AN ABSTRACT OF THE THESIS OF

Dongwha Sohn for the degree of Master of Science in Oceanography presented on June 18, 2009.
Title: Ecology of Greenland Halibut (*Reinhardtius hippoglossoides*) during the Early Life Stages in the Eastern Bering Sea and Aleutian Islands.

Abstract approved:

_____
Lorenzo Ciannelli

Greenland halibut (*Reinhardtius hippoglossoides*) have decreased in the eastern Bering Sea and Aleutian Islands since the 1970s. The reasons behind the poor recruitment are unknown, and important knowledge gaps of the ecology of the early life stages have been identified. The objectives of thesis research were (1) to examine geographic distributions and drift pathways from egg to settled juveniles (age-1) by a retrospective analysis in order to understand connectivity and different habitat utilization through ontogeny, (2) to describe vertical egg distribution using a one-dimensional model in order to understand patterns of vertical egg distribution and their association with water column hydrography and currents through the egg developmental stages, (3) to investigate diet of Greenland halibut larvae and pelagic juveniles diet using stomach content in order to understand foraging behavior, and (4) to examine otolith microstructure of Greenland halibut larvae and pelagic juveniles using otolith analysis in order to establish aging guidelines and other features related to bio-ecological changes (e.g. hatching, mouth opening etc.). The results of the thesis indicate that Greenland halibut early life stages from eggs to newly settled juveniles

have a long duration in the plankton and are subject to extended drift pathways. In the eastern Bering Sea and Aleutian Islands, Greenland halibut spawn along the continental slope between Akun Island and the Pribilof Islands, and between Umnak Island and Akun Island in the Aleutian Islands. Spawning most likely occurs in winter from December to January. At-sea observations of egg density ranged from 1023.5 kg/m^3 to 1027.8 kg/m^3. Based on modeling results, variability of egg density would affect vertical egg distributions. Eggs were found between 50 m and 400 m, in particular, most eggs were concentrated between 200 m and 300 m. Hatching probably occurs in deep water, below 500 m, and larvae rapidly rise in the water column to depths above 45 m. The mechanisms of slope-shelf connectivity appear to be related to the Bering Slope Current in the vicinity of both Bering and Pribilof Canyons. Some larvae cross to the continental shelf from March to May through Bering Canyon, while others are transported through Pribilof Canyon. Pelagic juveniles are mostly found around the Pribilof Islands over the middle shelf (50 m - 100 m isobaths) in July, and settling likely occurs during late summer on the middle shelf near St. Matthew Island. However, given that age-1 juveniles were primarily found on the outer shelf, juvenile Greenland halibut appear to actively move to deeper water, presumably selecting appropriate habitat based on a suite of environmental factors after settlement. Greenland halibut larvae and pelagic juveniles are vigorous carnivores and their feeding habits change as they grow. The clearly defined rings observed in the otoliths might be biological transition marks. This study shows that Greenland halibut have extensive horizontal ontogenetic migrations in the Bering Sea,

and utilize a range of geographic areas over the Bering slope and shelf at different life history stages. 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 and by size variations of suitable nursery locations.

Ecology of Greenland Halibut (*Reinhardtius hippoglossoides*) during the Early Life
Stages in the Eastern Bering Sea and Aleutian Islands

by
Dongwha Sohn

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented June 18, 2009
Commencement June 2010

Master of Science thesis of <u>Dongwha Sohn</u> presented on <u>June 18, 2009.</u>

APPROVED:

_____

Major Professor, representing Oceanography

_____

Dean of the College of Oceanic and Atmospheric Sciences

_____

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

_____
Dongwha Sohn, Author

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

LIST OF FIGURES

LIST OF FIGURES (Continued)

LIST OF TABLES

Ecology of Greenland Halibut (*Reinhardtius hippoglossoides*) during the Early Life Stages in the Eastern Bering Sea and Aleutian Islands

CHAPTER 1: INTRODUCTION

Greenland halibut

Greenland halibut (*Reinhardtius hippoglossoides,* Walbum 1792) is a member of the Pleuronectidae family (the right eye flounders) of the Pleuronectiformes (the flatfishes) order. Greenland halibut has a circumpolar distribution, occurring in the North Pacific, Arctic, and North Atlantic Oceans (Alton *et al*. 1988, Chiperzak *et al*. 1995; Fig. 1). The species is broadly distributed from 20 to 2200 m within sea temperatures ranging from -2.1 to 10 °C (Jensen 1935, Fedorov 1971, Templeman 1973 cited in Alton *et al*. 1988, Boje and Hareide 1993, Jørgensen 1998). 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, generally deeper than 500 m depth, from late winter to early spring (Jensen 1935, Fedorov 1971, Bulatov 1983, Godo and Hang 1989, Albert *et al*. 2001a), but year round spawning has also been hypothesized in the Barents and Norwegian Seas (Fedorov 1971).

Although many aspects of Greenland halibut life history have been widely studied in the Atlantic Ocean, little is known about the ecology and biology of the populations in the Pacific Ocean. This is especially true for early life stages. From studies in the Atlantic Ocean, it is known that Greenland halibut has a protracted pelagic phase, during which eggs and larvae undergo dramatic changes in buoyancy, and vertical and horizontal location (Godø and Haug 1989, Stene *et al*. 1999).
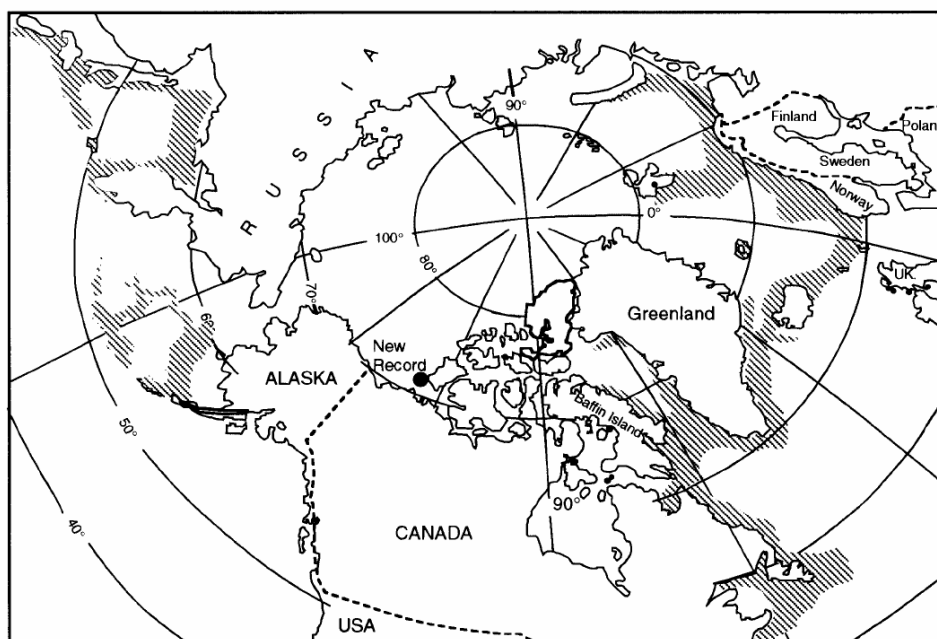
Figure 1. Geographical distribution of Greenland halibut, *Reinhardtius hippoglossoides* (from Chiperzak *et al*. 1995).

