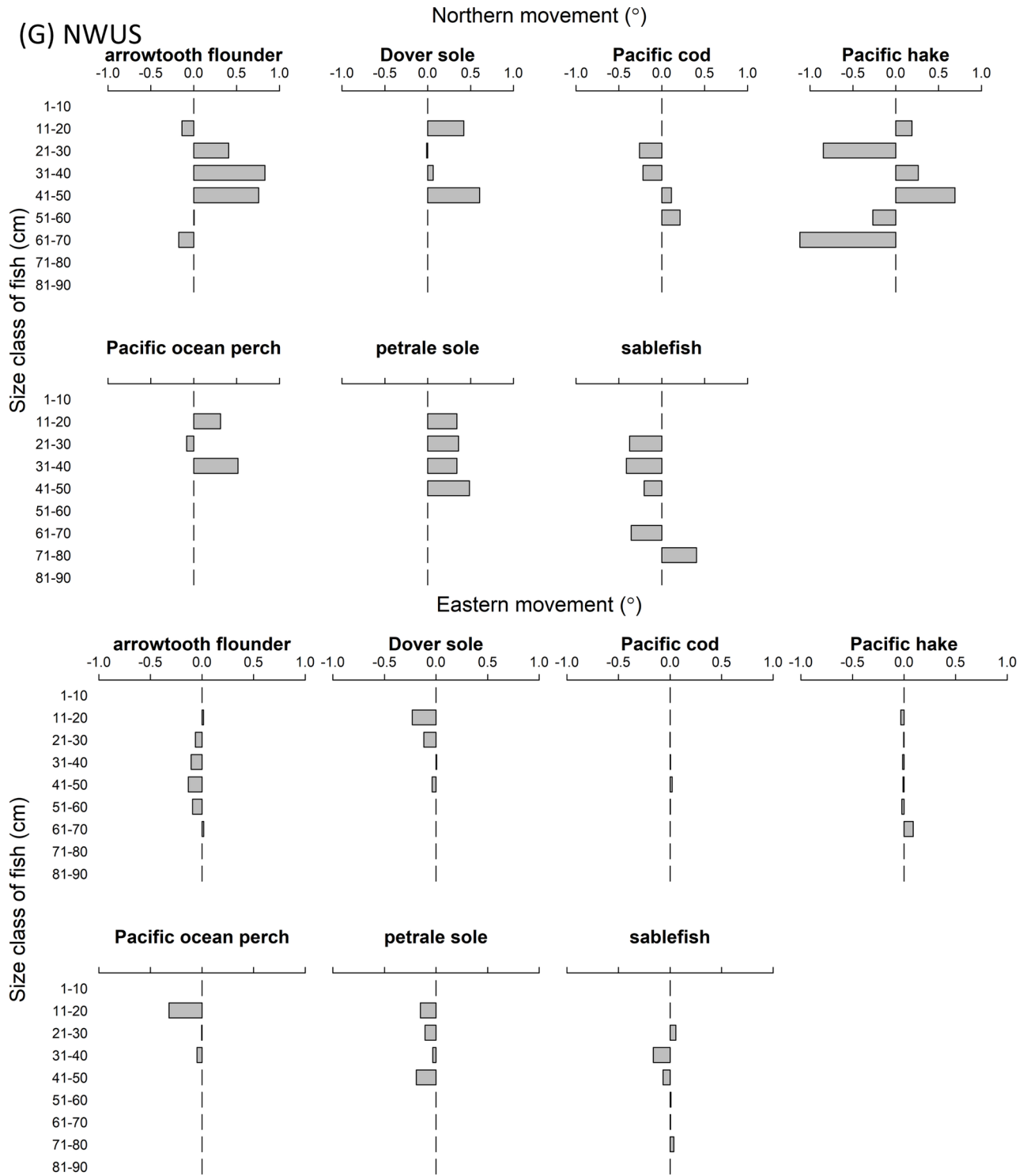


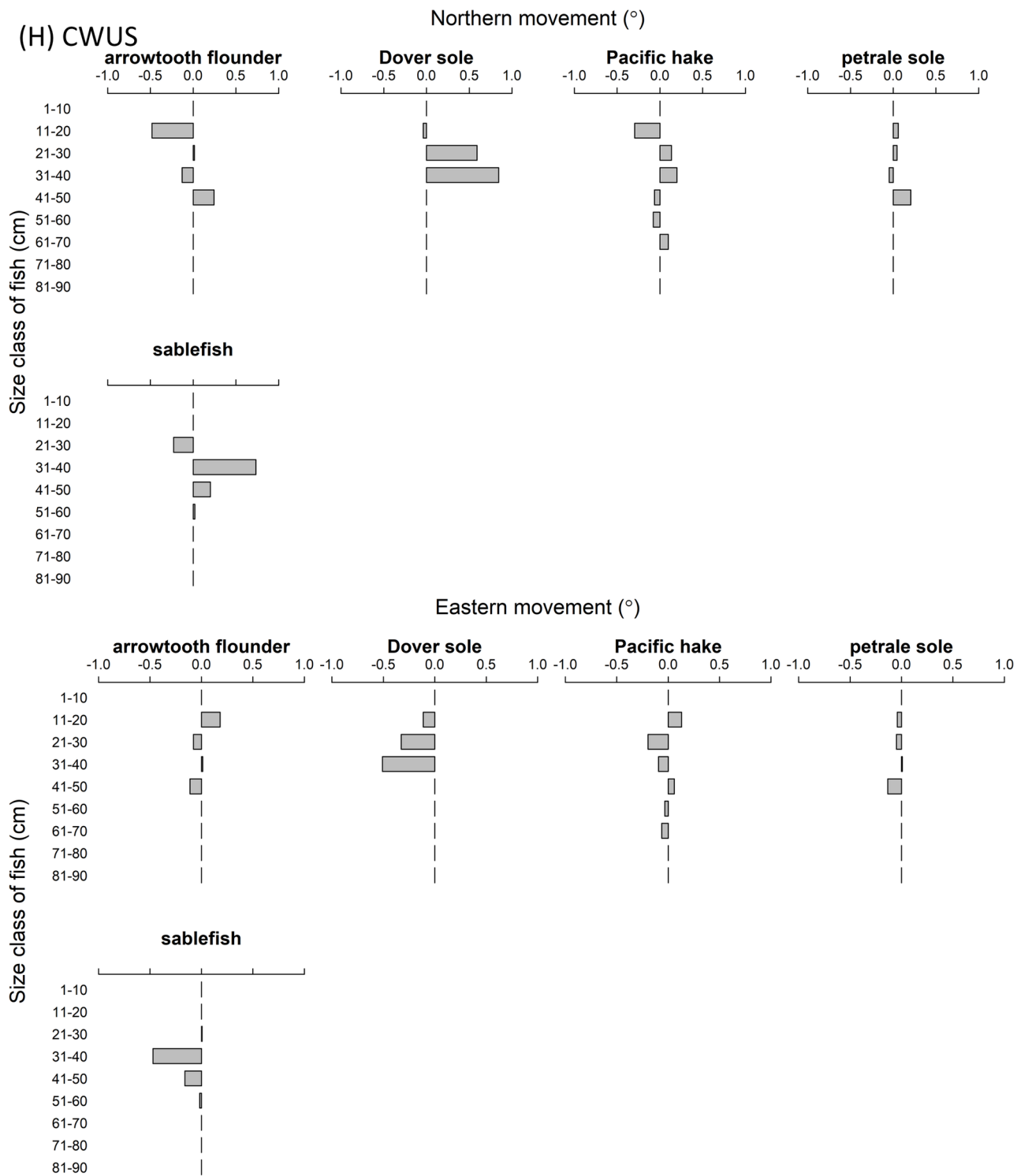


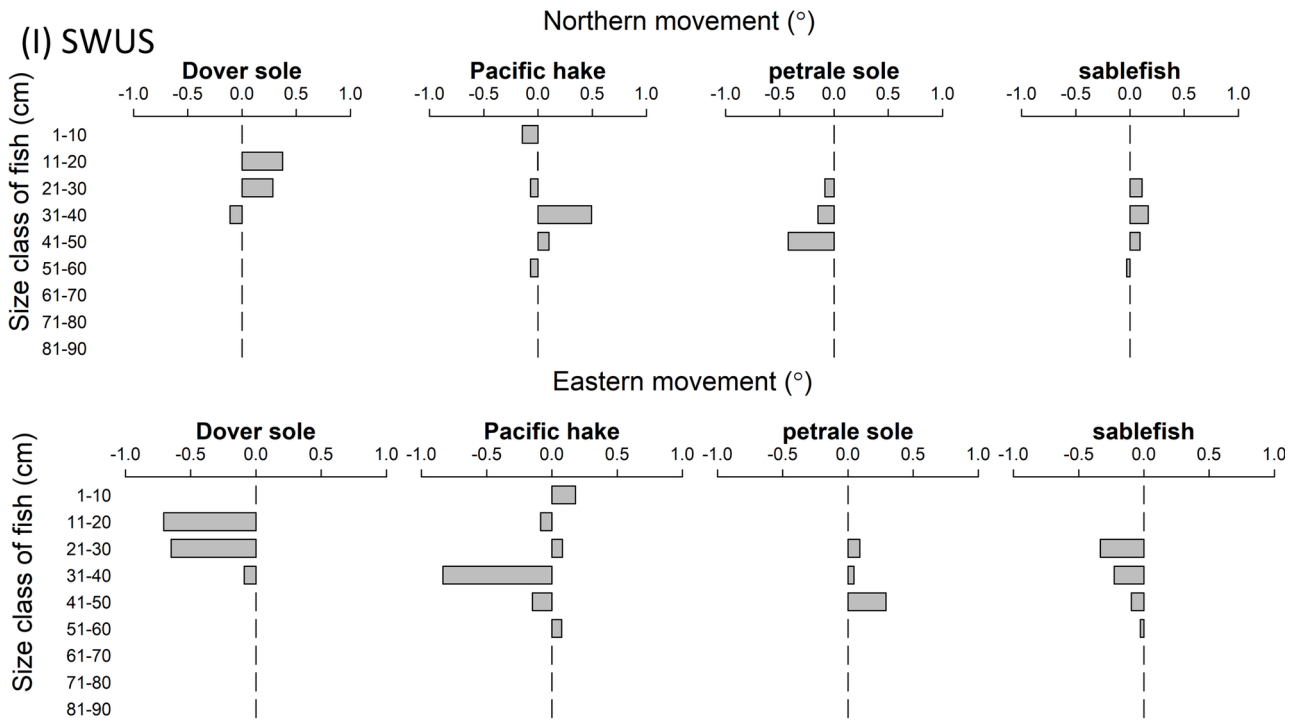




