Distribution and drift pathways of Greenland halibut (*Reinhardtius hippoglossoides*) during early life stages in the eastern Bering Sea and Aleutian Islands

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ABSTRACT

We describe the spatial distribution and dispersal pathways of Greenland halibut (*Reinhardtius hippoglossoides*) early life stages based on historical field data from the eastern Bering Sea and adjacent water along the eastern Aleutian Islands. Our results indicate that Greenland halibut from preflexion larvae to newly settled juveniles have a long pelagic duration and are subject to extended drift pathways. Hatching may occur in deep water, below 530 m, and larvae rise in the water column as they grow. Flexion/postflexion larvae are mostly found around the Pribilof Islands over the middle shelf (50–100-m isobaths) in July, and settling occurs during late summer on the middle shelf near St. Matthew Island. However, given that age-1 individuals were primarily found on the outer shelf, it appears that Greenland halibut actively move to deeper water with age (or size). The mechanisms of slope–shelf connectivity in preflexion larvae may be related to the Bering Slope Current in the vicinity of both Bering and Pribilof Canyons. This study shows that Greenland halibut early life stages have extensive horizontal ontogenetic migrations in the Bering Sea, and utilize a range of geographic areas over the basin and slope along the Aleutian Islands and in the eastern Bering Sea. Based on these results, it is hypothesized that settlement success and recruitment of Greenland halibut may be influenced by variability in currents and flows of the Bering Sea slope and shelf during their transport.

INTRODUCTION

Greenland halibut, *Reinhardtius hippoglossoides*, has a circumpolar distribution, occurring in the North Pacific, Arctic, and North Atlantic Oceans. The species is broadly distributed from 20 to 1600 m at temperatures ranging from −1 to 10°C (Jensen, 1935; Fedorov, 1971; Templeman, 1973 cited by Alton *et al.*, 1988). Greenland halibut can live over 36 years and reach up to 120 cm in length and 44.5 kg in weight (Jensen, 1935; Gregg *et al.*, 2006). Spawning typically occurs along the continental slope between 400 and 1100 m from late winter to early spring (Jensen, 1935; Hognestad, 1969; Nizovtsev, 1969; Smidt, 1969 cited by Godø and Haug, 1989; Fedorov, 1971; Albert *et al.*, 2001a), but year-round spawning has also been hypothesized in the Barents Sea/Norwegian Sea (Fedorov, 1971).

Many aspects of Greenland halibut life history have been widely studied in the Atlantic Ocean; however, little is known about the ecology and biology of the populations in the Pacific Ocean, particularly for early life stages. From studies in the Atlantic Ocean it is known that Greenland halibut have very large eggs (4.0–4.5 mm diameter) with mesopelagic distributions (600–1000 m depth) (Jensen, 1935; Smidt, 1969; Godø and Haug, 1989; Stene *et al.*, 1999). The length of newly hatched larvae reared from eggs collected from the Barents Sea in the laboratory is about 6 mm (Stene *et al.*, 1999). Larvae are epi- and mesopelagic, but they are found progressively shallower in the water column as they develop (Jensen, 1935). Larvae have a long pelagic period before settlement and are found in the water column up to 70 mm length (Jensen, 1935). Although certain life history characteristics may be similar among ecosystems, we cannot assume a conclusive understanding of Greenland halibut life history

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in the Pacific Ocean based on investigations in the Atlantic Ocean (Bailey *et al.*, 2005).

In the Pacific Ocean, Greenland halibut is primarily found in the eastern Bering Sea (EBS) and the western Bering Sea along the Aleutian Islands (AI) (Fig. 1; Alton *et al.*, 1988; Ianelli *et al.*, 2007). Greenland halibut used to be a commercially important flatfish species and is still a target species in the region (Ianelli *et al.*, 2007). However, due to population declines beginning in the late 1970s, the commercial importance of this stock is relatively low. Commercial harvests of Greenland halibut peaked near 80 000 tons in the late 1970s, but the current catch is only about 2000–3000 tons annually (Ianelli *et al.*, 2007). Other flatfish stocks (e.g., arrowtooth flounder, *Atheresthes stomias*) have increased substantially over the same period in the Bering Sea. Even with reduced catch limits, Greenland halibut spawning biomass remains low due to poor recruitment (Ianelli *et al.*, 2007). Although there are signs of improved recruitment in recent years (2007–2008), the reasons behind the poor recruitment over the previous years are unknown, and important knowledge gaps during the early life stages have been identified (Alton *et al.*, 1988; Ianelli *et al.*, 2007).

Dispersal and drift pathways associated with the prevailing direction of ocean currents have been shown to play a key role in flatfish recruitment and year-class strength (Fargo, 1994; Van der Veer *et al.*, 1998;

Wilderbuer *et al.*, 2002; Bailey *et al.*, 2005). This is particularly true in slope-spawning species like Greenland halibut, as their larvae must be transported from the continental slope up over the shelf, often perpendicular to prevailing currents, to reach suitable nursery locations in shallower water (Bailey and Picquelle, 2002; Bailey *et al.*, 2008). These nursery locations can be distant from offshore spawning grounds. It is essential to characterize early life drift pathways given the long journey that the eggs and larvae undertake from spawning to juvenile nursery locations, as well as the importance of successful settlement for flatfish species (Haug *et al.*, 1989; Albert *et al.*, 2001b).

In this paper, we examine the horizontal distribution patterns of Greenland halibut early life stages to describe potential drift pathways of their preflexion larvae, flexion/postflexion larvae, and settling locations of juvenile (age-0 and age-1) individuals. We also make a more limited examination of vertical patterns in preflexion larvae based on available data.

MATERIALS AND METHODS

Study area

The study area for this paper was the Bering Sea, and particularly the EBS and adjacent water along the eastern AI regions (Fig. 1). The Bering Sea is divided into the basin and the western and eastern shelf
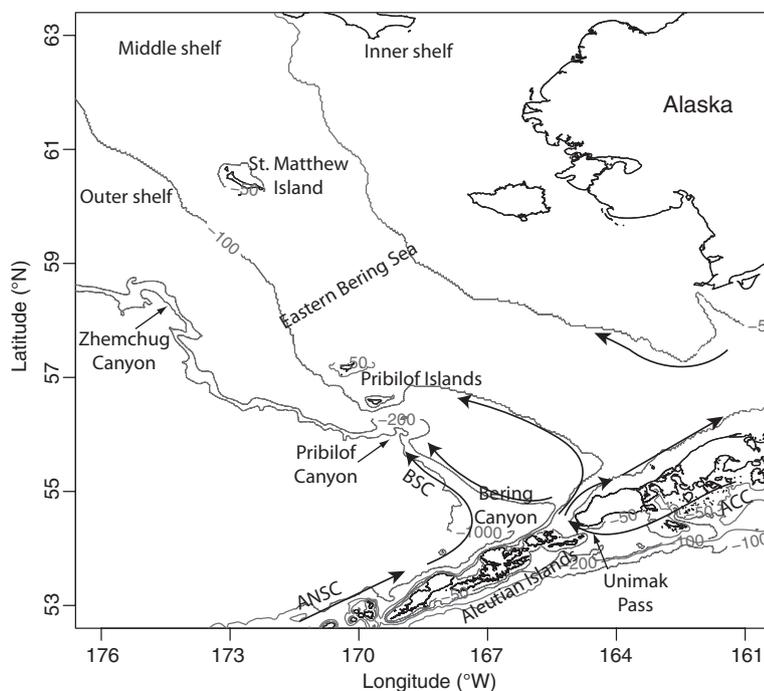