Greenland halibut in the Atlantic are known to have very large eggs (3.8 - 4.7 mm diameter) with mesopelagic distributions (600 m - 1000 m depth; Jensen 1935, Smidt 1969, Godo and Hang 1989, Stene *et al*. 1999). After fertilization in the laboratory, the density of artificially spawned eggs ranges from 1024.69 kg/m^3 to 1026.91 kg/m^3 and increases with developmental stage (Stene *et al*. 1999). Eggs from the Barents Sea hatch around 50 days at ca. 2 °C; eggs were between 4 °C and 5 °C for the first 5 days and then eggs were transferred to ca. 2 °C (Stene *et al*. 1999). Newly hatched larvae reared from eggs are about 6 mm (Stene *et al*. 1999). Larvae are epi- (surface to 200 m depth) and mesopelagic (between 200 – 1000 m depth), but they are found progressively shallower in the water column as they develop (Jensen 1935). They have a long pelagic period before settlement and pelagic individuals up to 70 mm length are found in the water column west of Greenland (Jensen 1935). Larvae (30 mm – 68 mm) mostly feed on calanoid copepods (Haug *et al*. 1989) in the eastern Norwegian and Barents Seas. Although certain life history characteristics may be similar among ecosystems, we cannot assume a conclusive understanding of Greenland halibut life history in the Pacific Ocean based on investigations in the Atlantic Ocean (Bailey *et al*. 2005).

Stock status and management

In the Pacific Ocean, Greenland halibut is found around the Chukchi Peninsula (Federov, 1971), in the Okhotsk Sea (Shuntov 1965, Nikolenko 1998), in the eastern Bering Sea and in the Aleutian Islands (Musienko 1970, Waldron 1981, D'yakov 1982, Bulatov 1983, Alton *et a*l. 1988). Also, the species rarely occurs off British Columbia (Westrheim and Pletcher, 1966), in California (Schott, 1966), and around Baja

California of Mexico (Hubbs and Wilimovsky, 1964). Among occurring regions, Greenland halibut is the most abundant in the eastern Bering Sea (EBS) and Aleutian Islands (AI; Alton *et al*. 1988, Ianelli *et al*. 2007), where they are a commercially important flatfish species (Ianelli *et al*. 2007). However, due to population declines beginning in the late 1970s, the current 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 2,000 to 3,000 tons annually (Ianelli *et al*. 2007). Other flatfish stocks (e.g., arrowtooth flounder, *Atheresthes stomias*) have increased substantially over the same period in the EBS and AI, but Greenland halibut spawning stock biomass has decreased less than 200,000 tons and recruitment has declined to less than 10 millions since 1979 (Fig. 2).

Annual catch limits for the species are set and strictly enforced by the National Marine Fisheries Service (NMFS) of National Oceanic and Atmospheric Administration (NOAA). The data for in-season management is collected by NMFS certified scientific observers, and the actual catch limit recommendations are developed through the North Pacific Fishery Management Council process. Prior to 1985, Greenland halibut and arrowtooth flounder catch limits were combined (Ianelli and Wilderbuer 1995, Ianelli *et al*. 2007). Given recent low catch limits, NMFS often keeps directed Greenland halibut fisheries closed (e.g., the directed Greenland halibut trawl fishery has remained closed since 1996; Ianelli *et al*. 2007). These closures are to ensure that incidental catches of Greenland halibut from other directed fisheries remain below the overall catch limit. Even with reduced catch limits, Greenland halibut spawning biomass remains low due to low recruitment (Ianelli *et al*. 2007).
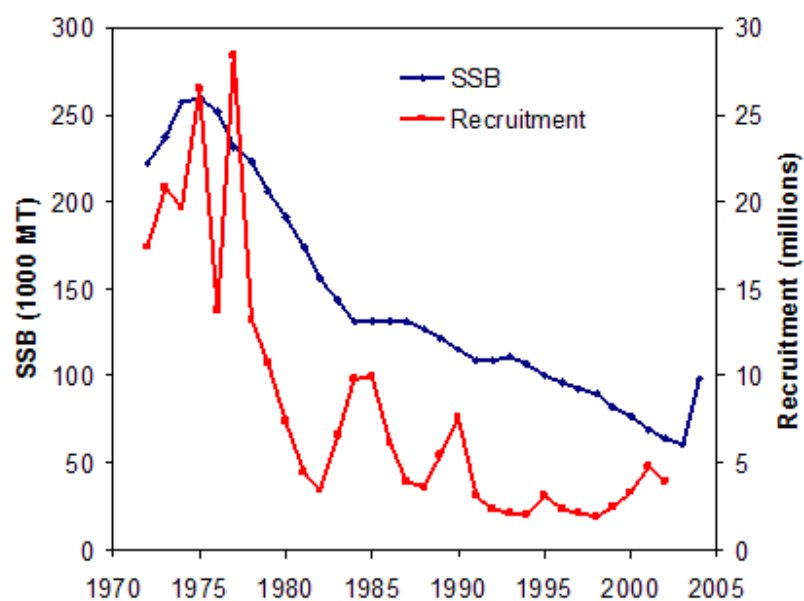
Figure 2. Status of spawning stock biomass (SSB) and recruitment of Greenland halibut in the eastern Bering Sea and Aleutian Islands (courtsey James Ianelli).

Although there are signs of improved recruitment in recent years (2007-2008), the reasons behind the poor recruitment over the previous 15 years are unknown, and important knowledge gaps during the early life stages have been identified (Alton *et al*. 1988, Ianelli *et al*. 2007).

Recruitment theories and variation generating factors

Understanding the ecology and biology of marine fish species during the early life stages, particularly the egg and larval stages, is very important since their survival determines year class strength and recruitment (Hjort 1914, Cushing 1975, Lasker 1975, Hunter 1984, Leggett and DeBlois 1994). Mortality during fish early life stages is often determined by combination of physical (i.e. temperature, salinity, turbulence, and currents) and biological factors (i.e. starvation, predation/cannibalism) (Hjort 1914, Cushing 1975, Lasker 1975, Houde 1987, Parrish *et al*. 1983, Fargo 1994, Sinclair 1988, Miller *et al*. 1988, Leggett and DeBloise 1994). Hjort (1914) proposed that mortality or survival rate during the fish larval stage is influenced by not only starvation ("critical period hypothesis"), but also by transport via oceanic currents to unfavorable nursery areas ("offshore transport hypothesis"). Historically, the first hypothesis has been of greater focus than the second hypothesis, but more recently, however, the second hypothesis has received substantial attention. Numerous studies on marine fish have shown that larval fish advection by oceanic currents are one of the critical processes in the variation of recruitment and the determination of population structure (Parrish *et al*. 1981, Nielsen et al 1998, Van der Veer *et al.* 1998, Wilderbuer *et al*. 2002).

In flatfish, dispersal and drift pathways associated with the prevailing direction of ocean currents have been also shown to play a key role in recruitment and year-class strength (Fargo 1994, Van der Veer *et al*. 1998, Wilderbuer *et al*. 2002, Bailey *et al*. 2005). Wilderbuer *et al*. (2002) reported that flatfish recruitment strength was related to broad-scale wind patterns and associated dispersal of early life history stages in the EBS. 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, in order to reach suitable nursery locations in shallower water (Bailey *et al*. 2008). These nursery locations can be distant from offshore spawning grounds, therefore, it is essential to characterize drift pathways during early life stages to gain insight into Greenland halibut recruitment dynamics (Haug *et al*. 1989, Albert *et al*. 2001b).

