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Distribution of early life Pacific halibut and comparison with Greenland halibut in the eastern Bering Sea

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ABSTRACT

Information about spatial distribution patterns during early life stages of fish is key to understanding dispersal trajectories and connectivity from spawning to nursery areas, as well as adult population dynamics. More than 30 years of historical field data were analyzed in order to describe the horizontal and vertical distributions of Pacific halibut early life stages (larvae to juveniles) in the eastern Bering Sea and to compare the distributions between Pacific halibut and Greenland halibut. Our results indicate that spawning for both species likely occurred in Bering and Pribilof canyons, along the slope between the two canyons, and on the eastern side of the Aleutian Islands during winter, but Pacific halibut spawning was protracted until early spring. Larvae of both species rose to shallower depths in the water column as they developed, but Pacific halibut larvae had an abrupt movement toward shallower depths. Geographically, larvae for both species either advected northwestward along the Bering Sea Slope or crossed onto the shelves from the slope regions, but the timing in Pacific halibut larval progression onto the shelf and along the slope was earlier than for Greenland halibut larvae. Pacific halibut juveniles (≤90 mm total length (TL)) were mostly found in the inner shelf between Bristol Bay and Nunivak Island, along the Alaskan Peninsula, and in the vicinity of the Pribilof Islands. The range of Greenland halibut juvenile (≤90 mm TL) distribution was expanded to south of the Pribilof Islands in the middle shelf and to the inner shelf. Although the two species share some attributes (i.e., spawning location) during early life stages, there were species-specific differences associated with spatial distribution (vertically and horizontally), timing differences in larval progression onto the shelves, pelagic larval duration, and juvenile nursery areas.

1. Introduction

Knowledge of the distribution and dispersal trajectories of marine fish during early life is critical for understanding recruitment and adult population dynamics. The early life stages of marine fishes are influenced by interactions between abiotic (i.e., currents, geographical feature, temperature, and dissolved oxygen) and biotic (i.e., food availability, predation, growth, body-length, and behaviors) factors. Changes in prevailing currents induced by variable atmospheric forcing play an important role in variations of dispersal trajectories and recruitment of marine fish (Van der Veer et al., 1998; Wilderbuer et al., 2002; Bailey et al., 2005; Cowen and Sponaugle, 2009). Currents may transport fish larvae to unsuitable areas resulting in high mortality rates and low recruitment (Houde, 2008). Flatfish may be particularly vulnerable to advective loss due to their long pelagic phases as larvae (Bailey et al., 2005) and their strict benthic habitat requirements as juveniles (Petitgas et al., 2013). It has been shown in several studies that slope-spawning flatfish may be vulnerable to changes in currents during their dispersal phases, when they rely on extensive drift to connect from spawning to settlement areas (Wilderbuer et al., 2002; Bailey et al., 2008; Duffy-Anderson et al., 2013; Vestfals et al., 2014; Duffy-Anderson et al., in press). Further, variations in connectivity between spawning and nursery habitats influence recruitment in flatfish populations (Hufnagl et al., 2013; Petitgas et al., 2013).

Pacific halibut (*Hippoglossus stenolepis*) and Greenland halibut (*Reinhardtius hippoglossoides*) are two ecologically and commercially important slope-spawning flatfish in the eastern Bering Sea (EBS). Both species are piscivorous and substantial predators — adults feed on abundant juvenile gadid species (e.g., walleye pollock (*Gadus chalcogrammus*), cod (*Gadus macrocephalus*)) and other flatfish species in the EBS (Aydin and Mueter, 2007). The abundances of Pacific halibut and Greenland halibut in the EBS have differentially fluctuated during the last three decades although they share many life history attributes. Pacific halibut had been stable prior to 2000, but over the last decade, biomass has continuously decreased because of poor recruitment and decreasing adult body-size at age (Stewart et al., 2013). Greenland halibut has decreased since late 1970s due to low recruitment and spawning biomass, however, there are signs of improved recruitment after 2006 (Barbeaux et al., 2013).

Distribution, dispersal trajectory, and population dynamics of Greenland halibut and Pacific halibut may be affected differently by

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changes in environmental conditions (e.g., changes in water temperature and currents) due to species-specific differences (i.e., vertical distribution, pelagic duration, and settlement location) during the early life stages. Greenland halibut is a circumpolar species while Pacific halibut is a subarctic species and comparing the two species may provide insight on how environmental variability affects the two species with contrasting ecological niches. The EBS has exhibited a prolonged cold period (2007–2012) after a prolonged warm period (2001–2005) with respect to variations in the timing of sea ice retreat and water temperature (Stabeno et al., 2012). The habitat occupied by Greenland halibut juveniles and adults has expanded to the south in the middle shelf with a series of cold periods in the EBS (Ianelli et al., 2011). Previous studies showed that differences in advective connectivity in flatfish are influenced by depth-discrete currents (Lanksbury et al., 2007; Duffy-Anderson et al., 2013). Therefore, it is important to understand the spatial distribution (vertically and horizontally), dispersal trajectories, and connectivity between spawning and nursery areas for the two species of halibut in order to understand their diverging population dynamics.

Little is known about Pacific halibut early life history in the EBS. From studies in the Gulf of Alaska (GOA) it is known that Pacific halibut spawn in relatively deep water (>400 m) along the continental slope during the winter, from December to March. Pacific halibut eggs have been found at depths between 100 and 400 m water, and newly hatched larvae below 425 m, along the continental slope (Thompson and Van Cleve, 1936; Skud, 1977). Pacific halibut hatching time was 20 days at 5 °C (Forrester and Alderdice, 1973). Larvae were reported to move to shallower depths as they developed, and 3 to 5 months after hatching were found at 100 m or shallower. The larvae are advected by currents from offshore to inshore and settle in shallow nursery habitat in May and June, 6 to 7 months after spawning (Skud, 1977; Norcross et al., 1997). In the EBS, Best (1981) mentioned that Pacific halibut spawn at depths between 250 and 550 m along the continental edge from Unimak Island and the Pribilof Islands and along the Aleutian Islands between December and January based on an International Pacific Halibut Commission (IPHC) cruise data. St-Pierre (1989), using 1985 and 1986 field survey data, reported that Pacific halibut postflexion larvae (16–25 mm) were found in Unimak Pass, along the eastern side of the Aleutian Islands, and along Unimak Island. Best (1974, 1977) and Best and Hardman (1982) showed that settled juveniles (<100 mm) and larger individuals were found in shallower water along the Alaskan Peninsula and in the inner shelf (<50 m isobaths) near Bristol Bay. Recently, Seitz et al. (2011) based on tagging data, found that localized spawning population may exist in the EBS. However, the horizontal and vertical distributions and dispersal trajectories of Pacific halibut larvae in the EBS are yet unknown. These knowledge gaps impede an understanding of whether and how dispersal and circulation differently affect Pacific halibut and Greenland halibut recruitment variability.

In contrast to Pacific halibut, there have been more studies about Greenland halibut ecology and biology during early life stages in the EBS, particularly in recent years. Alton et al. (1988) reported on the history of harvest and management for Greenland halibut and distribution of adult stages. Swartzman et al. (1992) showed that Greenland halibut adults moved to deeper water as they grew. McConnaughey and Smith (2000) found that the spatial distribution of Greenland halibut (>141 mm fork length (FL)) was related to sediment characteristics – a mixture of mud and fine sand. Distribution and dispersal trajectories of Greenland halibut during the early life stages have been studied based on observational data or/and passive modeling approaches (Sohn et al., 2010; Duffy-Anderson et al., 2013). Greenland halibut spawn along the slope near Bering Canyon and along the eastern Aleutian Islands during winter. Eggs have been found at depths between 200 and 600 m and larvae have been found between surface and 600 m (Sohn, 2009; Duffy-Anderson et al., 2013). After hatching, Greenland halibut larvae slowly move upward in the water column as they develop. Settlement areas are located over the middle shelf in the vicinity of St. Matthew Island (Sohn et al., 2010). Greenland halibut have a long pelagic larval duration of over six months from spawning to settling areas (Sohn et al., 2010).

The goals of this study are to (1) characterize the distribution and dispersal trajectories for Pacific halibut larvae by ontogenetic stage, (2) describe age-0 nursery habitats for Pacific halibut, and (3) compare the larval progression (horizontally and vertically) of Pacific halibut larvae to that of Greenland halibut. Using more than 30 years of historical data (1979 to 2012), we examined the spatial (horizontal and vertical) distributions of larval Pacific halibut (preflexion, flexion, and postflexion) abundance and body length, and then compared these results to a similar set of results for Greenland halibut. We also examined Pacific halibut age-0 distribution using historical field survey data. This study provides important fundamental early life history information about the ecology and biology of two commercial flatfish species in the EBS, especially for Pacific halibut. The comparison between the two species will be useful for studying habitat usages and predator–prey interactions, as well as conducting biophysical modeling, and climate impact projects for the two species and also other flatfish in the EBS.