Figure 1. Study area with major currents in the eastern Bering Sea and Aleutian Islands region. Aleutian North Slope Current (ANSC), Bering Slope Current (BSC), and Alaska Coastal Current (ACC).

regions. The EBS is partitioned into three shelves by hydrographic features often associated with different isobaths: the inner or coastal shelf (<50 m isobath), the middle shelf (between the 50 and 100 m isobaths), and the outer shelf (between the 100 and 200 m isobaths) (Coachman, 1986; Schumacher and Stabeno, 1998). There are two dominant currents at the shelf break: the Aleutian North Slope Current (ANSC) and the Bering Slope Current (BSC). The ANSC flows eastward along the AI from Amchitka Pass to Akun Island, and the BSC flows northward along the slope of the eastern shelf (Stabeno *et al.*, 1999). These currents, as well as weaker cross-shelf currents, have important roles within the EBS, including bringing nutrients from the basin to the shelf and modulating larval fish dispersal (Springer *et al.*, 1996; Stabeno *et al.*, 1999; Lanksbury *et al.*, 2007).

Data collections

Our retrospective analysis is based on samples collected by the NOAA Fisheries Alaska Fisheries Science Center (AFSC) in Seattle, WA. We define Greenland halibut early life stages based on different size ranges and various gear types used to collect them.

1 Preflexion larvae including yolk-sac larvae: 8.8–24.9 mm standard length (SL). Caught with 60 cm bongo nets (60BON) and a 1-m^2 multiple opening and closing net and environmental sampling system (MOCNESS).
2 Flexion/postflexion larvae: 25.0–59.9 mm SL. Caught by modified bottom trawl (MBT) and Methot trawl (MT).
3 Newly settled juveniles: 60–90 mm fork length (FL). Caught by bottom trawl (BT).
4 Age-1 individuals: 140–220 mm FL. Caught by BT. These categories are based on the facts that the smallest larva was 8.8 mm SL collected from 60BON, notochord flexion begins between 25 and 27 mm SL (Jensen, 1935), the smallest newly settled juvenile observed from the BT was 60 mm FL, and sizes of age-1 individuals based on stock assessment models are between 140 and 220 mm FL (Ianelli *et al.*, 2007).

Table 1. Data information of Greenland halibut from the Alaska Fisheries Science Center's EcoFOCI Program Ichthyoplankton database. Information on tows from which Greenland halibut specimens were collected (positive tows) as well as those including the zero catches (total tows) is reported in the table.

Year	Gear	No. of positive tows (No. of total tows)	Duration of positive tows	Duration of total tows
1988	60BON	8 (61)	March 19–April 2	March 17–April l4
1991	60BON	15 (81)	March 11–May 7	March 11–May 8
1992	60BON	9 (36)	April 16–April 18	April 16–April 18
1993	60BON	79 (119)	April 15–April 30	April 15–April 30
1994	60BON	37 (128)	April 15–April 29	April 15–April 30
1995	60BON	26 (362)	April 17–May 16	April 17–May 18
1996	60BON	3 (5)	May 15	May 15
1997	60BON	10 (66)	April 16–May 13	April 16–May 13
1999	60BON	3 (16)	May 19	May 15–May 20
2002	60BON	11 (81)	May 13–May 21	May 13–May 21
2005	60BON	2 (133)	May 19–May 20	May 16–May 20
1992	MOCNESS	6 (8)	April 16–April 22	April 16–April 22
1993	MOCNESS	15 (17)	April 17–April 28	April 17–April 28
1994	MOCNESS	7 (9)	April 16–April 24	April 16–April 27
1994	MT	4 (14)	July 16–August 19	July 15–September 6
1996	MT/MBT	7 (66)	July 22–August 3	July 21–August 7
1997	MT/MBT	35 (73)	July 5–September 12	July 5–September 17
1998	MBT	1 (25)	July 29	July 25–July 30
1999	MT/MBT	10 (58)	July 28–September 14	July 26–September 14
2000	MBT	1 (21)	July 29	July 28–August 1
2001	MBT	6 (23)	July 21–July 24	July 21–July 24
2002	MBT	1 (26)	August 5	August 1–August 9
2004	MBT	2 (25)	July 30–August 1	July 28–August 4
2005	MBT	1 (24)	July 18	July 15–July 21

60BON, 60 cm Bongo net; MOCNESS, Multiple Opening/Closing Net and Environmental Sampling System; MBT, Modified Beam Trawl; MT, Methot Trawl.

Preflexion larvae

Historical Greenland halibut larval data were obtained from archival records in the Ichthyoplankton Database (ICHBASE) housed at the AFSC (Table 1). Preflexion larvae were collected on research cruises conducted over a period of 20 years using both depth-integrated and depth-discrete approaches (Matarese *et al.*, 2003). Depth-integrated ichthyoplankton samples were collected using the 60BON (505 or 333 μm mesh) fitted with flowmeters. Nets were towed from various depths from the surface. Net depth was measured at each station using a Sea-Bird SBE 19 profiler attached in-line between the wire terminus and the bongo net frame. Depth-discrete ichthyoplankton samples were collected using the MOCNESS (Wiebe *et al.*, 1976) at a variety of stations over the EBS slope and shelf. The 60BON sampling occurred in March–May from 1988 to 2005, and depth-discrete MOCNESS sampling occurred in April from 1992 to 1994 (Table 1). All samples were preserved in buffered 5% formalin and were sorted at the Plankton Sorting and Identification Center in Szczecin, Poland. Taxonomic identifications were verified at the AFSC in Seattle, WA. All fishes were measured for standard length to the nearest mm SL.

Flexion/postflexion larvae

Flexion/postflexion larvae were collected from a series of cooperative research cruises between scientists at the ASFC and Graduate School of Fisheries Hokkaido University, Japan, on the T/S *Oshoro Maru*. Flexion/postflexion larvae were also collected from research cruises conducted by the AFSC. The larvae were sampled using either MBT (mouth opening 5 m^2) with 3 × 2 mm oval mesh net and a l-mm mesh cod end, or a 6-ft frame MT with 3-mm mesh netting and a 1-mm mesh cod end. MBT was designed to collect late larval and early juvenile stage fishes in the mid-water and is similar to MT (Methot, 1986). MBT differs from MT in not having a depressor but instead a weighted frame (Duffy-Anderson *et al.*, 2006); otherwise the two gears are very similar. A flowmeter fitted inside both frames was used to determine the filtered volume. All tows were oblique and were primarily made 10 m off bottom to the surface. Net depth was measured using an acoustic netsound. MBT sampling occurred from July to August in 1996–2005 and MT sampling was conducted from July to September in 1994–1999 (Table 1). All samples were preserved, sorted, and all fish flexion/postflexion larvae were identified and measured (mm SL).