Information on fish egg density is vital to describe vertical egg distribution. In turn, egg vertical distribution is needed to model horizontal transport of eggs and larvae (Sundby 1991, Ådlandskik *et al*. 2001, Boyra *et al*. 2003). Horizontal advection of eggs in the water can be strongly depended on their vertical distribution, particularly if there is a reverse of the flow through the water column (Cushing 1982, Coombs *et al.* 1990). Therefore, knowledge of vertical egg distribution is essential to better understanding egg and larval drift pathways. Moreover, a better knowledge of vertical egg distribution can be used to achieve a more precise and efficient egg sampling strategy.

Given starvation and predation induced mortality during fish early life stages, it is important to understand foraging behaviors and growth (Mayer and Wahl 1997).

Food serves an essential function for larval growth and abundance, as does temperature. Larvae must feed on adequate prey after yolk sac absorption for their survival. At the first feeding, food condition (quality and quantity) in time and space affect directly larval survival and growth. When food is not abundant, it leads to starvation or slow growth. Larval size and growth are also associated with resistance to starvation and predation; bigger size and faster growth are better to avoid predators and to catch prey (Houde 1989, Miller *et al*. 1988). The growth of larval fish can be determined by counting daily rings on otoliths of fish from the field (Campana & Neilson 1985). Feeding habit and ecology change with ontogeny due to higher energy requirements of larger fish. Identifying prey items of species is the basic step to understand feeding habit and growth related to survival.

Not only does the duration of the pelagic stages affect recruitment variation, but the duration of the settled juvenile phase has significant effects as well (Miller *et al*. 1991, Van der Veer and Leggett 2005). Flatfish transition their body from being bilaterally symmetrical to a pronounced asymmetry in the juvenile form. After the metamorphosis phase, flatfish require settlement in suitable benthic habitat for the juvenile stage. Mortality in the early settled stages on the bottom is particularly high due to settlement in unsuitable time and space (Gibson 1994, Bailey 2005, Van der Veer and Leggett 2005).

Study objectives

To improve understanding of the ecology and biology of Greenland halibut including age and growth, trophic ecology, and behavior during early life stages in the EBS and AI, I focused my research on the following objectives:

(1) To examine geographic distributions and drift pathways from egg to settled juveniles (age-1) by a retrospective analysis in order to understand connectivity and different habitat utilization through ontogeny.

(2) To describe vertical egg distribution using a one-dimensional model in order to understand patterns of vertical egg distribution and their association with water column hydrography and currents through the egg developmental stages

(3) To investigate diet of Greenland halibut larvae and pelagic juveniles diet using stomach content in order to understand foraging behavior.

(4) To examine otolith microstructure of Greenland halibut larvae and pelagic juveniles using otolith analysis in order to establish aging guidelines and other features related to bio-ecological changes (e.g. hatching, mouth opening etc.).

CHAPTER 2: MATERIALS AND METHODS

Study area

This study took place in the EBS and AI regions of the Bering Sea (Fig. 3). The Bering Sea is divided into the basin and western and eastern shelf regions. The EBS shelf is partitioned into three domains by bathymetric and hydrographic features; the inner or coastal domain, less than 50 m isobath, the middle domain, between the 50 m and 100 m isobaths, and the outer domain, between the 100 m 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 Bering Slope Current (BSC), which parallel the continental shelf edge (Stabeno *et al.* 1999). 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 1996, Stabeno *et al.* 1999, Lanksbury *et al.* 2007).
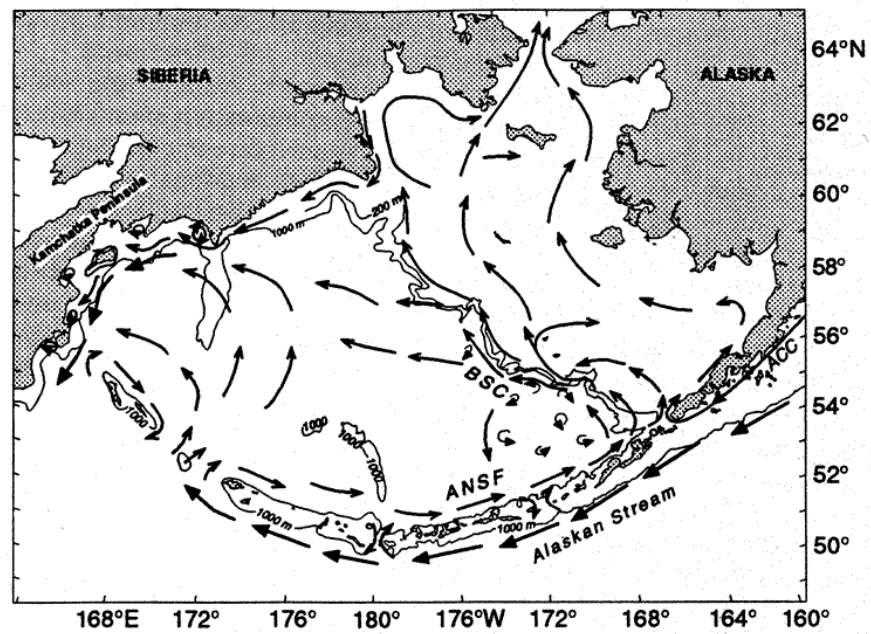
Figure 3. A schematic of flow on the Bering Sea in the upper 40 m of water column (Modified from Stabeno *et al*. 1999). BSC: Bering Slope Current, ANSF: Aleutian North Slope Flow, and ACC: Alaska Coastal Current.

Data

Research survey data collected by the NOAA Fisheries Alaska Fisheries Science Center (AFSC) were utilized to study the distribution, feeding habits, and otolith microstructure of Greenland halibut during early life stages from eggs to age-1 in the EBS and AI.

Collection of eggs

In preserved egg samples one of the primary characteristics to identify Greenand halibut eggs is their size (3.4 - 3.84 mm). However, in the Bering Sea historical egg data could not be analyzed due to an overlap in egg size between Pacific (3.12 - 3.4 mm) and Greenland halibut, which results in uncertainty of egg species classification. However, more conclusive taxonomic information is available for recent catches. In February, 2008 (45 tows) and 2009 (30 tows), Greenland halibut eggs were collected in the EBS using a paired, 60 cm Bongo net (60BON; 505 or 333 μm mesh) fitted with flowmeters during ichthyoplankton surveys of the AFSC (Table 1). Nets were towed obliquely from a maximum of 600 m to 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. Eggs were sorted directly from the net 2 side of the paired net, measured for diameter (mm), and staged for development according to a 20-stage scheme adapted from Blood *et al*. (1994; Table 2). Conductivity Temperature Depth (CTD) casts were also conducted at selected stations. Depth-discrete ichthyoplankton samples were collected using a 1 m^2 Multiple Opening and Closing Net and Environmental Sampling System (MOCNESS; Wiebe *et al*. 1976). Nine MOCNESS tows were conducted at selected stations over

the continental slope in 2008, but no tows were performed in 2009 due to rough weather. MOCNESS tows were to approximately 500 m maximum depth.

Collection of larvae

Historical Greenland halibut larval data were available from archival records in the Ichthyoplankton Database (ICHBASE) housed at the AFSC. Larvae were 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 300 m, 400 m, 500 m, or 600 m to 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. MOCNESS tows at a variety of stations were conducted over the EBS slope and shelf. Bongo sampling occurred intermittently in March – May from 1982 to 2007, and MOCNESS sampling occurred over the continental slope in April of 1992 and 1994, with most tows occurring at night (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 fish were measured to the nearest mm standard length (SL).