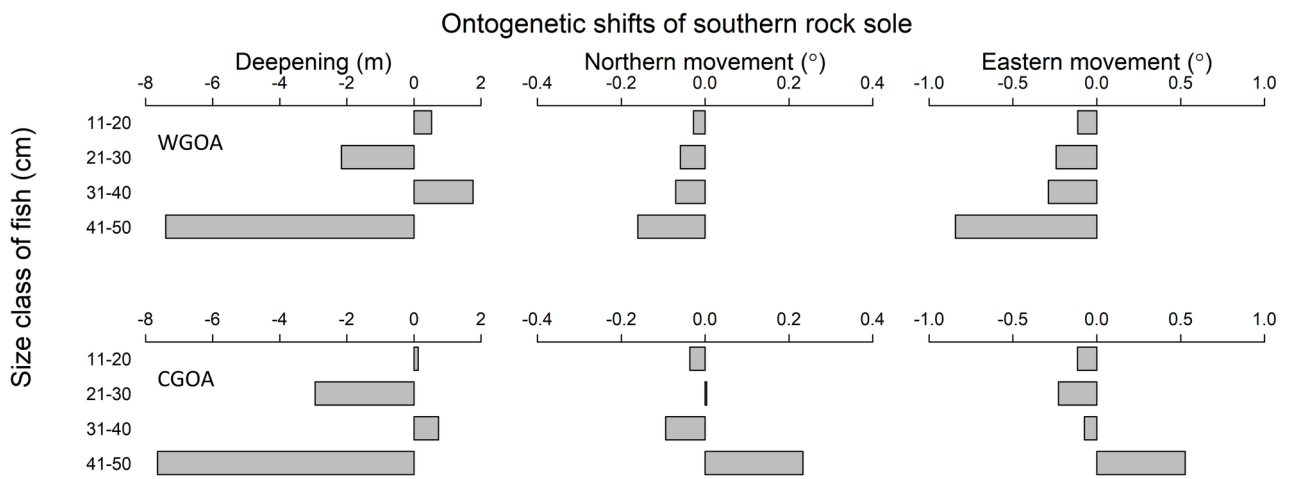




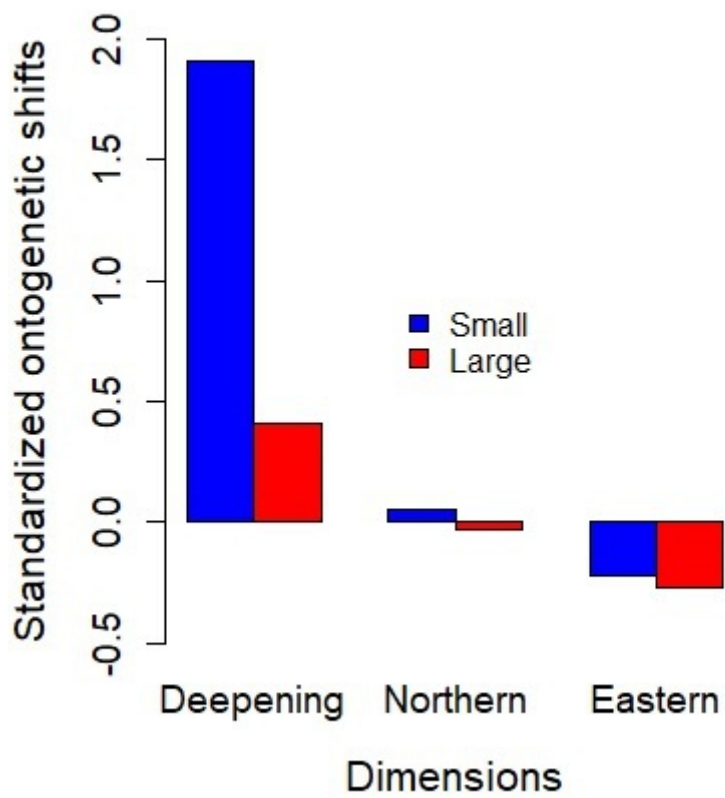