Newly settled juveniles and age-1 fish

Data on newly settled juvenile and age-1 individuals were obtained from the Resource Assessment and Conservation Engineering database (RACEBASE) maintained by the AFSC's Groundfish Assessment Program. Groundfish surveys using bottom trawls from 1982 to 2007 were utilized (Table 2). These surveys have been conducted annually beginning as early as May and extending as late as October, although most recently, surveys were conducted in summer months. These surveys provide extensive geographic coverage over the EBS shelf (http://www.afsc.noaa.gov/RACE/groundfish/gfprof_coverage.htm) and give an excellent representation of adult and sub-adult distributions. Briefly, the gear used 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. Estimates of net width are used in calculations of area swept. Samples were collected from a grid with spacing of 20 × 20 nautical miles, and tows are typically 30 min in duration.

Physical data

Physical data including temperature, salinity, and gear depth collected by Sea-Bird SBE 19 profiles from 60 cm bongo net sampling were used. If the Sea-Bird profiles were not available, physical data derived from conductivity, temperature, and depth (CTD) casts taken in nearby geographic locations and archived on the NOAA/EPIC website (http://www.epic.noaa.gov/epic/) were used.

Data analyses

Horizontal and vertical distributions of Greenland halibut early life stages were analyzed separately by gear type to eliminate differences in gear capture efficiency. The spatial and temporal limitations of data collection, coupled with the fact that Greenland halibut early life stages are comparatively rare in collections, necessitated pooling of data sets to some degree. The abundances of preflexion and flexion/postflexion larvae were expressed as the number of individuals caught per 10-m^2 surface area. The abundances of newly settled juveniles and age-1 individuals were standardized by calculating the number of individuals caught per 10 000 m^2 swept. We calculated mean abundance and length of Greenland halibut during different life stages by month (Table 3).

To examine the horizontal distribution patterns of preflexion larvae associated with environmental or other relevant factors, we used a generalized additive

Table 2. Data information of Greenland halibut from Bottom Trawl (BT) sampling in the Alaska Fisheries Science Center's Groundfish Assessment Program survey database. Information on tows from which Greenland halibut specimens were collected (positive tows) as well as those including the zero catches (total tows) is reported in the table.

Stage	Year	No. positive tows (No. total tows)	Date of positive tows	Date of total tows
Newly settled juveniles	1983	1 (353)	July 17	June 7–August 1
	1985	3 (358)	July 9–July 12	June 8–October 5
	1986	7 (354)	July 4–July 27	June 3–August 1
	1987	1 (360)	July 23	May 27–June 30
	1989	1 (373)	July 11	June 6–August 11
	1990	10 (371)	July 5–July 29	June 4–August 1
	1991	3 (372)	August 6– August 7	June 7–August 13
	1993	1 (375)	July 7	June 4–July 26
	2000	1 (372)	July 11	May 23–July 20
	2001	1 (400)	July 12	May 29–July 19
	2002	2 (375)	June 27–July 14	June 2–July 24
	2004	1 (375)	July 21	June 5–July 25
	2006	1 (405)	July 2	June 2–July 25
	2007	4 (376)	July 15–July 20	June 11–July 28
Age-1 fish	1982	25 (334)	June 17–July 30	May 29–August 1
	1983	8 (353)	July 16–August 1	June 7–August 1
	1984	6 (355)	August 11–August 15	June 9–August 19
	1985	7 (358)	July 14–September 10	June 8–October 15
	1986	14 (354)	July 4–July 28	June 3–August 1
	1987	22 (360)	July 20–July 28	May 27–July 30
	1988	20 (373)	July 13–July 28	June 4–July 30
	1989	22 (373)	July 11–August 2	June 6–August 11
	1990	19 (371)	July 13–August 1	June 4–August 1
	1991	54 (372)	July 17–August 13	June 7–August 13
	1992	18 (356)	July 11–August 3	June 5–August 3
	1993	18 (375)	July 20–July 24	June 4–July 26
	1994	6 (376)	July 21–July 22	June 3–July 26
	1995	4 (376)	July 11–July 21	June 4–July 22
	1996	11 (375)	July 24–July 26	June 8–July 28
	1997	12 (376)	July 12–July 24	June 7–July 26
	1998	17 (375)	July 24–July 29	June 9–July 29
	1999	8 (373)	July 7–July 9	May 23–July 11
	2000	10 (372)	July 7–July 13	May 23–July 20
	2001	18 (400)	July 11–July 19	May 29–July 19
	2002	24 (375)	June 27–June 21	June 2–July 24
	2003	21 (376)	July 14–July 19	June 2–July 22
	2004	12 (375)	July 18–July 24	June 6–July 25
	2005	2 (402)	July 15–July 18	June 3–July 22
	2006	2 (405)	July 19–July 20	June 2–July 25
	2007	12 (376)	July 18–July 25	June 11–July 28

model (GAM; Hastie and Tibshirani, 1990; Wood, 2006). GAM is a nonparametric and additive regression model that correlates a dependent variable with independent variable(s) through nonparametric smooth functions (Wood, 2006). By using GAM there is no need *a priori* to specify the functional form between the response variable and each explanatory variable (Wood, 2006). Furthermore, GAM allows us to predict the conditional effect of each explanatory

variable on the response variable. Thus, using GAM we can standardize for the uneven sampling design by including season and year effects (Wood, 2006).

We constructed a GAM model with a Gaussian family distribution and an identity link function that only used positive catch data for preflexion larvae. Including zero catches in the GAM would make the analysis nearly impossible due to the preponderance of zero data (see Table 1). Because we were ultimately

Table 3. The mean and standard deviation (SD) of Greenland halibut size (mm standard length or mm fork length) and abundance (number of individuals per 10 m^2 or number of individuals per 10 000 m$^{2)}$) from preflexion larvae to age-1.

Stage	Gear	Month	Mean size ± SD (mm)	Mean abundance ± SD of positive catch	Mean abundance ± SD of total catch	No. of positive tows (No. of total tows)
Preflexion larvae	60BON	3	11.9 ± 1.2 SL	35.13 ± 61.03	8.52 ± 33.01	16 (66)
	60BON	4	17.9 ± 1.9 SL	22.24 ± 22.57	6.13 ± 15.45	147 (533)
	60BON	5	20.4 ± 2.5 SL	14.33 ± 12.12	1.17 ± 5.21	40 (489)
Flexion/postflexion larvae	MT/MBT	7	35.3 ± 5.0 SL	0.51 ± 0.53	0.12 ± 0.34	59 (239)
	MT/MBT	8	38.0 ± 8.8 SL	0.35 ± 0.23	0.02 ± 0.10	4 (62)
	MT	9	56.6 ± 4.2 SL	1.52 ± 3.17	0.14 ± 0.97	5 (54)
Newly settled juveniles	BT	6	90 FL	0.21	0.00008 ± 0.00424	1 (2452)
	BT	7	88.4 ± 5.7 FL	0.31 ± 0.18	0.004 ± 0.040	32 (2495)
	BT	8	90 FL	0.213 ± 0.005	0.003 ± 0.027	3 (175)
Age-1 fish	BT	6	145.0 ± 7.0 FL	0.21 ± 0.02	0.00009 ± 0.00446	2 (4659)
	BT	7	195.1 ± 25.9 FL	0.89 ± 1.30	0.06 ± 0.43	347 (4589)
	BT	8	197.8 ± 21.7 FL	2.36 ± 2.89	0.41 ± 1.50	42 (239)
	BT	9	220.0 FL	0.98	0.07 ± 0.26	1 (14)

The units are number of individuals per 10 m^2 for abundance of preflexion and flexion/postflexion larvae, while the units are number of individuals per 10 000 m^2 for abundance of newly settled juveniles and age-1.