Collection of pelagic juveniles

Pelagic juveniles were collected from a series of cooperative research cruises between scientists at the AFSC and the Graduate School of Fisheries Hokkaido University, Japan, on the T/S *Oshoro Maru*. Pelagic juveniles were sampled using either a modified beam trawl (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 Methot trawl (MT) with 3 mm mesh

netting and a 1 mm mesh cod end. MBT was similar to MT in all regards except that MBT had a weighted frame instead of a depressor (Duffy-Anderson *et al*. 2006). A flowmeter fitted inside both frames was used to determine the filtered volume. All tows were oblique and made from 200 m (or 10 m off bottom) to the surface. Net depth was measured using an acoustic netsound. MBT was designed to collect late larval and early juvenile stage fishes in the midwater, and is similar to MT (Methot 1986). Utilized MBT sampling occurred from July to August in 1996 – 2005 and MT sampling was conducted from July to September in 1994 and in July 1997 (Table 1). All samples were preserved, sorted, identified and measured using similar protocols to those described above.

Collection of newly settled juveniles and age-1 fish

Data on age-0 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 (BT) have been conducted from 1982 to 2007 (Table 3). This survey has been conducted annually beginning as early as May and extending as late as October, though most of the recent surveys were conducted in summer months. The survey provides extensive geographic coverage over the EBS shelf (http://www.afsc.noaa.gov/RACE/groundfish/gfprof_coverage.htm) and gives an excellent representation of adult and subadult distributions. Briefly, the gear used was a 25.3 x 34.1 m eastern otter trawl with a 25.3 m headrope and a 34.1 m footrope. The net was attached to paired chains and dandylines, and a net mensuration system was used to measure net height and width while towing. Estimates of net width are used in

calculations for the area swept. Samples were collected from a grid with spacing of 20

x 20 nautical miles, and tows were typically 30 minutes in duration.

Table 1. Cruise information for positive catches of Greenland halibut from the Alaska Fisheries Science Center's EcoFOCI Program Ichthyoplankton database.

Cruise	Year	Gear*	Number of tows	Start date	End date
1OC88	1988	60BON	61	March 17	April 4
0MF91	1991	60BON	20	March 11	March 15
2MF92	1992	60BON	36	April 16	April 18
3MF93	1993	60BON	119	April 15	April 30
4MF94	1994	60BON	128	April 15	April 30
6MF95	1995	60BON	137	April 17	April 30
7MF95	1995	60BON	134	May 4	May 18
6MF97	1997	60BON	32	May 4	May 13
3MF02	2002	60BON	81	May 13	May 21
4MF07	2007	60BON	24	May 7	May 18
2MF92	1992	MOCNESS	1	April 16	April 16
2MF92	1992	MOCNESS	7	April 20	April 22
2MF93	1993	MOCNESS	2	April 17	April 21
2MF93	1993	MOCNESS	15	April 23	April 28
2MF94	1994	MOCNESS	8	April 16	April 16
2MF94	1994	MOCNESS	1	April 22	April 27
1MF08	2008	MOCNESS	7	February 17	February 27
1OM96	1996	MBT	33	July 22	July 29
1OM97	1997	MBT	28	July 21	July 29
1OM98	1998	MBT	25	July 25	July 30
1OM99	1999	MBT	20	July 26	August 1
1OM00	2000	MBT	21	July 28	August 1
1OM01	2001	MBT	23	July 21	July 24
1OM02	2002	MBT	26	August 1	August 9
1OM03	2003	MBT	22	July 20	July 25
1OM04	2004	MBT	25	July 28	August 4
1OM05	2005	MBT	24	July 15	July 21
7MF94	1994	MT	15	July15	September 6

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

Table 2. A 20 stage scheme of embryonic development of Greenland halibut (after Blood *et al*. 1994).

	Embryonic development stage
1	Precell
2	2 cell
3	4 cell
4	8 cell
5	16 cell
6	32 cell
7	Blastodermal cap
8	Early germ ring
9	Germ ring 1/4 down yolk
10	Germ ring 1/2 down yolk
11	Germ ring 3/4 down yolk
12	Late germ ring
13	Early middle (blastopore closure)
14	Late middle (tail bud thickens)
15	Early late (tail bud lifts from yolk)
16	Tail 5/8 around yolk
17	Tail 3/4 around yolk
18	Tail 7/8 around yolk
19	Full circle around yolk
20	Tail 1-118 around yolk

Table 3. Bottom trawl (BT) stations where newly settled juveniles (<100 mm SL) and age-1 (140 mm - 220 mm SL) of Greenland halibut have been caught. Data from the Alaska Fisheries Science Center's Groundfish Assessment Program survey database.

Cruise	Year	Number of tows	Start date	End date
198201	1982	10	July 24	July 30
198203	1982	16	June 16	July 11
198301	1983	5	July 12	July 30
198303	1983	12	July 12	August 1
198402	1984	6	August 11	August 15
198501	1985	17	July 9	September 10
198601	1986	8	July 1	July 10
198602	1986	16	July 4	July 28
198701	1987	22	July 20	July 28
198801	1988	34	July 13	July 29
198901	1989	26	July 11	August 2
199001	1990	35	July 3	August 1
199101	1991	43	July 17	August 13
199201	1992	24	July 11	August 3
199301	1993	23	July 7	July 24
199401	1994	7	July 19	July 22
199501	1995	12	July 3	July 21
199601	1996	15	July 8	July 26
199701	1997	13	July 11	July 24
199801	1998	19	July 24	July 29
199901	1999	7	July 7	July 9
200001	2000	23	June 25	July 13
200101	2001	21	July 11	July 19
200201	2002	24	June 27	July 22
200301	2003	20	July 14	July 19
200401	2004	13	July 8	July 24
200501	2005	6	July 14	July 18
200601	2006	5	July 2	July 20
200701	2007	42	July 2	July 25

Data analysis

Egg specific gravity and vertical distribution

In 2008 and 2009, live eggs collected from net 2 of the bongo array were used to measure instantaneous specific gravity with an Egg Density Gradient Apparatus (EDGAR: Coombs 1981, Kendall and Kim 1989; Fig. 4). Individual eggs were placed in the density gradient columns, which were made with two salinity solutions (approximately 30 ‰ and 40 ‰) and six beads of known density (1022.815 kg/m^3, 1023.716 kg/m^3, 1024.816 kg/m^3, 1026.817 kg/m^3, 1028.318 kg/m^3, and 1029.319 kg/m^3 at 5 °C). After each egg in the water column had stabilized (approximately 1 hour), the height of the egg and beads from the bottom of the graduated column was recorded. Position of the eggs relative to the beads was graphed for each experiment and a linear interpolation between beads determined specific gravity for each egg. A simple linear regression was used to test the influence of egg development stage or egg size on the egg density and to test the relationship between the density and size or stages.