2. Materials and methods

2.1. Study area

The EBS includes both the basin and the continental shelf that support one of the highly productive marine ecosystems from phytoplankton to mammals (Fig. 1). The shelf can be divided into three domains based on bathymetry: the inner shelf (<50 m isobaths), the middle shelf (50 m–100 m isobaths), and the outer shelf (100 m–200 m isobaths) (Fig. 1; Coachman, 1986). There are two dominant currents; the Aleutian North Slope Current (ANSC), flowing eastward along the Aleutian Islands, and the Bering Slope Current (BSC), flowing northwestward along the Bering Slope of the EBS (Fig. 1; Stabeno et al., 1999). In addition, part of the Alaska Coastal Current (ACC) flows from the GOA into the EBS through Unimak Pass and flows eastward parallel to the 50 m isobath along the Alaska Peninsula (Fig. 1; Stabeno et al., 2002). A portion of the ACC continues westward and enters into the Bering Sea through other passes including Samalga, and some of the Aleutian Stream flows through Amukta and Amchitka Passes along the Aleutian Islands (Stabeno et al., 1999; Ladd et al., 2005; Stabeno and Hristova, 2014). Submarine canyons, including Bering, Pribilof, and Zhemchug Canyons, are located on the continental margin edge along the Bering Slope and serve as spawning grounds for skates (Rajidae), Pacific halibut, Greenland halibut (Fig. 1; St-Pierre, 1984; Seitz et al., 2007; Hoff, 2010; Sohn et al., 2010; Duffy-Anderson et al., 2013) and nursery grounds for Pacific Ocean perch (*Sebastes alutus*) and skates (Brodeur, 2001; Hoff, 2008), as well as conduits for slope-shelf exchanges of nutrients and larvae (Stabeno et al., 1999; Mizobata et al., 2006).

2.2. Data sources

To characterize the horizontal and vertical distributions of Pacific halibut larvae and to compare the horizontal and vertical distributions between Pacific halibut and Greenland halibut larvae in the EBS, we obtained historical Pacific halibut larval abundance and body-length data including sampling date, sampling location (latitude and longitude), and bottom depth at each sampling location between 1979 and 2012 from the ichthyoplankton survey database (EcoDAAT) at the National Oceanic and Atmospheric Administration (NOAA)'s Alaska Fisheries Science Center (AFSC; Table 1). During the surveys, Pacific halibut larvae were collected by various gear types including 60 cm bongo (BON), 1 m^2 Tucker trawl (TUCK), modified beam trawl (MBT; used in midwater towing), 5 m^2 frame Methot trawl (METH; Methot, 1986), and 1 m^2 Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS; Wiebe et al., 1976). The gears including BON,

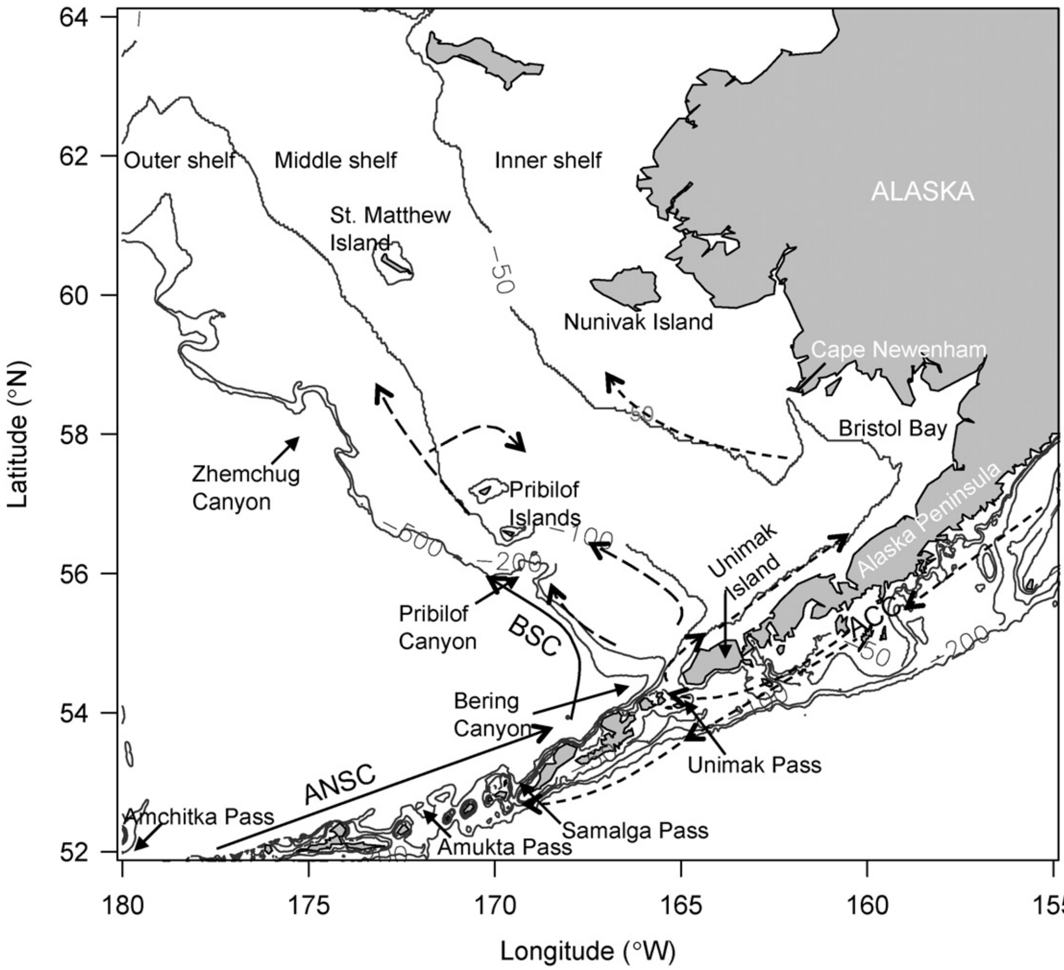

Fig. 1. Study area with schematic representation of the major currents — the Aleutian North Slope Current (ANSC; black line), Bering Slope Current (BSC; black line), Alaska Coastal Current (ACC; dashed line), flows (long dashed line) along the isobaths in the shelf in the eastern Bering Sea.

MOCNESS, and TUCK were equipped with 333 or 505 μm mesh size nettings. Both MBT and METH were equipped with 3 mm mesh size nettings. Tows were conducted from the surface to various depths in the shelf and slope/basin — mostly tows were to 10 m off bottom in the shelf and to about 200 or 500 m in the slope and basin. All tows were oblique. All sampling gears were fitted with flow meters to estimate the volume of water filtered. Ichthyoplankton samples were preserved in buffered 5% formalin and were sorted at the Plankton Sorting and Identification Center in Szczecin, Poland. All larvae were measured to the nearest 1.0 mm standard length (SL). Larval identifications were verified at the AFSC in Seattle, Washington, USA. More detailed sampling protocols can be found in Matarese et al. (2003).

To describe nursery habitats for Greenland halibut and Pacific halibut juveniles in the EBS, we utilized abundance and body-length data for juvenile stages (≤90 mm total length (TL)) and associated environmental data at each sampling station. Most of the historical catch data were acquired from the AFSC's EBS summer bottom trawl groundfish surveys which were conducted by the Groundfish Assessment Program (hereafter: Groundfish Survey) between 1982 and 2011 (Table 2). The Groundfish Survey has been conducted annually beginning as early as May and extending as late as October, although most recently, surveys have been conducted during June and July. These surveys provide extensive geographic coverage over the EBS shelf (http://www.afsc.noaa.gov/RACE/groundfish/gfprof_coverage.htm). The Groundfish Survey covered about 376 standard stations within 20 × 20 nautical mile grids. The gear is 25.3 × 34.1 m eastern otter trawl with 25.3 m headrope and 34.1 m footrope. The net is attached to paired chains and dandylines, and a net mensuration system is used to measure net height and width while towing. Tows are typically 30 min. in duration. Estimates of net width are used in calculations of area swept. All individual fish that were captured were measured to the nearest mm TL for flatfish or FL for other fish. More specific information about the Groundfish Surveys can be found in Lauth (2011). Other Pacific halibut and Greenland halibut juveniles catch data were also obtained from the AFSC juvenile flatfish surveys that were conducted in September in 2010 and 2012 using a 3.05-m plumb staff beam trawl rigged with 7 mm mesh, a 4 mm cod end liner, and tickler chains (Gunderson and Ellis, 1986). The 2010 survey was primarily conducted at shallow depths (<50 m depth) between Nunivak Island and Cape Newenham, whereas the 2012 survey was conducted over the inner, middle, and outer shelves between 55° N and 60° N. Each fish length was recorded to the nearest mm TL. A total of 123 stations were sampled between the two surveys. More specific information about these surveys can be found in Cooper et al. (2014).