The units are mm standard length (SL) for size of preflexion and flexion/postflexion larvae, while the units are mm fork length (FL) for size of newly settled juveniles and age-1 fish.

60BON, 60 cm Bongo Nets; MBT, Modified Beam Trawl; MT, Methot Trawl; BT, Bottom Trawl.

interested in spatial distribution of Greenland halibut in the Bering Sea and not absolute estimates of abundance, the removal of zero catch in the analyses would still give a very clear indication of where preflexion larvae had occurred in previous sampling effort. A full model was constructed with the natural logarithm of preflexion larval abundance as a responsible variable. Independent variables in the full model included factor of year, day of year, sampling location (latitude, longitude), maximum gear depth of 60 cm bongo nets, water depth (isobath), each temperature and salinity at maximum gear depth, sea surface temperature, and sea surface salinity. A stepwise backwards selection process was used for determining the best-fit model by minimizing the model generalized cross-validation (GCV). The GCV is a measure of the predicted mean squared error of the fitted model. GAMs were implemented using the mgcv library in R (Wood, 2004; R Statistical Computing Software, http://www.r-project.org/).

Similar GAM analysis on the horizontal distribution of other stages including flexion/postflexion larvae, newly settled juveniles, and age-1 individuals could not be accomplished because of limited sample size (see Tables 1 and 2) and because it was during the larval phase that the sampling design was most variable and therefore in need of standardization. To describe the horizontal distribution of the other stages, we plotted descriptive maps using pooled data across years.

MOCNESS sampling was conducted over the continental slope in April from 1992 to 1994 with most tows occurring at night. To describe the vertical distribution of preflexion larval abundance and length with respect to depth, we limited the data analyses to MOCNESS sampling conducted in 1993. This year was chosen because MOCNESS sampling was conducted from the surface to the greatest depth represented (530 m depth) (cf. 200 and 300 m depth in 1992 and 1993, respectively), and it was also the year with the greatest number of tows (15 tows). To account for spatial variability of vertical distribution, we grouped the tows in three different locations, including the slope, Bering Canyon, and shelf regions. The slope consisted of seven tows within the geographic area bounded by 54.8°N, 168.4°W, and between the 2000 and 3000 m isobaths, Bering Canyon consisted of four tows in the geographic area bounded by 54.4°N, 166.4°W, and between the 500 m and 1000 m isobaths, and the shelf consisted of four tows in the region bounded by 55°N, 166°W, and <200 m. For the slope and Bering Canyon locations, the discrete depth strata of MOCNESS sampling were divided into five categories of water column depth: 0–100, 100–200, 200–300, 300–400, and 400–530 m. For the shelf location, the discrete depth strata were divided into two categories: 0–60 and 60–120 m. We then tested for differences in the vertical patterns of larval abundance within water depth strata, as well as

differences in larval length in separate analyses. An analysis of variance (ANOVA) and pairwise *post hoc* testing using a Tukey honestly significant difference (HSD) test were used to examine differences in larval abundance between water depth strata in each of the three locations. When the assumptions of normality and homoscedasticity were not satisfied, natural log transformation was used to normalize the data. For the vertical distribution of larval length with respect to water depth strata, a simple linear regression analysis was used to test for differences in mean larval size as function of depth in each three locations.

RESULTS

Horizontal preflexion larval distribution

Preflexion larvae were found over the outer continental shelf, the continental slope, and the basin of the EBS and eastern AI from March to May (Fig. 2). Preflexion larvae were mostly found in adjacent water along the eastern AI and over the basin and slope between Bering Canyon and Pribilof Canyon in the EBS. During the spring, it appears that some preflexion larvae drifted from the slope eastward across Bering Canyon onto the outer shelf. The highest abundances of Greenland halibut preflexion larvae were observed in March (Table 3). Preflexion larval lengths ranged from 8.8 to 24.4 mm [mean = 17.45 mm; standard deviation (SD) = 3.11 mm].

The best-fitted GAM explained 61.1% of the deviance in observed preflexion larval abundance. The GAM results indicated that the larval abundances were significantly influenced by sampling location (latitude and longitude), the day of year, maximum gear depth of 60 cm bongo nets, and water temperature and salinity at maximum gear depth (Figs 2 and 3). The effect of spatial position on larval abundance was the highest along the slope and over the basin (<1000 m isobath) between 54 and 56°N (Fig. 2). The timing of larval abundance peaked around the 120th day of the year, which corresponds to April 29 (Fig. 3a). The abundance of preflexion larvae tended to increase with increasing maximum towing depth (Fig. 3b). Notably, the highest larval abundance was found in tows that reached around 450 m of maximum towing depth. This result could be driven by the fact that (i) preflexion larvae are more abundant in deeper water than shallow water, and/or (ii) sampling using 60 cm bongo nets collects more preflexion larvae with increasing towing depth or sampling time if larvae are patchy. Larval abundance was positively and linearly correlated with the bottom water temperature (Fig. 3c). The effect of bottom water salinity was U-shaped, with the lowest concentration at 33.0 (Fig. 3d).

Vertical preflexion larval distribution

Preflexion larvae were collected throughout the water column to a depth of 530 m (Fig. 4). In April, the