A one-dimensional steady state model, which has been developed by Sundby (1983 and 1990) was utilized to describe the vertical distribution of Greenland halibut eggs. In a steady state (i.e., no change of vertical egg distribution over time), the vertical diffusion flux (related to turbulence) is balanced by the vertical convection flux (related to egg size and specific gravity). This balance can be written as:

$$K \frac{\partial C(z)}{\partial z} - (-w(z) * C(z)) = 0 ,$$
(1)

where K is the vertical eddy diffusivity (m^2/s), z is the depth (m), $C(z)$ is the
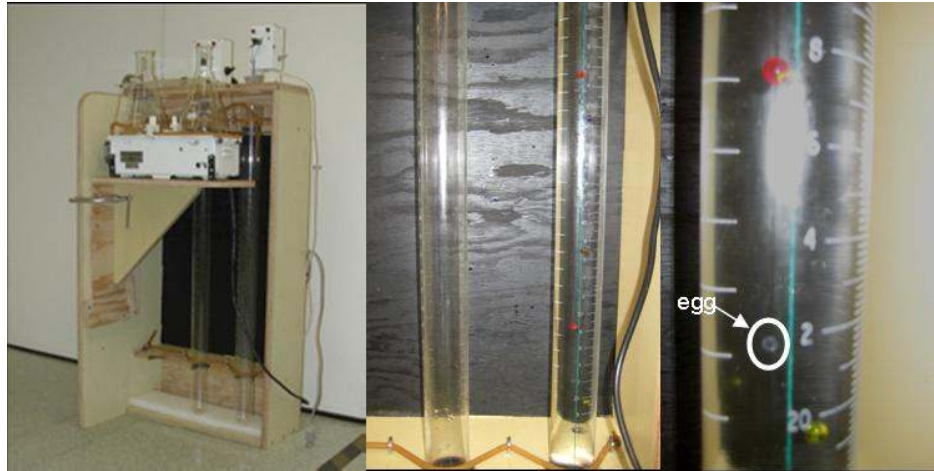
Figure 4. Pictures of Egg Density Gradient Array and density-gradient column with beads and egg.

concentration of fish eggs, and w is the terminal velocity (m/s). When the Reynolds number for flow around the egg is less than 0.5, meaning the viscosity force is dominant, the terminal velocity (w) of eggs is given by Stokes' law:

$$w = \frac{gd^2\Delta\rho}{18\nu} \tag{2}$$

where g is the gravity acceleration (m/s), d is the egg diameter (m), $\Delta\rho$ is the density difference between the egg and the ambient sea water (kg/m^3), and ν is the dynamic molecular viscosity of sea water (kg/ms). For bathypelagic eggs, Sundby (1991) reported that vertical egg distribution depends on vertical density stratification of the pycnocline, in addition to the turbulence. In a linear density gradient, the vertical velocity (w) is re-written:

$$w(z) = m(z - z_A) \tag{3}$$

where m is a constant and is independent of z, but depends on egg density and stratification, z_A is the depth where density difference between water and egg is 0. Therefore, equation (1) analytically solves to:

$$C(z) = C_A \exp[-\frac{m}{2K}(z - z_A)^2] \tag{4}$$

where C_A is the egg concentration at depth z_A. Based on (4), the eggs have a normal distribution in the vertical where the standard deviation is:

$$\sigma = \sqrt{\frac{K}{m}} \tag{5}$$

Also, equation (3) is re-written for m:

$$m = \frac{d^2\rho_w N^2}{18\nu} \tag{6}$$

where N is the Brunt–Väisälä frequency, which is the frequency at which a vertically displaced parcel will oscillate within a statically stable environment.

The one-dimensional egg vertical distribution model was parameterized using average water density, which is calculated using field-derived Seacat data from the seven MOCNESS sampling stations near Bering Canyon region where eggs were collected. Also, three selected specific gravity of eggs, which are 25% = 1026.20, 50% = 1026.55, and 75% = 1026.90 quantile based on measured egg specific gravity that are higher than the lowest water density (1024.89 kg/m^3), were used as input values for the model. I used $K = 10^{-4}$ m^2/s for the modeling (Gregg 1998).

Distribution and drift pathways during early life stages

We defined Greenland halibut early life stages based on different size ranges and various gear types used to collect them. From 60BON and MOCNESS samplings, the smallest larva was 8.8 mm. According to Matarese *et al*. (1989), notochord flexion begins. Here, post flexion larvae are called pelagic juveniles.

· Larvae: 8.8 – 25 mm SL. Caught by 60BON and MOCNESS.

· Pelagic juveniles: 25.1 – 59 mm SL. Caught by MBT and MT.

· Newly settled juveniles: 60 – 90 mm fork length (FL). Caught by BT.

· Age-1 juveniles: 140 – 220 mm FL. Caught by BT.

Horizontal and vertical distributions of Greenland halibut early life stages from larvae to age-1 were analyzed separately by gear type to eliminate differences in gear capture efficiency. Before data analyses, locations with zero catch were removed, however, the non-catch locations were included in descriptive maps (Fig. 6, Fig. 12, and Fig. 15-17). Catch per unit effort (CPUE) was expressed as the number of larvae

or pelagic juveniles caught per 10 m^2 surface area. CPUE was normalized by a logarithmic transformation for statistical analysis. An analysis of variance (ANOVA) was used to compare differences of mean larval abundance and lengths among months and years. A linear regression was used to examine the effect of maximum gear depth on larval abundance. Catch depth of MOCNESS sampling were separated into six categories: 0 – 45 m, 46 - 99m, 100 - 199 m, 200 – 299 m, 300 - 399 m, and 400 – 530 m. Linear regression analyses were used to test for differences in larval mean size within the depth strata from MOCNESS sampling. An ANOVA was used to test for the variation of mean pelagic juvenile abundance and juvenile size among months and years from combined MBT and MT sampling. For BT sampling, Greenland halibut individuals from RACEBASE were separated into two length-size classes: < 100 mm FL (newly settled juveniles) and 140 - 220 mm FL (age-1 individuals) based on stock assessment models (Ianelli *et al.* 2007). CPUE was calculated for newly settled and age-1 juveniles by dividing the number of fish caught by the area swept.

Stomach content analyses

Sixty larvae and thirty-six pelagic juveniles were randomly selected from historical sampling for stomach content analyses. The larvae were sampled from different cruises occurring in 1993 and 2007 (Table 4 and Fig. 5). Pelagic juveniles were sampled from various cruises conducted in 1994 and 1997 (Table 4 and Fig. 5). The size (mm) and weight (g) of larvae and pelagic juveniles were measured. Stomach contents were identified to lowest possible taxa. Identified stomach contents were enumerated using a dissecting microscope. The stomach content analysis was described using percentage frequency of occurrence, which was calculated relative to

the number of non-empty stomachs given by the equation (6) as below (Hyslop 1980, Bowen 1983):

$$F_i = (N_i / N) *100 \qquad (6)$$

where F_i is frequency of occurrence of the i food item in the sample, N_i is the number of stomachs in which the i item is found, and N is total number of stomachs with food in the sample.

Otolith analyses

Sixteen pairs of otoliths (sagitta) were extracted from larvae collected along the Bering Sea Slope in May 2007. Before removing the otoliths, the SL and body weight (BW) of the larvae were measured. The extracted otoliths could not be weighed because they were too small (62-110 um), but their diameters were measured. The otoliths were mounted to microscope slides with clear acrylic nail polish for daily ring measurements under a compound microscope following the procedures of Brown and Bailey (1992).

Table 4. Samples used in stomach content analyses.