2.3. Data analyses

The use of data from different gears is necessary in order to capture the larval distribution of Pacific halibut and Greenland halibut throughout their different early life history stages. PH and GH larval catch data from BON, MOCNESS, and TUCK with 333 and 505 μm mesh and MBT and METH with 3 mm mesh were utilized for analysis. The difference between MBT and METH is that the former has a weighted frame instead of having a depressor (Methot, 1986; Duffy-Anderson et al., 2006), therefore larval abundance data from these two gears were combined.

Table 1
Cruise information for Pacific halibut (PH) and Greenland halibut (GH) larvae from the Alaska Fisheries Science Center's EcoFOCI Program Ichthyoplankton database. *Bongo (BON), Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS), Tucker trawl (TUCK), modified beam trawl (MBT), and Methot trawl (METH).

Year	Cruise	Gear*	Total no. of tows	Positive tows of PH	Positive tows of GH	Sampling duration
1992	2MF92	MOCNESS	8	4	6	4/16–4/22
1993	3MF93	MOCNESS	17	7	15	4/17–4/28
1994	4MF94	MOCNESS	9	1	7	4/16–4/27
1995	7MF95	MOCNESS	6	0	0	5/5–5/17
2005	5MF05	MOCNESS	21	3	0	5/10–5/17
2006	3MF06	MOCNESS	12	5	0	5/9–5/15
2007	4MF07	MOCNESS	3	2	2	5/9–5/15
2008	1MF08	MOCNESS	8	4	4	2/19–2/26
2009	1KN09	MOCNESS	55	4	1	6/14–7/10
2010	1TT10	MOCNESS	90	3	2	7/1–7/12
1979	3MF79	BON	126	1	8	6/1–7/23
1986	MF862	BON	48	1	1	2/16–2/28
1988	1DN88	BON	46	5	0	4/11–5/8
	1OC88	BON	61	7	8	3/17–4/4
1991	0MF91	BON	20	6	10	3/11–3/15
	1MP91	BON	61	1	5	4/14–5/8
1992	2MF92	BON	36	11	9	4/16–4/18
1993	3MF93	BON	119	33	79	4/15–4/30
1994	4MF94	BON	128	34	37	4/15–4/30
1995	2MF95	BON	1	1	0	3/8
	6MF95	BON	137	30	15	4/17–4/30
	7MF95	BON	134	14	10	5/4–5/18
1996	6MF96	BON	5	2	3	5/15
1997	4WE97	BON	66	1	2	7/1–7/13
	5MF97	BON	34	5	3	4/16–4/25
	6MF97	BON	32	5	7	5/4–5/13
1999	1MF99	BON	37	1	0	4/14–4/18
	4MF99	BON	16	3	3	5/15–5/20
2002	3MF02	BON	81	14	11	5/13–5/21
2003	4MF03	BON	60	5	0	5/18–5/24
2004	1KR04	BON	3	2	0	8/10–8/22
2005	5MF05	BON	91	17	1	5/10–5/20
	6MF05	BON	2	2	0	5/22
	3TT05	BON	42	0	1	5/16–5/27
2006	1TT06	BON	92	0	1	4/15–5/9
	3MF06	BON	90	10	2	5/9–5/18
	4MF06	BON	3	2	0	5/22
2007	1HE07	BON	64	2	2	4/11–5/11
	4MF07	BON	101	18	25	5/8–5/18
2008	1AR08	BON	14	1	0	6/3–6/16
	1MF08	BON	44	23	18	2/18–2/26
	3DY08	BON	65	4	1	5/13–5/21
2009	1DY09	BON	27	11	5	2/26–3/4
	2DY09	BON	12	3	1	4/27–5/3
	3DY09	BON	87	7	6	5/9–5/18
2010	1AK10	BON	21	1	0	6/6–6/26
	2DY10	BON	102	1	8	5/6–5/17
2011	1DY11	BON	37	1	0	5/21–5/28
	2AK11	BON	10	1	0	6/25–7/11
2012	1DY12	BON	58	10	7	4/29–5/9
	2DY12	BON	195	6	6	5/17–6/1
1979	3MF79	TUCK	128	2	0	6/2–7/23
1986	MF862	TUCK	12	1	0	2/16–2/26
1993	3MF93	TUCK	8	6	0	4/16
1995	6MF95	TUCK	13	1	0	4/17–5/1
1997	4WE97	TUCK	25	1	0	7/6–7/13
1996	1OM96	MBT	34	0	4	7/21–7/29
1997	1OM97	MBT	28	0	12	7/21–7/29
1998	1OM98	MBT	25	0	1	7/25–7/30
1999	1OM99	MBT	20	0	6	7/26–8/1
2000	1OM00	MBT	21	0	1	7/28–8/1
2001	1OM01	MBT	23	0	6	7/21–7/24
2002	1OM02	MBT	26	0	1	8/1–8/9
2004	1OM04	MBT	25	0	2	7/28–8/4
2005	1OM05	MBT	24	1	1	7/15–7/21
1992	1MM92	METH	4	1	0	7/9–7/14
1994	7MF94	METH	15	0	4	7/15–9/6
1996	9MF96	METH	32	0	2	7/21–8/7
1997	4WE97	METH	32	9	22	7/5–7/13
	9MF97	METH	13	0	1	9/11–9/17
1999	7MF99	METH	38	0	2	9/4–9/14

We analyzed the horizontal and vertical distributions of Pacific halibut and Greenland halibut larvae separately by gear to avoid complications due to differences in capture efficiency. Larval abundance was expressed as individuals per 10 m^2 for analysis of horizontal distributions. The larval abundance data of Pacific halibut and Greenland halibut from nets at different MOCNESS sampling depths were integrated to provide a whole-water column estimate when examining horizontal larval distribution. We pooled data over years because larvae for the two species were rarely collected in each ichthyoplankton survey. However, to characterize the dispersal progression throughout the ontogeny, the distribution is shown for different months. Pacific halibut larvae were grouped in development stages based on their body-length: preflexion larvae (6.0–13.5 mm SL), flexion larvae (13.6–17.8 mm SL), and postflexion larvae (17.9–27.9 mm SL) (Thompson and Van Cleve, 1936; Matarese et al., 1989). Greenland halibut larvae were also grouped in development stages: preflexion larvae (9.0–19.2 mm SL), flexion larvae (19.3–21.9 mm SL), and postflexion larvae (22.0–44.9 mm SL) (Sohn et al., 2010; Duffy-Anderson et al., 2013). Each stage was analyzed separately.

To characterize Pacific halibut dispersal trajectories and movement across bathymetry throughout early ontogeny, we examined the spatial and temporal progression of body length during the larval stage using a generalized additive model (GAM). The full model was constructed using a Gaussian family with an identity link function using individual larval body-length at each station as the response variable. Independent variables in the model (prior to variable elimination) were day of year, sampling location (latitude and longitude), and bottom depth. A stepwise backwards selection process was used to determine the best-fit model by minimizing the generalized cross-validation (GCV) and Akaike information criterion (AIC). The GCV is a measure of the predicted mean squared error of the fitted model. The AIC is a measure of the relative goodness of fit of a statistical model (likelihood), penalized by the number of parameters. The GAMs were implemented using the mgcv library in R (Wood, 2004; Wood, 2006; R Statistical Computing Software, http://www.r-project.org/). To consider the possibility of bias due to selectivity in larval body-length in relation to gear type, Welch's t-tests were applied (R Statistical Computing Software, http://www.r-project.org/): no significant differences were found in larval size between gear type (BON and MOCNESS) (t (df = 38) = 1.43; *p-value* = 0.16) or between mesh sizes (333 and 505 μm) (t (df = 29) = −0.05; *p-value* = 0.96). Sample sizes of larval length from other gear types including TUCK, MBT, and METH were insufficient to conduct statistical analysis.

For the analysis of vertical distributions, we utilized Pacific halibut larval data from MOCNESS samplings in 1992–1995 and 2005–2010 while Greenland halibut larval data were grouped in 1992–1994, 2007–2008, and 2010. We analyzed both larval body-length (mm SL) and density (expressed as individuals per 1000 m^3) distributions grouped over the following binned depth strata: 0–100 m, 101–200 m, 201–300 m, 301–400 m, and 401–530 m. The depth bins were grouped to a relatively low resolution because the sampled depth varied over survey years or stations.