Figure 2. Bubble plots show the observed horizontal distribution of Greenland halibut preflexion larvae (8.8–24.9 mm) during spring (March to May) collected from the 60 cm bongo net. The color image shows the conditional effect of station position on preflexion larval abundance estimated from the best-fit generalized additive model. Plus signs represent non-catch stations across years (1988–2005). Note that the patterns of GAM-predicted spatial effect and the observations are not necessarily expected to be similar, due to the effect of other variables included in the GAM analysis (see Fig. 3).
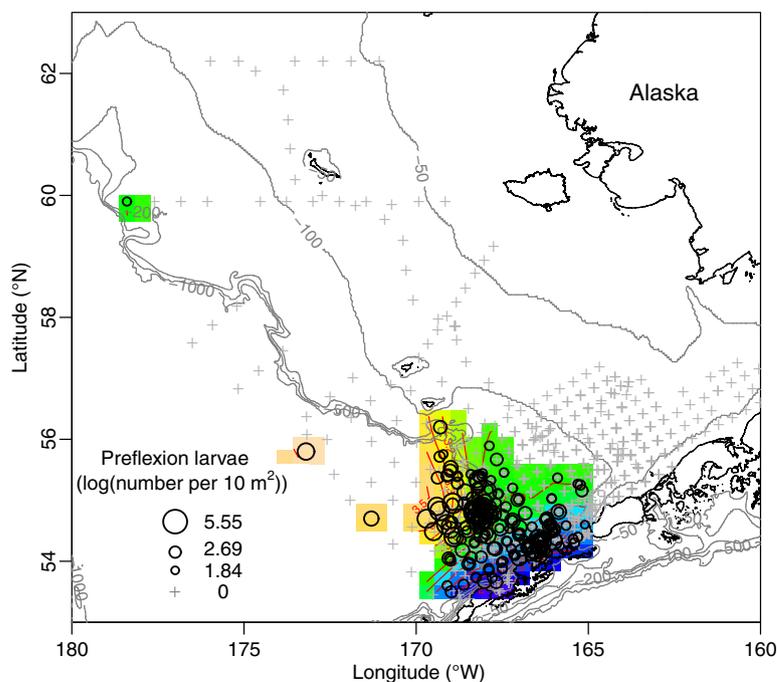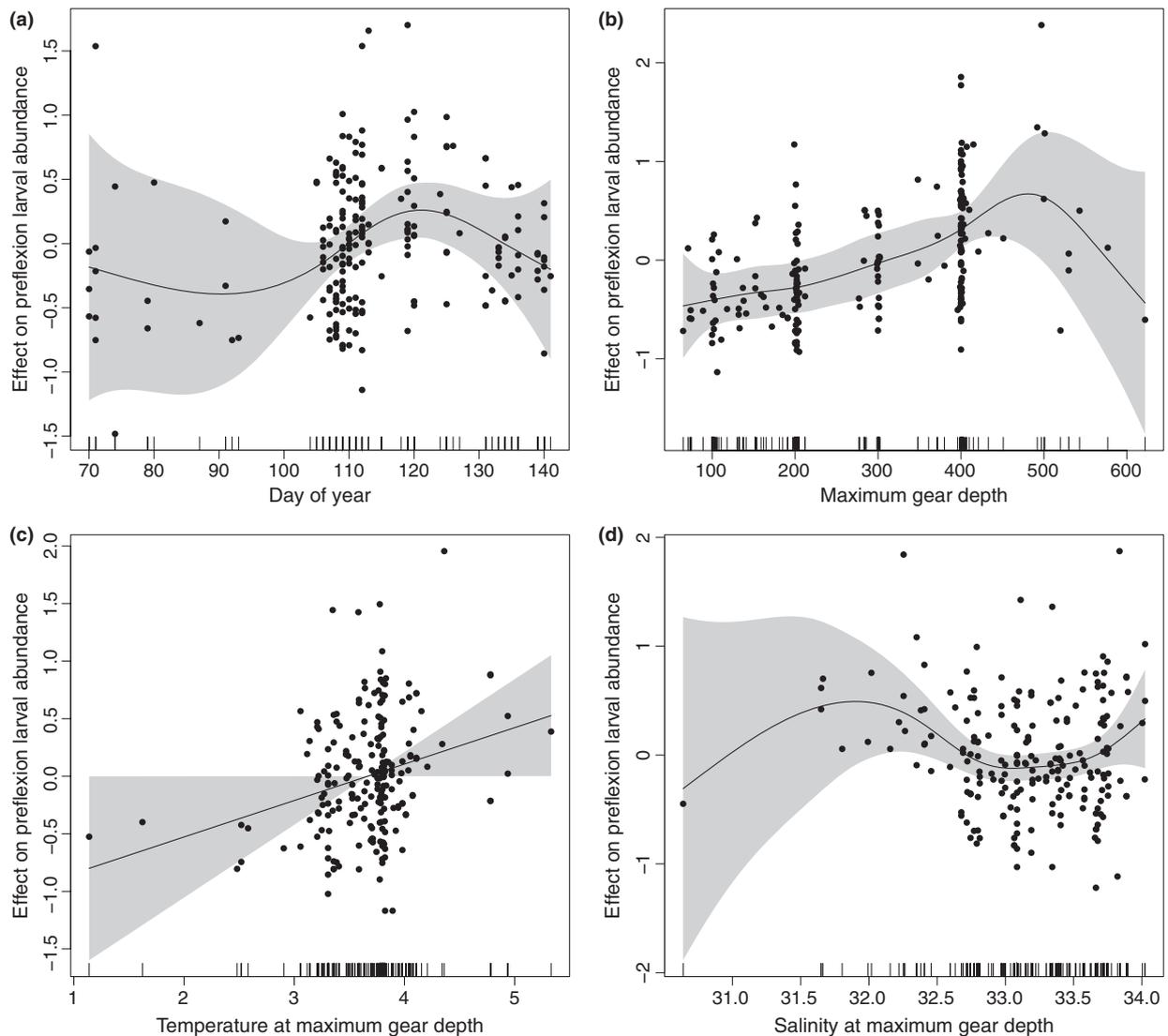
Figure 3. Effects of (a) day of year, (b) bottom water temperature, (c) maximum towing depth of 60 cm bongo net, and (d) bottom water salinity on preflexion larval abundance, estimated from the best-fitted generalized additive model. Shaded areas in each plot indicate 95% confidence intervals and dark circles in each plot indicate residuals.

length of the larvae varied from 12 to 22.4 mm. In April 1994, six preflexion larvae were found between 400 and 530 m depth strata. There was a significant difference in larval abundance between water depth strata in the slope location [ANOVA, $P < 0.05$, $F = 4.837$, and total degrees of freedom (df) = 26 (df = 22 in within groups and df = 4 between groups)], and mean larval abundance collected from both 0–100 and 300–400 m water depth strata were higher than other depth strata (Tukey HSD, $P < 0.05$). Statistically, mean larval abundance between 0 and 100 m and 300–400 m was not significantly different (Tukey HSD, $P < 0.05$). In the canyon location, preflexion

larvae were only collected in three depth strata including 0–100, 200–300, and 300–400 m, and no significant differences were detected. It was impossible to conduct any statistical analysis in the shelf location because Greenland halibut preflexion larvae were only found at one depth strata (0–60 m). In the analyses of vertical distribution with larval length, the linear regression in the slope location showed that preflexion larval size was significantly increased with decreasing water depth strata ($R^2 = 0.37$, $P < 0.0001$). This result indicates preflexion larval size increased by about 1 mm per decreasing water depth strata (100 m). In the canyon location, larval size was significantly