	Larvae				Pelagic juveniles		
Year	Name of Station	No. of fish	Time of day	Year	Name of Station	No. of fish	Time of day
1993	2	1	2:45 PM	1994	2	1	1:46 AM
1993	20	2	8:52 AM	1994	3	1	3:34 AM
1993	23	1	1:53 PM	1994	4	2	1:20 AM
1993	29	1	3:31 AM	1994	5	5	3:11 AM
1993	30	2	5:37 AM	1994	6	1	1:30 AM
1993	32	2	9:34 AM	1994	9	1	3:24 AM
1993	38	2	11:30 PM	1997	53	5	2:06 PM
1993	48	1	8:29 PM	1997	57	5	1:48 AM
1993	63	1	3:21 PM	1997	58	3	8:20 AM
1993	66	2	6:33 PM	1997	69	2	3:34 AM
1993	73	2	2:21 AM	1997	81	1	1:27 AM
1993	76	1	5:27 AM	1997	82	1	2:04 AM
1993	78	1	7:57 AM	1997	83	2	2:56 AM
1993	84	6	2:29 PM	1997	99	2	12:24 PM
1993	94	1	6:19 AM	1997	139	2	9:03 PM
1993	111	1	11:04 AM	1997	143	2	5:30 AM
1993	112	3	11:55 AM				
1993	118	1	6:15 PM				
1994	49	1	1:33 PM				
1997	78	1	7:57 PM				
2002	70	1	7:14 PM				
2007	40	1	1:03 AM				
2007	54	2	6:18 AM				
2007	57	3	3:33 PM				
2007	59	1	9:31 PM				
2007	60	2	2:07 AM				
2007	69	1	10:22 PM				
2007	71	2	3:33 AM				
2007	72	6	5:55 AM				
2007	78	1	1:20 AM				
2007	85	1	5:39 AM				
2007	87	1	6:34 AM				
2007	89	1	11:33 AM				
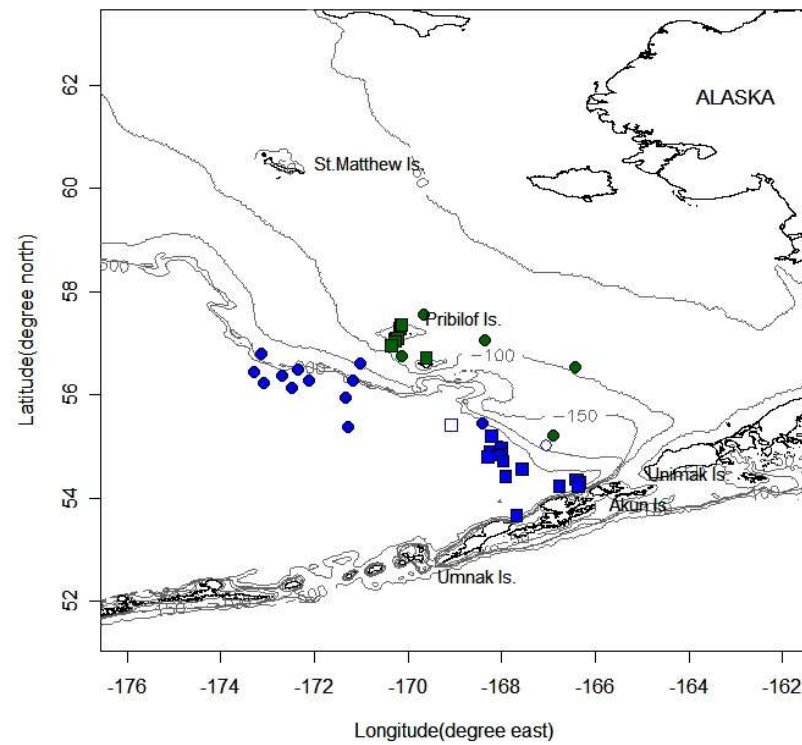
Figure 5. Distributions of larvae and pelagic juveniles used for stomach content analyses (blue square: 1993, blue circle: 2007, green square: 1994, and green circle: 1997).

CHAPTER 3: RESULTS

Egg specific gravity and vertical distribution

In February 2008 and 2009, 111 eggs and 6 eggs were collected, respectively. Eggs were found along the slope region near Bering Canyon (Fig. 6). Size of live eggs ranged in diameter from 3.8 mm to 4.4 mm. Instantaneous specific gravity was measured for 59 and 4 early-late stages of eggs in 2008 and 2009, respectively. The specific gravities of eggs ranged from 1023.5 kg/m^3 to 1027.8 kg/m^3 in 2008 and from 1026.4 kg/m^3 to 1026.5 kg/m^3 in 2009 at experimental temperatures between 0°C and 5°C. Few eggs in the early and middle stages were found. There were no significant relationships between egg size and specific gravity (Fig. 7; p-value > 0.05), or between egg stage and specific gravity (Fig. 8; p-value > 0.05).

Based on Seacat data from the seven MOCNESS sampling stations near the Bering Canyon region in February 2008, I obtained vertical profiles of water temperature, salinity, and density (Fig. 9). There were strong vertical mixing in the upper 50 m at some stations, but water column was well stratified below 50 m (Fig. 9). The specified one-dimensional egg vertical distribution model shows changes of vertical egg distribution associated with changes in egg density (Fig. 10).