To describe settlement locations for both Pacific halibut and Greenland halibut in the EBS, we used juvenile catch data with body-length ≤90 mm TL from the Groundfish Survey and the juvenile flatfish survey, which represent age-0. Pacific halibut and Greenland halibut juveniles (≤90 mm TL) were not collected in every year from the Groundfish Survey (Table 2). In the juvenile flatfish survey, Greenland halibut juveniles (≤90 mm TL) were only found in 2010. Due to low catches of the juvenile Pacific halibut and Greenland halibut in each survey year, it was necessary to pool datasets over the survey years. Abundance of Greenland halibut and Pacific halibut juveniles was calculated as the number of individuals caught per 10,000 m^2 swept.

Table 2
Data collected for Pacific halibut (PH) and Greenland halibut (GH) juveniles (≤90 mm total length) from the Alaska Fisheries Science Center's Groundfish survey (1) and juveniles flatfish survey (2) database.

Survey	Year	Gear	Total no. of tows	Positive tows of PH	Positive tows of GH	Sampling duration
1	1983	Bottom trawl	353	0	1	6/7–8/1
	1985	Bottom trawl	358	0	3	6/8–10/5
	1986	Bottom trawl	354	0	6	6/3–8/1
	1988	Bottom trawl	373	1	0	6/4–7/30
	1989	Bottom trawl	374	0	1	6/6–8/11
	1990	Bottom trawl	371	0	10	6/4–8/1
	1991	Bottom trawl	373	0	3	6/7–8/13
	1993	Bottom trawl	375	0	1	6/4–7/26
	1997	Bottom trawl	376	1	0	6/7–7/26
	1999	Bottom trawl	373	2	0	5/23–7/11
	2000	Bottom trawl	372	3	1	5/23–7/20
	2001	Bottom trawl	400	0	1	5/29–7/19
	2002	Bottom trawl	375	0	2	6/2–7/24
	2003	Bottom trawl	376	1	0	6/2–7/22
	2004	Bottom trawl	375	4	1	6/5–7/25
	2005	Bottom trawl	402	1	0	6/3–7/22
	2006	Bottom trawl	405	5	1	6/2–7/25
	2007	Bottom trawl	376	1	4	6/11–7/28
	2008	Bottom trawl	375	0	7	6/4–7/24
	2009	Bottom trawl	376	1	10	6/2–7/19
	2010	Bottom trawl	376	2	6	6/7–8/4
	2011	Bottom trawl	376	3	1	6/5–7/25
2	2010	Beam trawl	58	11	6	9/11–9/18
	2012	Beam trawl	64	1	0	8/20–10/7

3. Results

3.1. Horizontal distribution of Pacific halibut and Greenland halibut larvae

Pacific halibut preflexion larvae (n = 210) were collected during spring (February–May) from BON (n = 155), MOCNESS (n = 48), and TUCK (n = 7) samplings (Table 3). Smaller preflexion larvae (<8.3 mm SL) were found in February, March, and May (Table 3). Spatially, preflexion larvae were mostly found in the continental slope regions along the Bering Sea slope between Bering and the Pribilof Canyons and along the eastern end of the Aleutian Islands (Fig. 2. (a)). A few preflexion larvae were found in the middle shelf between 50 m

Table 3
Range, mean, and standard deviation (SD) of Pacific halibut standard length (mm) and catch per unit effort (CPUE; number of individuals per 10 m^2) over geographic area from preflexion to postflexion larvae. *Bongo (BON), Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS), Tucker trawl (TUCK), modified beam trawl (MBT), and Methot trawl (METH).

Stage	Month	Gear type*	Body-length range	Mean body-length (SD)	CPUE range	Mean CPUE (SD)	No. fish
Preflexion larvae	2	BON	6.1–12.8	9.4 (1.4)	3.4–12.1	7.8 (1.7)	78
	2	MOCNESS	7.0–13.5	9.6 (1.4)	0.7–1.4	1.1 (0.3)	29
	2	TUCK	11.1		2.7		1
	3	BON	6.0–11.8	9.7 (1.0)	5.2–17.2	8.1 (3.2)	43
	4	BON	10.0–13.5	12.6 (0.9)	5.4–14.2	8.7 (2.4)	19
	4	MOCNESS	10.0–13.0	12.0 (0.9)	1.8–4.4	2.9 (1.0)	17
	4	TUCK	11.0–13.0	12.2 (0.7)	2.8–3.8	3.3 (0.7)	6
	5	BON	8.2–13.5	12.2 (1.9)	3.8–9.8	6.8 (1.9)	15
	5	MOCNESS	11.0–13.5	12.3 (1.8)	1.2–2.1	1.6 (0.7)	2
Flexion larvae	2	BON	13.8		9.4		1
	2	MOCNESS	13.9		1.3		1
	3	BON	13.6–15.0	14.3 (1.0)	7.2–7.8	7.5 (0.4)	2
	4	BON	13.6–17.8	15.6 (1.1)	4.7–10.4	7.5 (1.1)	144
	4	MOCNESS	14.0–16.2	15.0 (0.8)	2.3–3.1	2.6 (0.3)	12
	4	TUCK	14.0–15.5	14.7 (0.8)	3.1		3
	5	BON	13.7–17.8	15.9 (0.9)	3.5–11.4	6.9 (1.5)	160
	5	MOCNESS	15.0–17.8	16.5 (0.8)	0.9–2.0	1.5 (0.3)	18
	6	BON	17.0–17.5	17.3 (0.4)	6.8–7.1	7.0 (0.2)	2
	6	MOCNESS	15.0–17.6	16.5 (1.0)	0.8–1.5	1.2 (0.3)	5
	7	METH	17.5		0.08		1
Postflexion larvae	2	BON	18.2		8.3		1
	4	BON	18.0–26.0	19.6 (2.6)	5.7–9.3	7.4 (1.1)	9
	5	BON	17.9–26.5	19.3 (1.7)	4.1–10.0	6.3 (1.3)	46
	5	MOCNESS	18.0–19.1	18.8 (0.4)	1.2–1.6	1.4 (0.2)	7
	6	BON	22.6		3.3		1
	6	MOCNESS	18.0–22.0	19.7 (1.5)	1.1–6.1	2.7 (2.0)	8
	6	TUCK	20.7		2.9		1
	7	BON	21.0–22.0	21.5 (0.7)	4.9–5.0	5.0 (0.1)	2
	7	MBT	21.0		1.0		1
	7	METH	18.0–23.2	20.6 (1.5)	0.0–0.3	0.1 (0.1)	15
	7	TUCK	18.5–22.8	20.7 (3.0)	0.01–1.3	0.7 (0.9)	2
	8	BON	22.0		3.7		1