Figure 4. Vertical abundance and standard length distribution of Greenland halibut preflexion larvae collected in three different locations of April 1993. Bar chart shows mean and two standard errors.
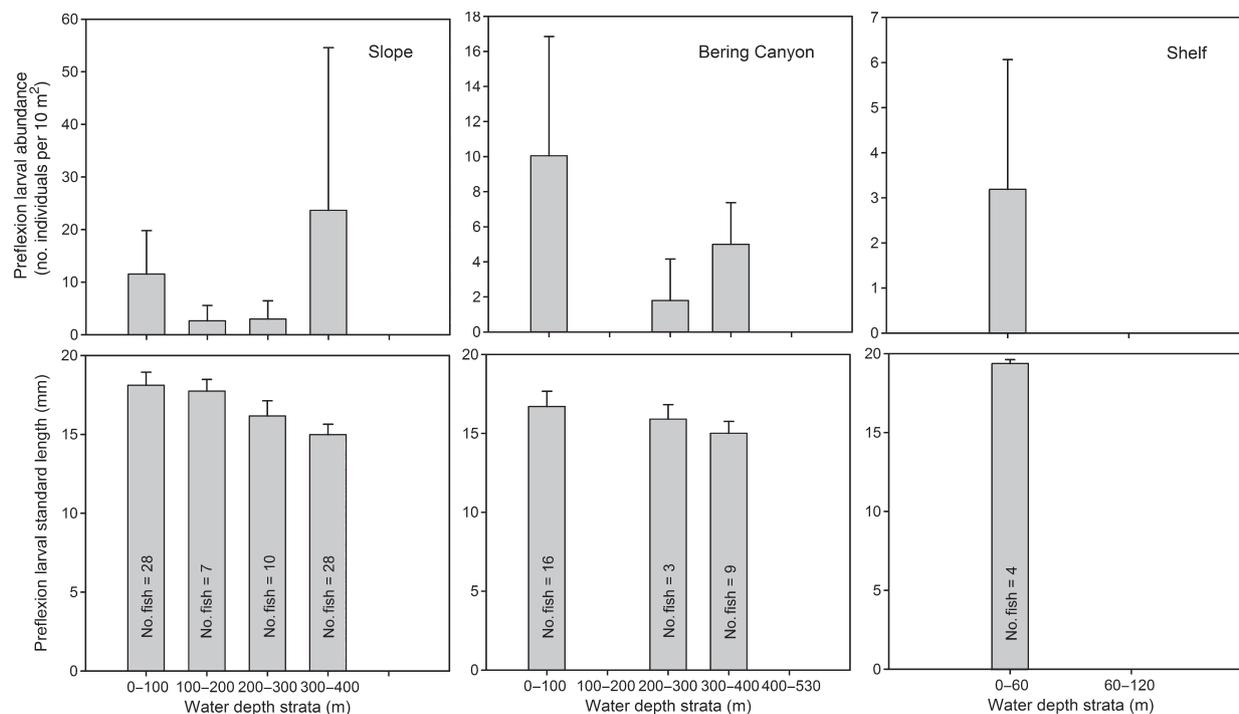
increased with decreasing water depth strata (R^2 = 0.20, P < 0.018). This result indicates preflexion larval size increased about 0.55 mm per decreasing water depth strata. Analyses were not conducted for the shelf location (see explanation above). The combined larval vertical distribution data from MOCNESS sampling may indicate that Greenland halibut eggs hatch deep in water below 530 m, and larvae then rise to shallower depths as they develop.

Horizontal flexion/postflexion larval distribution
Flexion/postflexion larvae were found over the middle and outer continental shelves between 56 and 58°N from July to September in MBT and MT samples (Fig. 5a). Some flexion/postflexion larvae were concentrated in Pribilof Canyon and near the Pribilof Islands, indicating that they likely crossed the continental slope through Pribilof Canyon. The length of these flexion/postflexion larvae ranged from 25 to 59.8 mm SL (mean = 35.86 mm, SD = 5.92 mm).

Horizontal newly settled juvenile distribution
Newly settled juveniles (60–90 mm FL) caught with BT gear were found over the middle shelf in the vicinity of St. Matthew Island between 58 and 62°N during summer (late June to early August; Fig. 5b). The smallest length of newly settled juveniles was
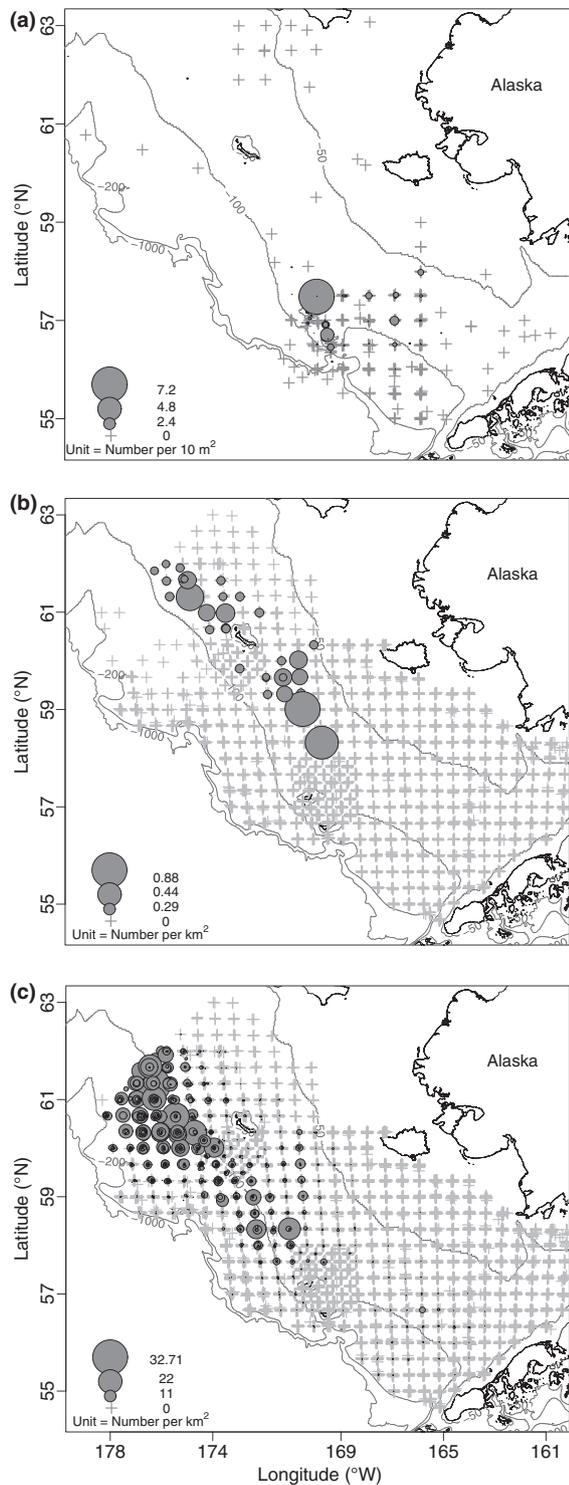
60 mm SL, occurring in late July. The mean length of newly settled juveniles was 88.38 mm FL with 5.53 mm standard deviation. No newly settled juveniles were collected south of the Pribilof Islands.

Horizontal age-1 distribution
Age-1 fish (length size class: 140–220 mm FL) were mostly concentrated over the outer shelf, although they also appeared over the middle shelf (Fig. 5c). The mean length of age-1 fish was 195.2 mm FL with 25.7 mm standard deviation. Greenland halibut age-1 fish moved to deeper water and westward compared to newly settled juveniles.

DISCUSSION

Prior to our study, little was known about the spatial distribution and connectivity between spawning and potential nursery locations during the ontogeny of Greenland halibut in the Bering Sea. This information is critical because early life drift pathways can affect settlement success and survival of flatfish (Van der Veer *et al.*, 1998; Wilderbuer *et al.*, 2002; Bailey *et al.*, 2005). Although the data used in our analysis were not originally meant to survey Greenland halibut early life stages, and therefore are sparse and variable, the information that we have derived has still proved very

Figure 5. Horizontal distribution of (a) flexion/postflexion larvae (25.0–59.9 mm) during summer (July to September) collected from the modified beam trawl and Methot trawl sampling; (b) Newly settled juveniles (<100 mm) during summer (June to August) collected from bottom trawl sampling; (c) Age-1 (140–220 mm) during summer (June to September) from bottom trawls. Bubbles in (a) indicate number of individuals per 10 m² and bubbles in both (b) and (c) indicate number of individuals per 10 000 m². Plus signs in each plot represent non-catch stations across years.