For MOCNESS samplings, eggs were found between 50 m and 400 m. The greatest numbers of eggs were concentrated between 200 m and 300 m (Fig. 11).
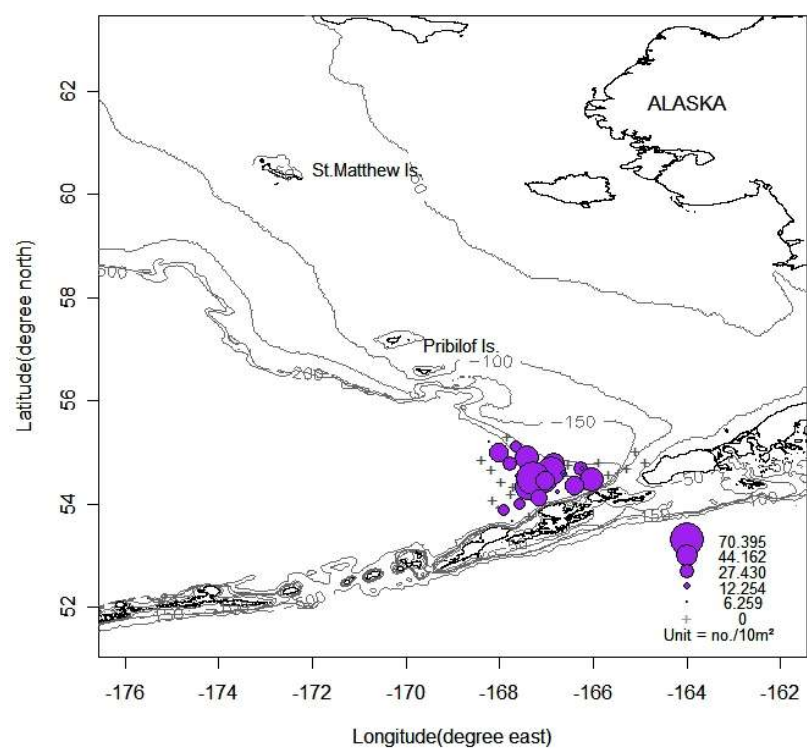
Figure 6. Distribution and abundance of Greenland halibut eggs in February 2008.
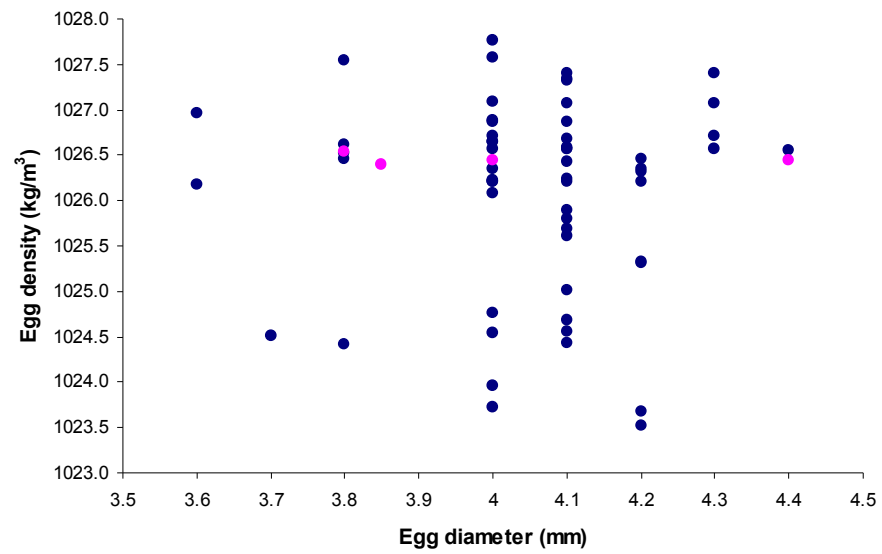
Figure 7. Relationship between egg density and egg diameter (blue circles: 2008 and pink circles: 2009; *p-value* > 0.05).
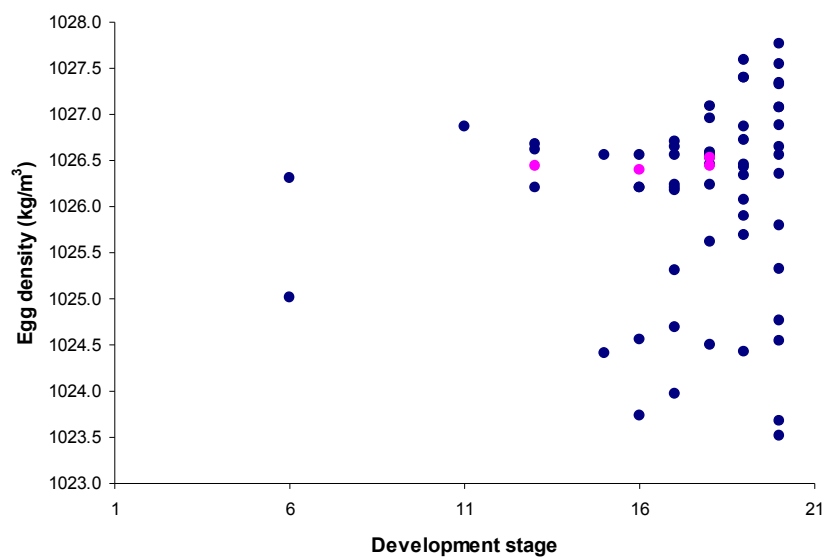
Figure 8. Relationship between egg density and developmental stage (blue circles: 2008 and pink circles: 2009; *p-value* > 0.05).
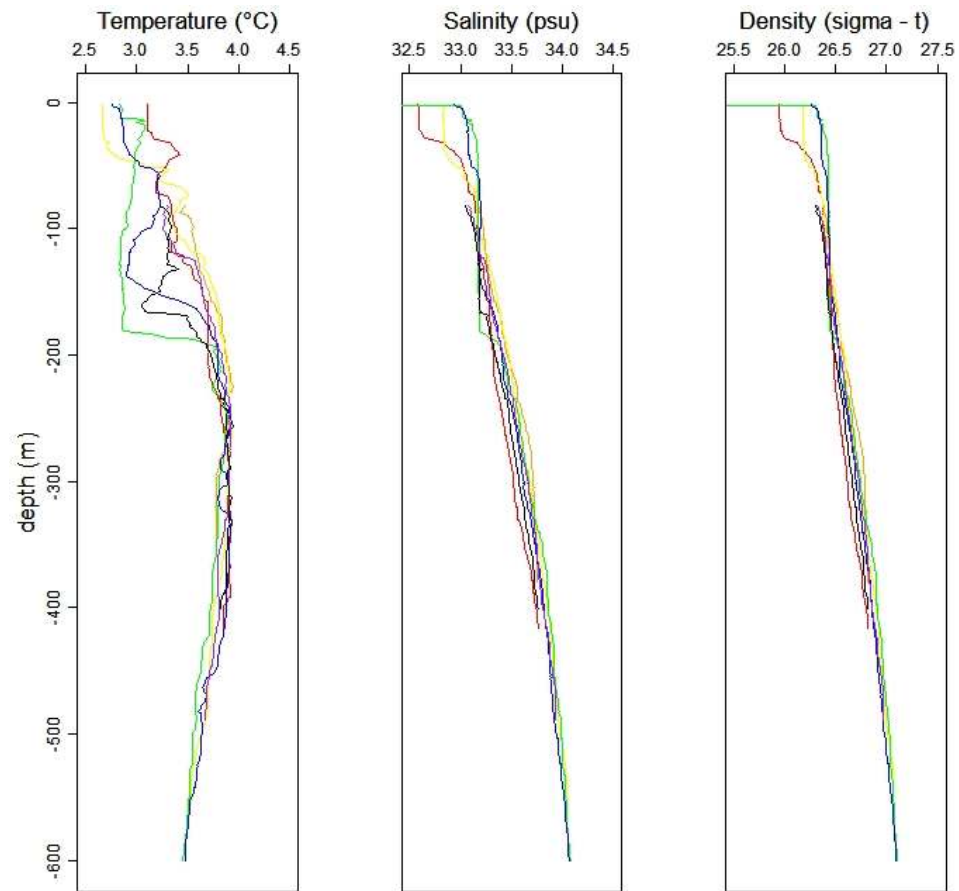
Figure 9. Sea-Bird Seacat SBE 19 Profiles of water temperature, salinity, and density at the seven MOCNESS sampling stations where eggs were collected near Bering Canyon region in February 2008 (red line: st.12, orange line: st. 44, yellow line: st. 45, green line: st. 46, blue line: st.47, purple line: st. 48, and black line: st. 49)
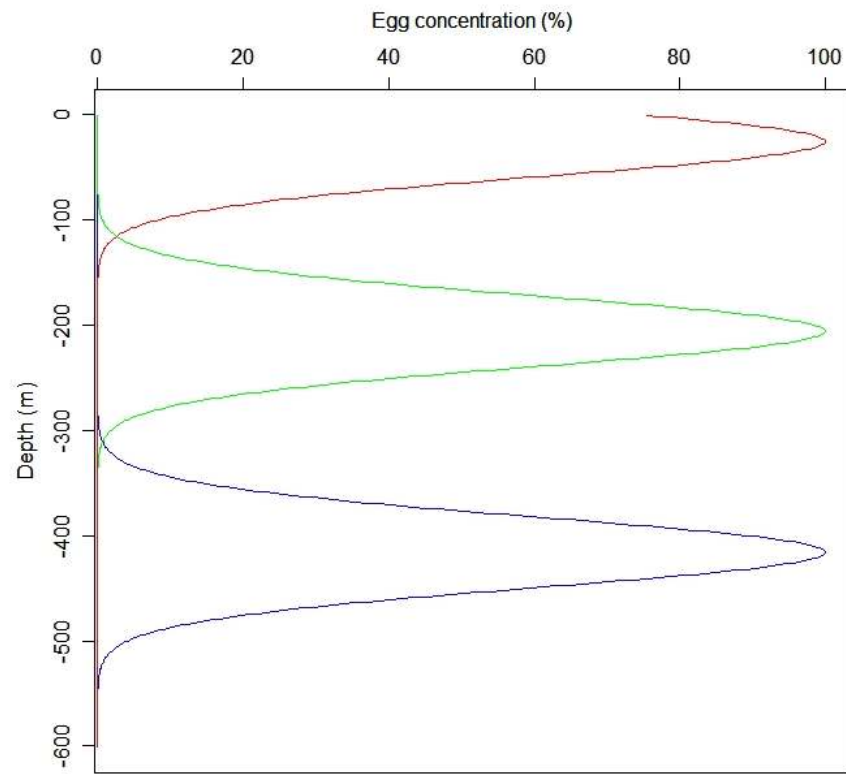
Figure 10. Change of vertical egg distribution with different egg specific gravity: 1026.20 (red line), 1026.55 (green line), 1026.90 (blue line) kg/m^3 at the seven MOCNESS sampling stations.
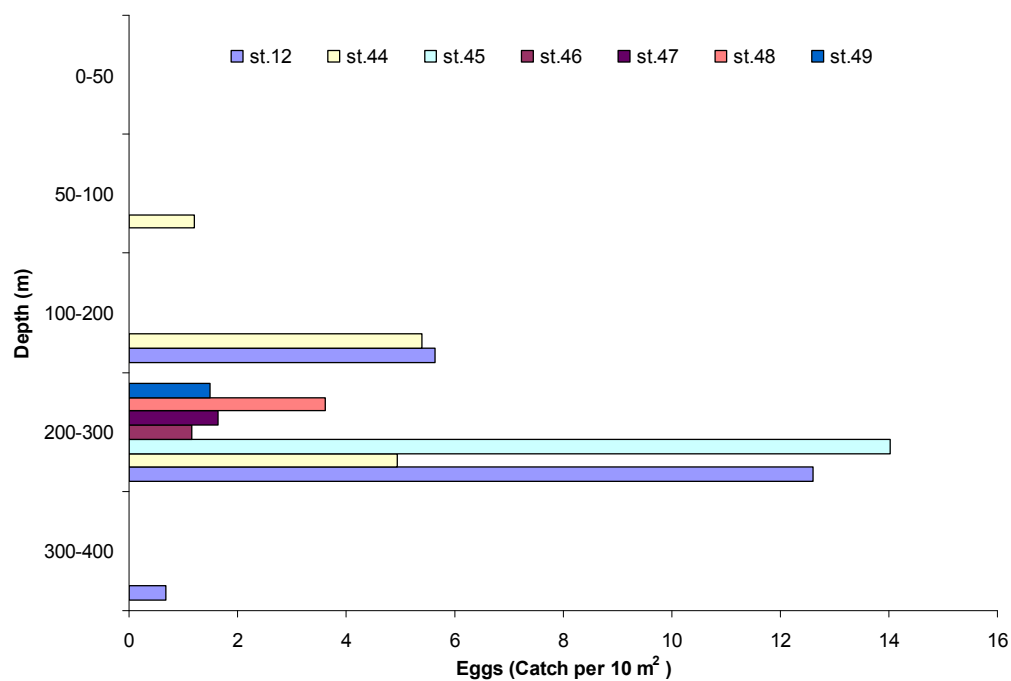
Figure 11. The vertical distribution of Greenland halibut eggs by eggs concentration collected in February from the Multiple Opening and Closing Net and Environmental Sampling System (MOCNESS) in February 2008.