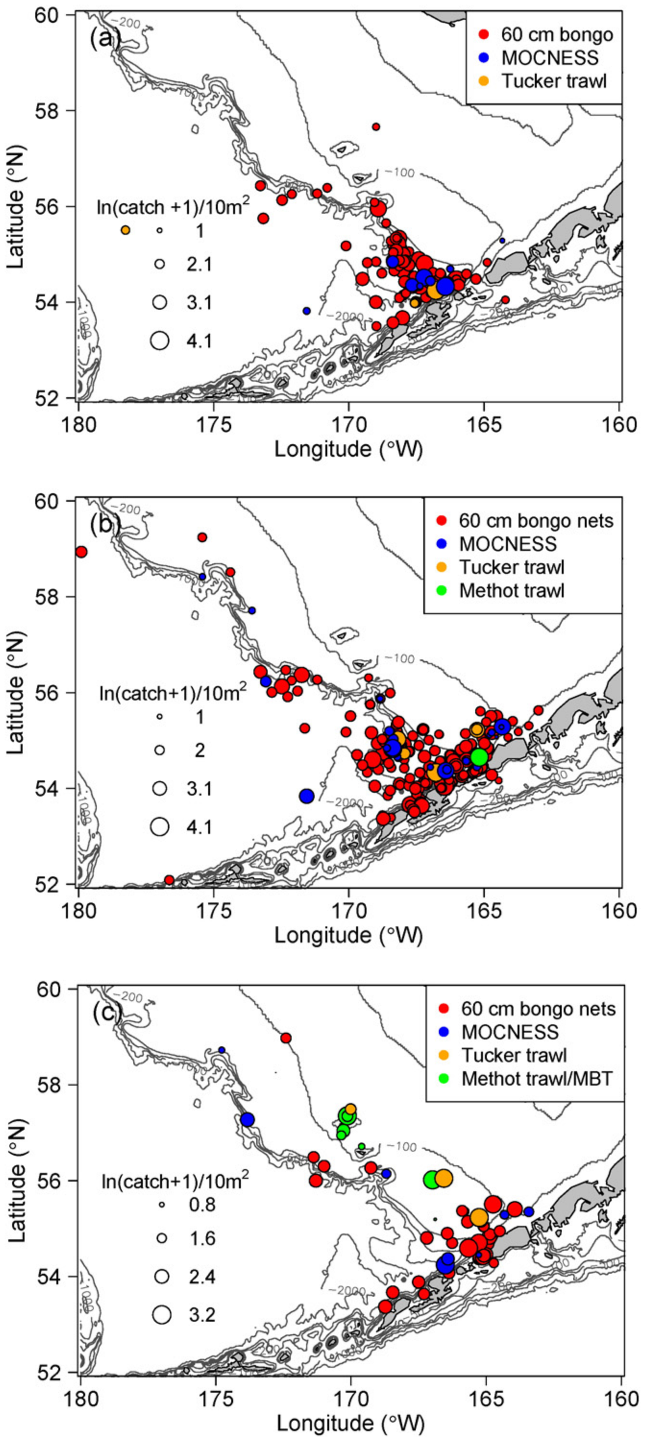

Fig. 2. Pacific halibut horizontal distribution of (a) preflexion larvae (6.0 mm–13.5 mm standard length (SL)) from February to August, (b) flexion larvae (13.6 mm–17.8 mm SL) from February to August, and (c) postflexion larvae (17.9 mm–28.0 mm SL) from February to August in the eastern Bering Sea. Bubble sizes are proportional to the log transformed catch per unit effort (CPUE) + 1. MOCNESS and MBT stand for Multiple Opening/Closing Net Sampling System and modified beam trawl, respectively. Gray lines indicate 50 m, 100 m, 200 m, 500 m, 1000 m, and 2000 m isobaths.

and 100 isobaths along Unimak Island and near St. Paul Island (Fig. 2. (a)). Pacific halibut flexion larvae (n = 349) were caught between February and July from BON (n = 309), MOCNESS (n = 36), TUCK (n = 3), and METH (n = 1) samplings (Table 3). Pacific halibut flexion larvae were mainly observed in three areas; the same area where the majority of preflexion larvae were found, the outer shelf (100 m–200 m isobaths), and at shallower depths (<50 m isobath) along the Alaskan Peninsula (Fig. 2. (b)). Flexion larvae were also found north of the Pribilof Islands near Zhemchug Canyon (Fig. 2. (b)). Pacific halibut postflexion larvae (n = 94) were captured between February and August from BON (n = 60), MBT/METH (n = 16), MOCNESS (n = 15), and TUCK (n = 3) samplings (Table 3). Postflexion larvae were mostly observed in the outer and middle shelves along the Unimak Island and around the Pribilof Islands (Fig. 2. (c)). Some postflexion larvae still remained in the slope edge along the eastern side of the Aleutian Islands and along the Bering Sea Slope between Pribilof and Zhemchug Canyons (Fig. 2. (c)). The best-fitted GAM (Model 3 in Table 4) explained 74.8% of the deviance in observed larval body-length (Table 4). Sampling location and day of year had significant effects on larval body-length (Table 4). Results of the GAM analysis showed that Pacific halibut larvae progress from the slope to the shelves through Bering Canyon and along the slope to northwest as they grow (Fig. 3 (a)). Some preflexion larvae were predicted along the central side of the Aleutian Islands (Fig. 3 (a)). Other preflexion larvae were predicted to occur along the slope between 55° N and 59° N (Fig. 3 (a)). Also, a preflexion larva was predicted to occur in the middle shelf around the Pribilof Islands between 57° N and 58° N (Fig. 3 (a)). Pacific halibut larval body-length increased over time (Fig. 3 (b)), at about 0.08 mm d^{-1}.

Greenland halibut preflexion larvae (n = 537) were also caught during spring (February – May) from BON (n = 441) and MOCNESS (n = 96) samplings (Table 5). Smaller preflexion larvae (<10.1 mm SL) were found between February and April (Table 5). Greenland halibut flexion larvae (n = 182) were collected between April and May from BON (n = 167) and MOCNESS (n = 15) samplings (Table 5). Greenland halibut postflexion larvae (n = 268) were captured between April and August from BON (n = 57), MBT/METH (n = 205), and MOCNESS (n = 6) samplings (Table 5).

Larvae of both Greenland halibut and Pacific halibut were mainly found along the Bering Sea slope between 53° and the 60° N and along the eastern side of the Aleutian Islands between February and April (Fig. 4). Larvae of the two species were also observed in the outer shelf between May and July (Fig. 4). However, Pacific halibut larvae were found in the middle shelf near Unimak Island in April and in the middle shelf and shallower areas (<50 m isobaths) along the Alaskan Peninsula in May and June (Fig. 4 (b)), but Greenland halibut were not. Pacific halibut larvae were also found through Unimak Pass (Fig. 4 (b)). A small number of Greenland halibut larvae were found in the north of St. Matthew Island, while Pacific halibut were observed south of St. Matthew Island (Fig. 4 (a) and (b)). The smallest body-length class for both species (<10 mm SL) was found along the Bering Sea slope near Bering Canyon. As they develop, larval distribution of Greenland halibut and Pacific halibut spreads northward along the slope and eastward over the shelf. A few Pacific halibut larvae (20.1–27.0 mm SL) were found on the shelf while many Greenland halibut larvae were found along the shelf-break and in the middle shelf near the Pribilof Islands. No Pacific halibut larvae (27.1–63.0 mm SL) were found in the water column in the outer and the middle shelves, while Greenland halibut larvae (27.1–63.0 mm SL) were still observed in this area.

3.2. Vertical distribution of Pacific halibut and Greenland halibut larvae

Vertically, both species rose to shallower depths in the water column as they developed — larger larvae were found at shallower depths while smaller larvae were found deeper (Fig. 5). However, the vertical distribution of Pacific halibut larvae was bi-modal with peaks at 0–100 m and 301–530 m depth while Greenland halibut larvae were found throughout the water column from the surface to 530 m depth (Fig. 5). Pacific halibut preflexion larvae, which were <13.6 mm SL, were found between 301 m and 530 m while both flexion and postflexion larvae that were between 14 and 20 mm SL were observed above 100 m depth.

Table 4
Model selection results of Generalized Additive Models for Pacific halibut larval standard length (mm) from 1979 to 2012 in the eastern Bering Sea. Estimated degrees of freedom are shown for independent variables with nonparametric terms. Asterisks denote significance at the following alpha levels: *0.1, **0.005, and ***0.001. GCV stands for generalized cross validation score and AIC stands for akaike information criterion. Bottom depth is log-transformed.

Model	No. fish	GCV	AIC	R-square	Deviance explained	Sampling location	Bottom depth	Day of year
1	651	3.414	2647.39	0.74	74.9%	0.1	0.004**	<2e-16***
2	651	3.454	2656.29	0.73	72.7%	Excluded	1.45e-08***	<2e-16***
3	651	3.441	2652.22	0.74	74.8%	4e-05***	Excluded	<2e-16***

3.3. Distribution of Pacific halibut and Greenland halibut settled juveniles

Pacific halibut juveniles (≤90 mm TL) were found over the shelf, especially in the inner shelf between Bristol Bay and Nunivak Island, along the west side of the Alaskan Peninsula, and in the vicinity of the Pribilof Islands (Fig. 6 (a) and (b)). The smallest Pacific halibut settled juvenile found in the juvenile flatfish survey was 33.7 mm TL and was found in shallow water (<50 m depth) along the eastern side of the Alaska Peninsula ((Fig. 6 (b)). The smallest settled juvenile collected from the Groundfish Survey was 40 mm TL and it was also found in the inner shelf (<50 m depth) near Bristol Bay (Fig. 6 (b)). Greenland halibut (≤90 mm TL) were mostly found in the middle shelf around St. Matthew Island and between 57° and 59° N in the inner shelf (Fig. 6 (c) and (d)). A few Greenland halibut juveniles were observed above 60° N and south closed to Unimak Island of the outer shelf (Fig. 6 (c) and (d)). The smallest Greenland halibut settled juvenile was 60 mm TL from the Groundfish Survey and 69 mm TL from the juvenile flatfish survey.