1000 km over a 6-month period with vertical excursion of over 500 m. Over this period, Greenland halibut occupy a variety of habitats for spawning, nursery, and settlement, and appear to utilize large swaths of the EBS shelf as nursery areas for immature stages. Based on our findings, we discuss the most salient characteristics of Greenland halibut early life drift as they complete their journey from spawning to settlement locations. We also provide a schematic representation of horizontal and vertical distribution of Greenland halibut, and of connectivity between preflexion larval stage and age-1 fish (Fig. 6).

Spawning location, depth, and timing (early larval distribution)

The spawning time and locations of Greenland halibut in the Bering Sea are still poorly defined, and what little is known is based on studies that are several decades old. Musienko (1970) reported that spawning occurs on the continental slope from St. Matthew Island to Cape Navarin between October and December, but Bulatov (1983) noted spawning along the continental slope off Unimak Pass during winter from February to March. Alton *et al.* (1988) inferred that Greenland halibut mainly spawns either over the slope area between Unimak Pass and the Pribilof Islands, or in the AI, based on trawl surveys.

Based on our retrospective analysis of larval distributions, we suggest that spawning could occur in adjacent water along the eastern AI during winter, as evidenced by early-stage larvae collected along the easternmost AI. Spawning could also occur along the south EBS slope during winter given the presence of early-stage larvae along the Bering Sea slope between Bering Canyon and Pribilof Canyon. Other evidence comes from a recent cruise in February 2008 (Sohn, 2009), which noted 111 Greenland halibut eggs in both the basin and slope along the eastern AI and along the southern Bering Sea slope between Bering Canyon and Pribilof Canyon. Available data indicate that Greenland halibut eggs hatch deep in the water,
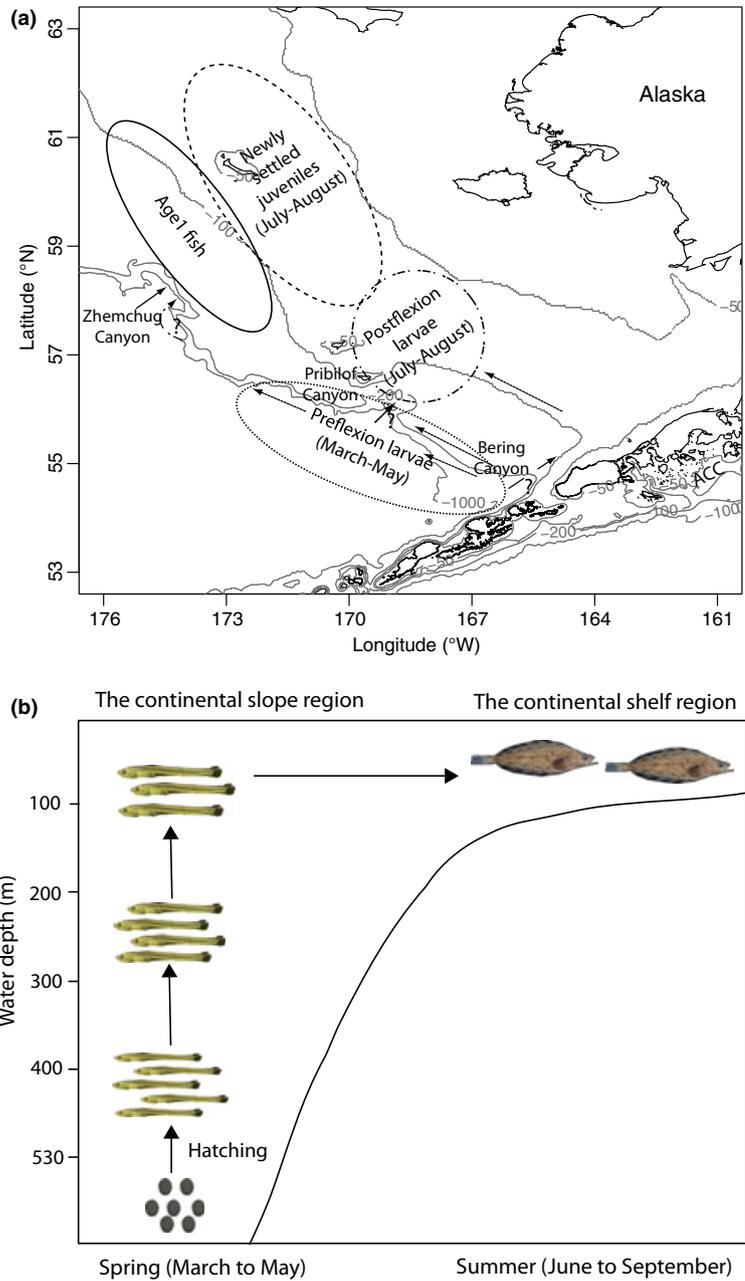
valuable. Our results indicate that Greenland halibut larvae have a long pelagic duration and are subject to extended drift pathways before settlement. The distance of probable drift to settlement location (near St. Matthew Island) in the Bering Sea is approximately

Figure 6. Schematic representations of Greenland halibut distribution and connectivity from preflexion larvae to age-1. (a) Horizontal distributions through different life history stages (dot circle: preflexion larvae, dot-dash circle: flexion/postflexion larvae, dash circle: newly settled juveniles, bold circle: age-1, dot arrows: possible preflexion larval transport routes, dot-dash arrows: possible postflexion larvae transport of movement routes (b) Vertical shifts also occurred with development. Knowledge gasp, particularly with regard to cross-shelf transport locations are indentified with question marks.

below 530 m, and then larvae rise to shallower depths as they develop and become more buoyant. Given those results, we may hypothesize the existence of three spawning scenarios in the EBS and eastern AI. First, that there is a single spawning group occurring in both the EBS and eastern AI slope, which spawns synchronously during the winter. A second possibility is that there is a single spawning group that begins to spawn from the eastern edge of the AI intermittently during migration from the AI to the EBS slope during

winter. Finally, there could be different spawning groups in each region with different spawning schedules.

With regard to spawning time, we found that the smallest Greenland halibut larva (8.8 mm SL) was collected in March. In the Atlantic, Stene *et al.* (1999) reported that egg development time of Greenland halibut was 53 days at 4°C after fertilization, and hatched larval size was approximately 6 mm. If we assume the hatching size and temperature in

the Pacific to be similar to the Atlantic, the smallest larvae in our study could have been spawned as early as December or January. Furthermore, eggs were collected in February 2008 in the same area (near Bering Canyon) as preflexion larvae (Sohn, 2009). Most eggs were in the late stages of development, indicating that spawning had likely commenced 1–2 months earlier.

Transport mechanisms

Slope currents, submarine canyons, predominant flow fields, and baroclinic eddies are important features to consider when studying transport of Greenland halibut during their early life stages.

Slope currents

The patterns of horizontal and vertical distribution of Greenland halibut preflexion larvae suggest that their dispersal and transport could be physically influenced by both the ANSC and the BSC. The ANSC may transport preflexion larvae eastward, and the BSC northward. In particular, the BSC in the shallower portion of the water column could be directly associated with dispersal of Greenland halibut preflexion larvae, as along the slope these were more found in greater numbers in the upper water column based on results of preflexion larval vertical distribution. Our results indicate ontogenetic changes in vertical distribution of Greenland halibut preflexion larvae; the largest larvae were mostly abundant at <100 m. Changes of larval vertical distribution could facilitate their transport and slope-shelf connectivity by the BSC. This assertion is consistent with the findings of Stabeno *et al.* (1999), who reported that advection and dynamics along the slope and slope-shelf exchange are processes influenced by the structure of the BSC.