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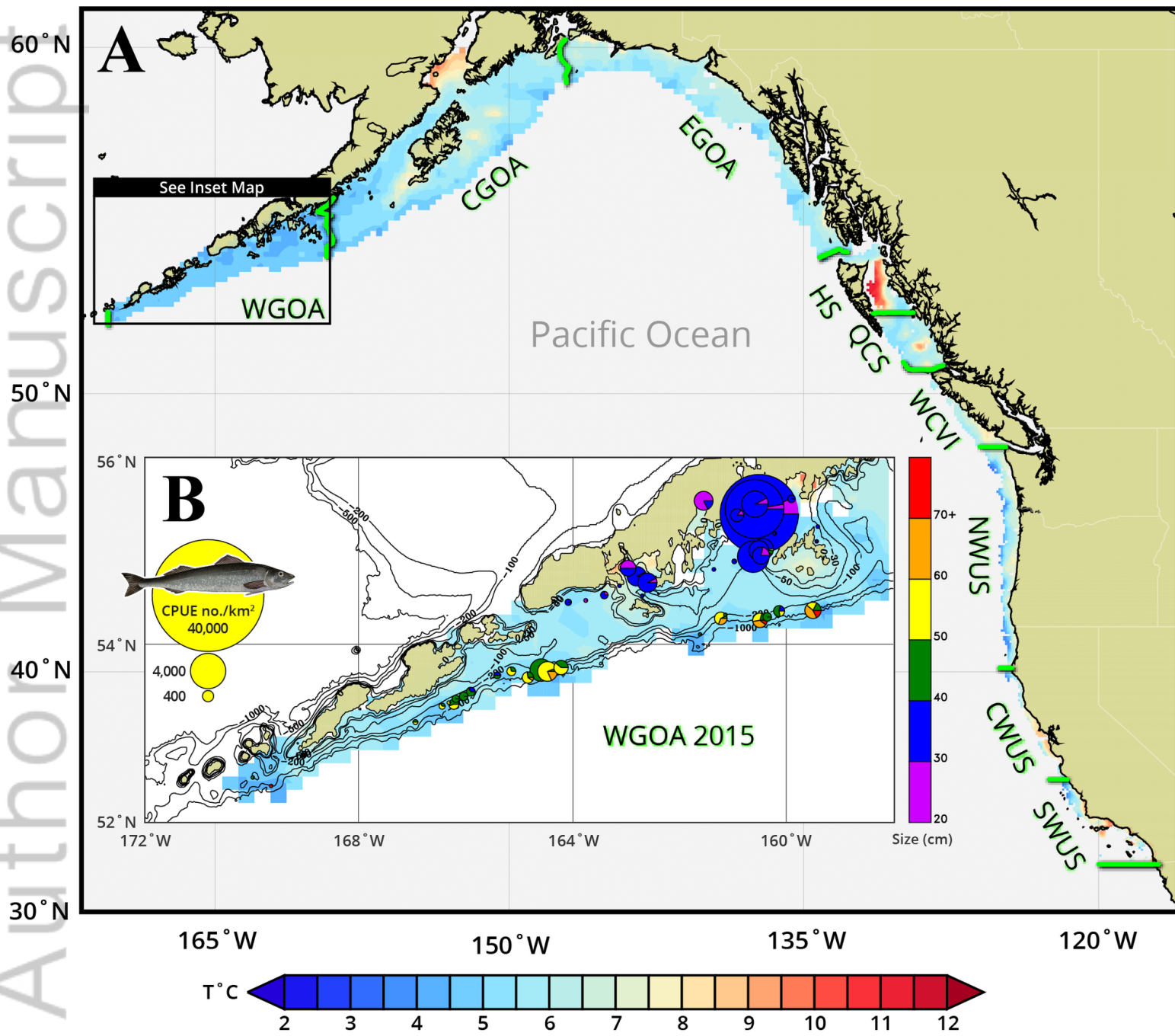


FAF\_12679\_Fig6 OS group.jpg



FAF\_12679\_Fig 4\_OS\_arrow.tif

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