4. Discussion

Given the distribution of Pacific halibut larvae from the analysis of the preflexion size data, it is likely that spawning occurs in both Bering and Pribilof Canyons, along the continental slope between Bering and Pribilof Canyons, and along the eastern side of the Aleutian Islands during winter and early spring in the EBS. This result is consistent with previous studies about spawning location in the EBS (Best, 1981; St-Pierre, 1984). Forrester and Alderdice (1973) reported that Pacific halibut hatching time was about 20 days at 5 °C and 14 days at 7 °C and that larval body-length at hatching ranged from 6.15 mm to 7.79 mm TL at 5 °C and from 5.33 mm and 7.62 mm TL at 7 °C. Furthermore, Liu et al. (1994) reported that time to hatching for Pacific halibut was about 14 days at 6.5 °C and newly-hatched larval body-length ranged from 6.0 mm to 6.6 mm TL. Our GAM results showed that Pacific halibut body-length between preflexion and postflexion larvae increased at about 0.08 mm d^{-1}. This is likely an underestimation of actual growth due to the continuous influx of newly hatched individuals. Liu et al. (1993) reported that the average daily body-length increment during 20 days after hatching was 0.17 mm at 8 °C. Considering Pacific halibut hatching time, larval body-length at hatching (Forrester and Alderdice, 1973; Liu et al., 1994) and larval body-length daily increment from our results, small larvae that were found in February, March, and May could have been spawned in January, February, and April, respectively. These results are in agreement with earlier studies which show spawning occurs from November through March in the EBS (Best, 1981; St-Pierre, 1984). Also, our results indicate that Pacific halibut have a protracted spawning window during winter and early spring (April) in the EBS.

From depth-discrete MOCNESS sampling, the smallest Pacific halibut larva (7 mm SL) was found between 401 and 530 m. Assuming that eggs slowly rise during embryogenesis, this suggests that Pacific halibut eggs are hatched below 500 m depth. However, the actual spawning depth of Pacific halibut in the EBS is still unknown because Pacific halibut and Greenland halibut eggs cannot presently be differentiated by morphological traits alone. In the GOA, Pacific halibut eggs have been found between 100 and 400 m water depth (consistent with our results), and newly hatched larvae below 425 m, along the continental slope (Thompson and Van Cleve, 1936; Skud, 1977). Based on female spawning behaviors from unpublished Pop-up Archival Transmitting (PAT) tagging study in the EBS, Pacific halibut may release their eggs between 200 and 400 m depth (Andrew Seitz, University of Alaska, personal communication). Egg densities of Pacific halibut that were fertilized and incubated at 33‰, increased from 1.025 and then stabilized at 1.026 between about 8 and 13 days after fertilization (Forrester and Alderdice, 1973). It is therefore likely that Pacific halibut eggs are released at relatively shallow depths (around 250 m), then sink due to change in their density. Additionally, vertical distribution of Pacific halibut larvae in the EBS is different than in the GOA. Pacific halibut larvae (<13 mm SL) in our study were observed between 301 and 530 m in

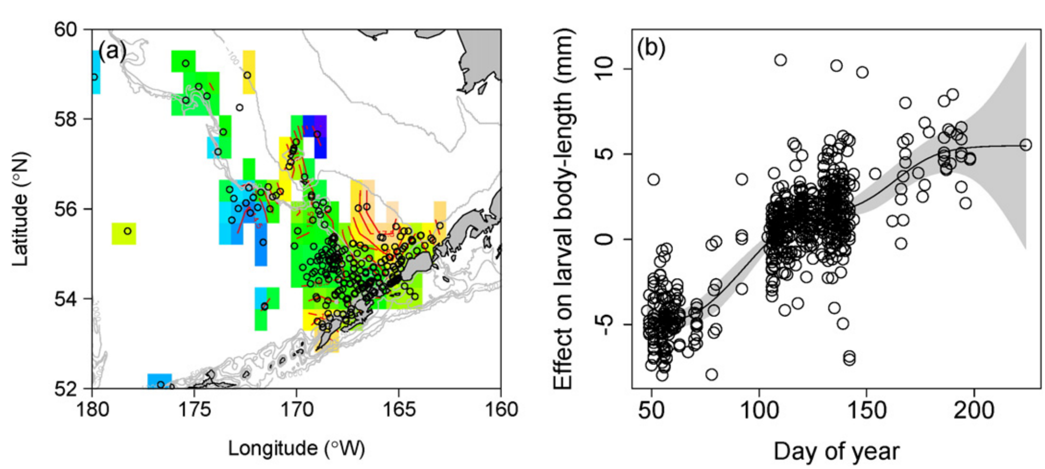

Fig. 3. Partial effects of (a) sampling location and (b) day of year on Pacific halibut larval body-length estimated from the Generalized Additive Model (GAM). Image color and red contour lines indicates predicted larval body-length from the GAM in which sampling location (latitude and longitude) and day of the year where included as covariate. The body-length increases going from blue to green and yellow being largest. Open circles in (a) and (b) indicate the observation data. Shaded areas on (b) are intervals of the modeled independent variables.

Table 5
Range, mean, and standard deviation (SD) of Greenland halibut standard length (mm) and catch per unit effort (CPUE; number of individuals per 10 m^2) over geographic area from preflexion to postflexion larvae. *Bongo (BON), Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS), modified beam trawl (MBT), and Methot trawl (METH).

Stage	Month	Gear type*	Body-length range	Mean body-length (SD)	CPUE range	Mean CPUE (SD)	No. fish
Preflexion larvae	2	BON	9.5–16.0	10.9 (1.6)	6.1–14.2	7.8 (1.9)	20
	2	MOCNESS	9.9–10.0	10.0 (0.1)	0.9–1.5	1.2 (0.4)	2
	3	BON	9.0–15.0	11.9 (1.2)	3.6–41.3	9.8 (9.3)	92
	4	BON	9.5–19.2	17.1 (1.6)	5.8–14.2	8.6 (1.4)	278
	4	MOCNESS	12.0 – 19.2	16.2 (1.4)	2.3–6.0	3.7 (1.1)	93
	5	BON	12.0–19.1	17.8 (1.4)	4.4–10.1	7.1 (1.6)	51
	5	MOCNESS	17.1		2.0		1
Flexion larvae	4	BON	19.4–21.2	20.1 (0.5)	5.8–15.2	7.9 (1.5)	104
	4	MOCNESS	19.5–21.8	20.1 (0.7)	2.0–5.1	3.4 (1.2)	13
	5	BON	19.3–21.9	20.7 (0.8)	4.0–10.1	7.4 (1.6)	63
	5	MOCNESS	20.6–21.1	20.9 (0.4)	2.0		2
Postflexion larvae	4	BON	22.0–22.8	22.2 (0.4)	7.3–9.0	8.2 (0.8)	5
	4	MOCNESS	22.0–22.4	22.2 (0.3)	2.8		2
	5	BON	22.0–25.5	22.8 (0.9)	4.9–9.3	7.3 (1.2)	39
	5	MOCNESS	22.0–25.0	23.5 (2.1)	1.3–2.0	1.7 (0.5)	2
	6	BON	22.0–34.6	27.1 (4.0)	3.9–7.2	6.3 (1.2)	9
	6	MOCNESS	30.0		6.7		1
	7	BON	35.1–39.0	36.9 (1.9)	5.4–6.9	6.0 (0.7)	4
	7	MOCNESS	32.9		1.7		1
	7	MBT	25.0–44.8	35.6 (4.5)	0.0–0.9	0.3 (0.3)	53
	7	METH	24.0–44.5	33.7 (4.4)	0.0–0.3	0.1 (0.1)	148
	8	MBT	38		0.6		1
	8	METH	29.8–39.5	33.4 (5.3)	0.0–0.2	0.1 (0.1)	3

the EBS, but they have been found between 150 and 380 m in the GOA (Bailey and Picquelle, 2002). This discrepancy in vertical depth might result from differences in environmental conditions (i.e., water temperature, salinity, and topographic features) influencing larval growth and distribution.

Interestingly, developmental stages of Pacific halibut co-occurred along the central (west of Samalga Pass and east of Amchitka Pass as defined by Mordy et al., 2005) Aleutian Islands, indicating the existence of separate spawning groups and the retention of larvae in this region. Previous studies suggested that there could be a separate spawning group in the Aleutian Islands. Nielsen et al. (2010) reported genetic differences between Pacific halibut in the Aleutian Islands and Pacific halibut in the EBS and the GOA. Moreover, Seitz et al. (2011) suggested localized spawning groups in the EBS and the Aleutian Islands regions based on tagging results. Alternatively or in addition to multiple spawning groups in the EBS, it is possible that Pacific halibut larvae enter the Aleutian Islands of the Bering Sea from the GOA through the central passes (i.e., Amukta, Seguam, Tanaga, and Amchitka Passes). Some of the Alaskan Stream flows through the central passes along the Aleutian Islands into the Bering Sea (Stabeno et al., 1999; Ladd et al., 2005; Mordy et al., 2005; Ladd and Stabeno, 2009).