Submarine canyons

The spatial distribution of preflexion larvae during summer indicates that some larvae are transported from the continental slope to the outer shelf via bathymetric steering of currents through the large canyons that punctuate the continental shelf edge. In the western Gulf of Alaska, Bailey *et al.* (2008) identified canyons and sea valleys as potential avenues of transport across the shelf edge for deepwater flatfishes there, and similar mechanisms are hypothesized here for slope-spawning species in the EBS. Our data show that the most preflexion Greenland halibut larvae were found over the basin and slope between Bering Canyon and Pribilof Canyon, along the eastern AI and Bering Sea slope in spring, and over the outer shelf near Bering Canyon. It is likely that larvae cross from the slope to the shelf via flows through Bering

and other submarine canyons. Those preflexion larvae that do not cross to the shelf through Bering Canyon may be swept northwards towards Pribilof or Zhemchug Canyons. Bering and Pribilof Canyons are known to be important conduits of slope-shelf exchange (Stabeno *et al.*, 1999, 2008; Mizobata and Saitoh, 2004), and we propose that these canyons also serve as important conduits for ingress of slope-spawned larvae, connecting offshore spawning grounds with important nursery areas over the continental shelf.

Cross-shelf flow

Once over the continental shelf, Greenland halibut larvae are advected eastward and then northward towards settlement areas over the middle shelf. Evidence from satellite-tracked drifters deployed by the Fisheries Oceanography Coordinated Investigations program at the AFSC over 15 years (D.S. Duffy-Anderson, personal observation) suggest weak, eastward-flowing cross-shelf currents that are consistent with this observation. Also, an individual-based modeling study shows eastward transport of snow crab (*Chionoecetes opilio*) larvae (Parada *et al.*, 2010). Greenland halibut larvae entrained in the sluggish cross-shelf flow maintain a slow but persistent advection eastward. It has been hypothesized that cross-shelf flow is maintained by variations in baroclinicity due to melting sea ice in the spring and temperature gradients (vertical, horizontal) in summer (Stabeno *et al.*, 2007). Further, mean wind direction over the shelf is well-characterized, and it is known that wind is primarily from the northeast from December to March ($\sim$2 m s^{-1}), which could propel near-surface larvae closer to juvenile settling areas (Stabeno *et al.*, 2007). Finally, the weak cross-shelf currents characteristic of spring and summer become somewhat stronger in the fall (Stabeno *et al.*, 2007), which could serve to enhance advection of those remaining flexion/postflexion larvae to the middle shelf before the onset of winter.

Baroclinic eddies

Meso-scale eddies that propagate along the shelf break are common features of the BSC and the southeast Bering Sea basin (Stabeno *et al.*, 1999), and there have been several studies on the role of eddies relative to the ecosystem over the shelf. Mizobata and Saitoh (2004) demonstrated that primary productivity over the outer shelf was correlated with the BSC eddy field, and Mizobata *et al.* (2008) showed that there was a 50–70% increase in on-shelf flux associated with the propagation of eddies in the vicinity of the Pribilof Islands. Given the significant degree of on-shelf flux provided by eddy circulation, it seems likely that larval

entrainment in meso-scale eddies is a possible mechanism of dispersal (Stabeno and Meurs, 1999). In the Gulf of Alaska, it has also been suggested that eddies are physical mechanisms for cross-shelf transport (Bailey *et al.*, 2008). However, it should be noted that because the formation and propagation of eddies are not consistent in space and time, they may have only an episodic role as a mechanism of connectivity for Greenland halibut early life stages.

Settlement, newly settled juveniles and age-1 distributions

Greenland halibut require specific habitat for settling and prefer different environmental conditions for their ontogenetic stages after settlement. The smallest newly settled juvenile in our data set (60 mm FL) was on the middle shelf near St. Matthew Island. Our observations indicate that this is a preferred settling location. It is usually surrounded by a cold water pool, with an average summer bottom temperature <2°C. Sediment is characterized by a mixture of mud and fine sand (McConnaughey and Smith, 2000; Ciannelli and Bailey, 2005), which may be a preferred habitat for settling Greenland halibut juveniles.

The dominant distribution of Greenland halibut age-1 over the outer shelf indicates that they move into deeper water with increasing age (or size). Our results confirmed observations of size-related variability of Greenland halibut spatial distribution between newly settled and age-1 juveniles. In the EBS, some studies have shown that Greenland halibut spatial distribution and abundance after settlement is associated with environmental variables such as depth, temperature, and sediment type (Swartzman *et al.*, 1992; McConnaughey and Smith, 2000). Swartzman *et al.* (1992) assumed that Greenland halibut distribution show a change associated with increasing size accompanying increased depth. McConnaughey and Smith (2000) found that the distribution and abundance of Greenland halibut larger than 141 mm were only weakly associated with sediment texture.

Future work

In this study there are certain limitations to the data. We could not use historical egg data archived at the AFSC due to the confounding effects of egg-size overlap between Greenland halibut and Pacific halibut (*Hippoglossus stenolepis*). Currently, efforts are underway to resolve this problem and these data should be available in the near future. Furthermore, sampling conducted at the AFSC often did not extend over the entire Bering Sea slope and shelf. In particular, there are extensive gaps in the coverage throughout the western portion of the AI and northern portion of the

EBS slope region. Adult distributions of Greenland halibut are known from catch by trawl, longline, and pot gears occurring along all of the AI and EBS (Ianelli *et al.*, 2007). The limited data that are available for early life history stages indicate that Greenland halibut eggs and preflexion larvae are predominantly found in the eastern AI and southern EBS slope. However, eggs and preflexion larvae could be found in other locations if the sampling area was extended. Timing of sampling is also critical. Preliminary data derived from a research cruise conducted by the AFSC in February 2008 suggest that Greenland halibut eggs were mostly at late stages of development (Sohn, 2009). To identify spawning location and timing accurately, samples of earlier stage eggs are needed, which requires the addition of early sampling periods in December and January.

It is likely that variations in dispersal pathways induced by changes in the BSC direction and strength play an important role in Greenland halibut recruitment. Greenland halibut have a very prolonged pelagic larval duration and rather strict habitat requirements during the settling phase; this, coupled with the fact that in the EBS water circulation and hydrography are inter-annually variable, makes it very likely that hydrographic and meteorological forcing influence Greenland halibut recruitment. For example, Wilderbuer *et al.* (2002) found, using an ocean surface current simulation model, above-average flatfish recruitment coincided with decadal scale changes in wind-driven advection of flatfish larvae to juvenile nursery grounds in the Bering Sea. Furthermore, using a depth-discrete model, Lanksbury *et al.* (2007) reported that differences in depth distribution affected dispersal trajectories of northern rock sole (*Lepidopsetta polysystra*) in the Bering Sea. These studies suggest that broad-scale shifts in climatological forcing factors and their associated changes in oceanographic processes affect the production, abundance, distribution, and dispersal of flatfishes. Future research efforts might include model simulations to identify potential drift pathways, which could then be compared with the patterns of larval distribution presented here.

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