Pacific halibut preflexion larvae were mostly observed over the slope while postflexion larvae were found in the shelf regions, indicating larval advection from the slope to the shelf as they grow. Vertically, Pacific halibut larvae have a bi-modal depth distribution between preflexion and flexion larval stages, indicating an abrupt movement toward shallower depths as they develop. This vertical ontogenetic migration might enhance cross-shelf transport from spawning locations over the slope to nursery areas on the shelves in the EBS. Based on modeling results, BSC transport from April to early September varies with water depth: below 30 m, flow is primarily northward along the slope edge, while above 30 m on-shore transport occurs (Regional Oceanographic Modeling System for the northeast Pacific (ROMS NEP version 4); Duffy-Anderson et al., 2013). Slope-shelf exchanges of Pacific halibut

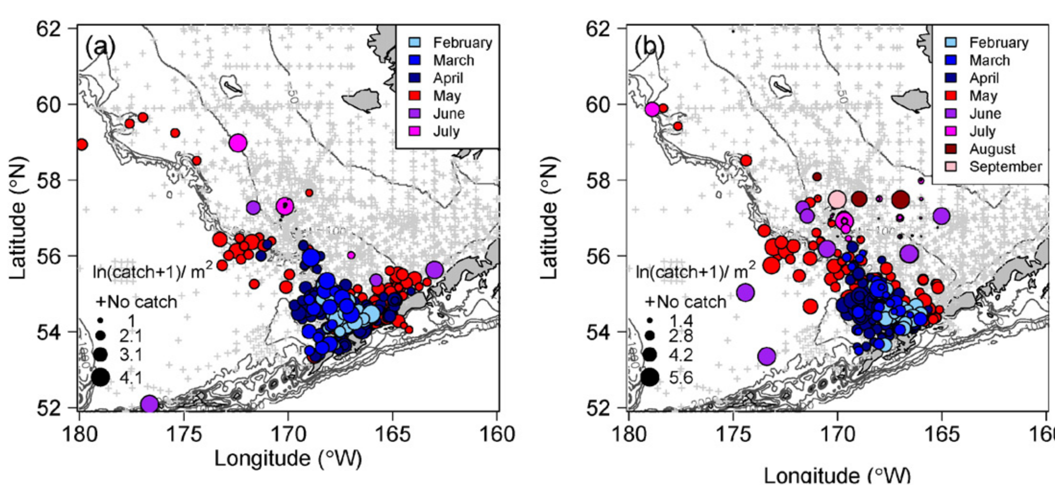

Fig. 4. Horizontal distributions of (a) Pacific halibut and (b) Greenland halibut larvae between February to September collected from 60 bongo (BON), modified beam trawl (MBT), and methot trawl (METH) samplings between 1972 and 2012. Plus signs represent non-catch stations across the sampling years. Gray lines indicate 50 m, 100 m, 200 m, 500 m, 1000 m, and 2000 isobaths.

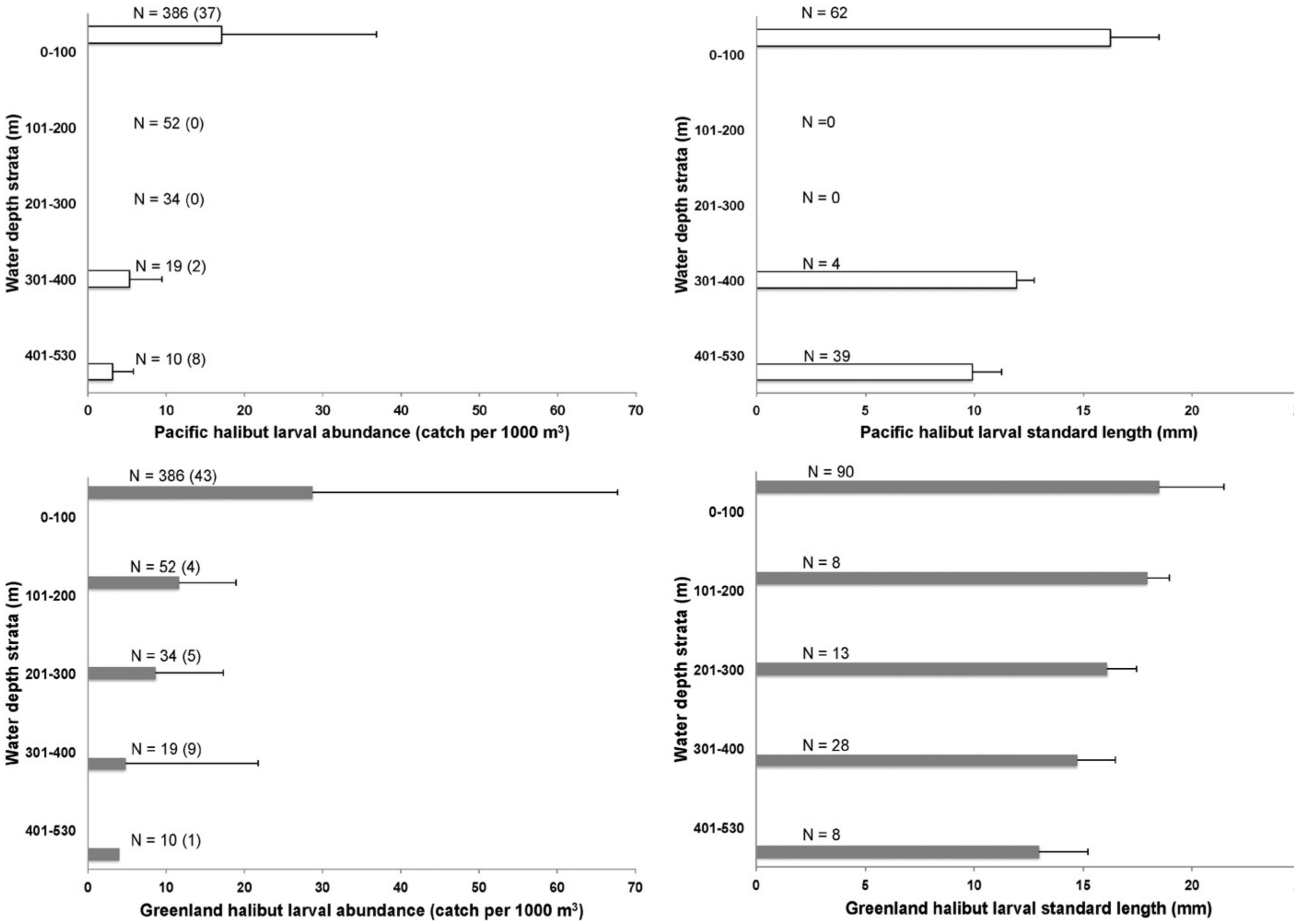

Fig. 5. Vertical distribution of Pacific halibut larval abundance (one standard deviation (line); top left) and standard length (standard deviation (line); top right) over 10 years (1992–1995 and 2005–2010) and vertical distribution of Greenland halibut larval abundance (standard deviation (line); bottom left) and standard length (one standard deviation (line); bottom right) in 1992–1994, 2007–2008, and 2010 in the eastern Bering Sea. N refers to number of tows (number of positive tows) for the left panel and number of fish for the right panel.

larvae in the EBS could be influenced by variability in the BSC. Satellite-tracked drifters, oceanographic models, and field observation data show seasonal and interannual variability in onshore and offshore transports in the EBS (Danielson et al., 2011; Stabeno et al., 2012; Ladd, 2014; Vestfals et al., 2014). Intra-annual variability in the BSC exists; the BSC is close to the slope edge during winter and far from the edge during the rest of year (Ladd, 2014). Interannual shifts in the BSC position are likely due to mesoscale variability, such as eddies or meanders (Ladd, 2014). Vestfals et al. (2014) found that Pacific halibut recruitment increased with increased cross-shelf transport through Bering and Pribilof Canyons, and decreased with increased transport along the Bering Sea slope (Vestfals et al., 2014). Thus, changes in the BSC could influence variations of distribution, dispersal trajectories, and habitat connectivity during Pacific halibut early ontogeny.

Flexion and postflexion Pacific halibut larvae were found in the Unimak Pass indicating some larvae observed in the EBS may have advected from the GOA through the eastern passes (passes east of Samalga Pass as defined by Ladd et al., 2005) including Unimak. This finding is in agreement with previous studies in which Pacific halibut larvae were found near the Unimak Pass and appeared to flow from the GOA to the EBS through the Unimak Pass associated with circulation pattern (Skud, 1977; Best, 1981; St-Pierre, 1989). Satellite-tracked drifter data support Pacific halibut larval connectivity between the EBS and GOA through Unimak Pass (Ladd et al., 2005). Unimak Pass is also known to be important for exchange of nutrients and other organisms (e.g., northern rock sole (*Lepidopsetta polyxystra*)) between the EBS and the GOA (Stabeno et al., 2005; Ladd et al., 2005; Lanksbury et al., 2007; Siddon et al., 2011). Furthermore, Nielsen et al. (2010) found that the genetic structure of Pacific halibut is not different between the GOA and southeast Bering Sea, but is different in the Aleutian Islands. Larvae could also enter the Bering Sea through other eastern passes. The portion of the Aleutian Stream flows through Aleutian passes, especially Amukta Pass and forms the eastward flowing the ANSC (Stabeno et al., 1999). The ACC flows in the EBS through Unimak Pass while a portion of the ACC continuously flows along the Aleutian Islands until Samalga Pass (Ladd et al., 2005; Stabeno and Hristova, 2014).

Based on our analysis of the juvenile data, Pacific halibut utilize specific settlement and nursery habitat for age-0 fish: water <50 m depth, between Bristol Bay and Nunivak Island, along the Alaska Peninsula, and around the Pribilof Islands in the inner and middle shelves of the EBS. These results are consistent with previous studies (Best, 1974, 1977; Best and Hardman, 1982). Best (1974 and 1977) and Best and Hardman (1982) found juveniles (<100 mm TL) in shallow depths (<50 m) along the Alaskan Peninsula, in the inner shelf between Bristol Bay and Nunivak Island, and in the middle shelf of southeastern Bering Sea. The smallest settled juvenile (33.7 mm TL) in our dataset was in the inner shelf along the Alaska Peninsula, suggesting that this body-length is a potential body-size at settlement for Pacific halibut. Best (1977) reported that many age-0 Pacific halibut in the EBS were found in bottom water temperature between 3.5 and 5.5 °C while few halibut were found at 2 °C or less than 2 °C. Thus, climate variability in the EBS can alter the distribution of Pacific halibut juveniles. Recently, the EBS has exhibited a prolonged cold

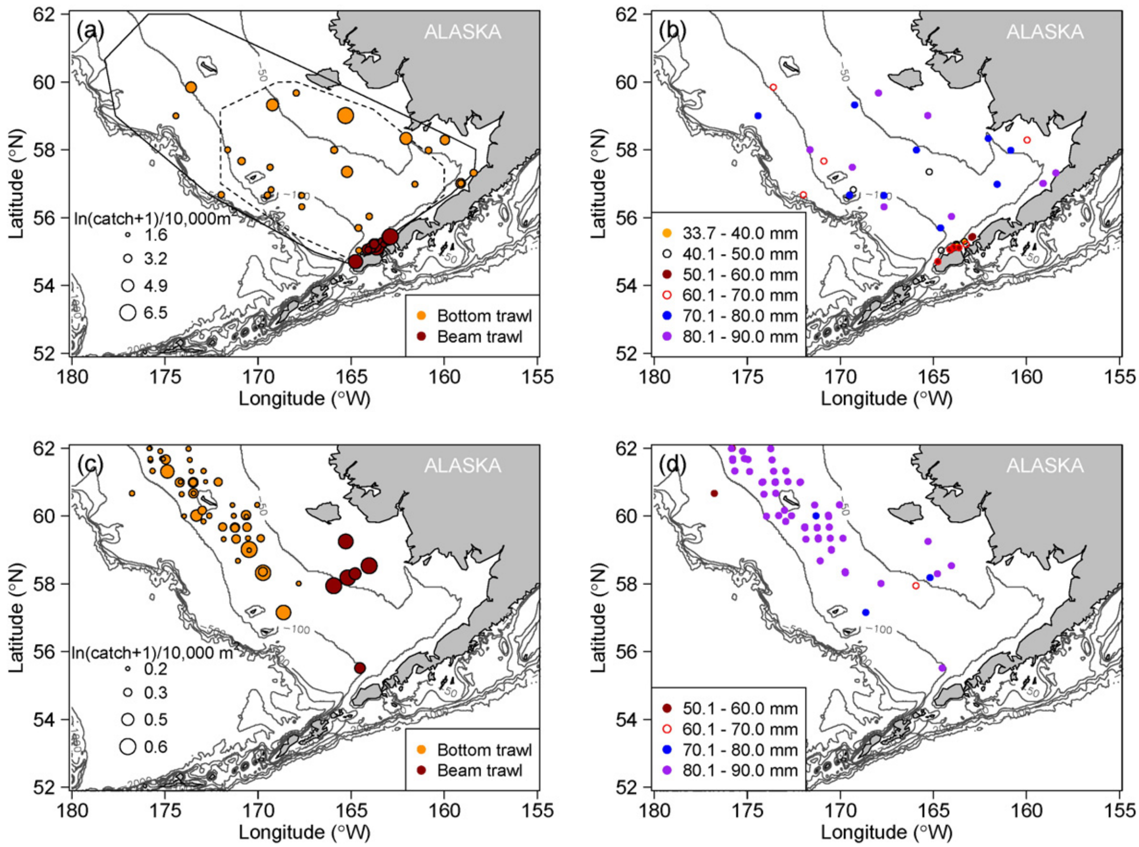

Fig. 6. Distributions of (a) abundance (ln (catch per unit effort (CPUE) + 1)) per 10,000 m^2 and of (b) body-length for Pacific halibut settled juveniles (33.7 mm–90.0 mm total length (TL)) and distributions of (c) abundance (ln (CPUE + 1)) per 10,000 m^2 and of (d) body-length for Greenland halibut settled juveniles (60.0 mm–90.0 mm TL) from the eastern Bering Sea summer bottom trawl (1982–2011) and beam trawl (2010 and 2012) surveys. Bubbles in (a) and (c) indicate natural log transformed CPUE + 1 and open circles in (b) and (d) indicate locations where individuals in each body-length category were found. Gray lines indicate 50 m, 100 m, 200 m, 500 m, 1000 m, and 2000 m isobaths. Black line polygon in (a) indicates geographic area sampled by bottom trawl while black dash line polygon indicates geographic area sampled by beam trawl.

period (2007–2012) after a prolonged warm period (2001–2005; Stabeno et al., 2012). Settled juvenile Greenland halibut (<100 mm TL) range has expanded to south of the Pribilof Islands, which is likely due to an increase in the extent of the cold pool (summer bottom temperatures <2 °C) and associated expansion of their habitat due to expanded winter sea ice coverage during the cold period (Ianelli et al., 2011). The distributions of age-0 and age-1 northern rock sole in the EBS also appears to be influenced by changes in water temperature and flows due to climate change (Cooper et al., 2014). Thus, it is possible that changes in size of suitable nursery habitat for Pacific halibut could be impacted between the warm and cold periods in the EBS, influencing Pacific halibut distribution and recruitment.

Although Greenland halibut and Pacific halibut share several attributes during early life stages, there are species-specific differences in vertical distribution, timing of cross-shelf transport (larval progression in time and space), and settlement locations. Both species spawn along the slope near Bering Canyon during winter, larvae ascend into surface waters after hatching, and are advected from the slope to the shelf for settlement. However, Pacific halibut spawning may be protracted until April. Also, Pacific halibut cross to the shelf earlier than Greenland halibut. Vertically, Pacific halibut have an abrupt vertical ascent through the water column. Furthermore, Pacific halibut settle earlier than Greenland halibut indicating that Pacific halibut pelagic larval duration is comparatively shorter than that of Greenland halibut. Both species occupy specific habitats for settlement. Greenland halibut settle in the middle shelf around St. Matthew Island at water temperatures ~1 °C (Sohn et al., 2010) though their settlement area can be expanded to south when water temperatures decrease (Ianelli et al., 2011). In contrast, Pacific halibut settle farther south in shallower depth (<50 m) along the Alaskan Peninsula, between Bristol Bay and Nunivak Island, and around the Pribilof Islands. These species-specific differences during early ontogeny in the same environment can cause different distribution and transport characteristics with climate variability in the EBS, which in turn may differently influence their settlement success, recruitment, and population dynamics.

Based on the results of our study, we propose that species-specific differences in early life stages for Pacific halibut and Greenland halibut could result in differences of recruitment success and population dynamics within the same oceanographic system. As a future study, particle-tracking models for Pacific halibut and Greenland halibut during early life stages, combined with outputs from regional ocean modeling systems may help to further elucidate the proposed hypothesis. In that regard, our results provide baseline data for future modeling work of drift trajectories for the Pacific halibut during early life history stages. Furthermore, our study provides fundamental or updated early life history information about ecology and biology for the two commercial flatfish species in the EBS that would be useful for studying habitat usages, predator–prey interactions, and climate impact projects for other flatfish species in the EBS.

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