Horizontal larval distribution

Larvae were found over the outer continental shelf domain, the continental slope, and the basin of the EBS and eastern AI from March to May (Fig. 12). Larvae from the easternmost AI appeared to be concentrated near the AI between Umnak and Akun Island, and those along the slope were noted between Akun Island and the Pribilof Islands in the EBS. Larvae were most abundant between 54°N and 55°N along the slope and throughout Bering Canyon. During the spring, some larvae appeared to have drifted from the slope eastward across Bering Canyon onto the shelf. The highest abundances of Greenland halibut larvae were observed in March (Table 5). Larvae tended to be associated with the deeper maximum gear depth from March to May (linear regression, *p-value* <0.05; Fig. 13). Notably, the highest abundances of larvae were found in tows that reached 400 m maximum gear depth. Larval lengths ranged from 8.8 to 24.4 mm (mean = 17.38 mm; sd = 3.15 mm). From March to May, the majority of larvae were between 16 and 21 mm, with larval size increasing throughout this period (ANOVA, *p-value* < 0.05) and larval abundance decreasing (ANOVA, *p-value* < 0.05; Table 5). Inter-annual variation of mean larval abundance was significant (ANOVA, *p-value* < 0.05).

Vertical larval distribution

Larvae were collected between the surface and 530 m depth (Fig. 14). Highest concentrations of larvae were noted near the surface in the upper 45 m of the water column (Fig. 14). In April, the length range of the larvae varied from 12 to 22.4 mm. Larvae in near surface waters were larger than those at depth (ANOVA, *p-value* < 0.05). The combined larval vertical distribution data from MOCNESS sampling

indicate that Greenland halibut eggs hatch below 530 m, and larvae rise to shallower water as they develop and become more buoyant.
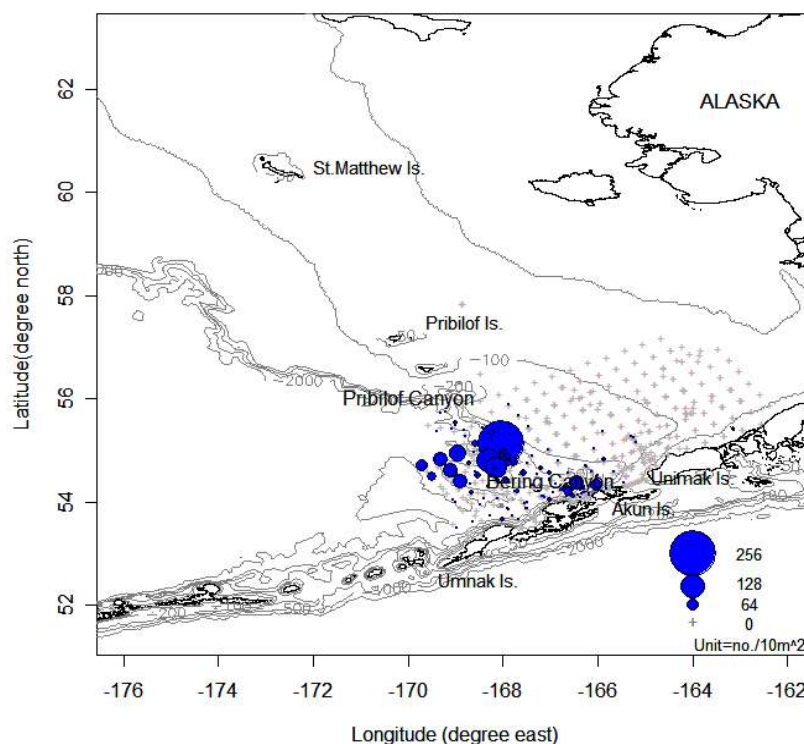
Figure 12. The horizontal distribution of Greenland halibut larvae collected during spring (March to May) from the 60cm bongo net. Bubble sizes indicate catch per unit effort, and plus signs represent non-catch stations.

Table 5. The mean and standard deviation (SD) of length and positive catch abundance of Greenland halibut before age-1 for each gear type.

Gear*	Month	Mean and SD of length (mm)	CPUE (no./10m^2)	Numbers of stations	Numbers of fish
60BON	March	11.92 ± 1.23	35.14 ± 61.04	11	77
60BON	April	17.99 ± 1.99	22.65 ± 22.85	139	380
60BON	May	21.03 ± 2.45	12.08 ± 8.04	28	51
MBT/MT	July	35.65 ± 4.83	0.52 ± 0.38	54	327
MBT/MT	August	45.00 ± 9.90	0.40 ± 0.21	2	2
BT	June-August	88.38 ± 5.53	0.30 ± 0.18**	37	37

*60 cm Bongo net (60BON), Modified Beam Trawl (MBT), Methot Trawl (MT), and Bottom Trawl (BT).
**unit = no./10,000 m^2
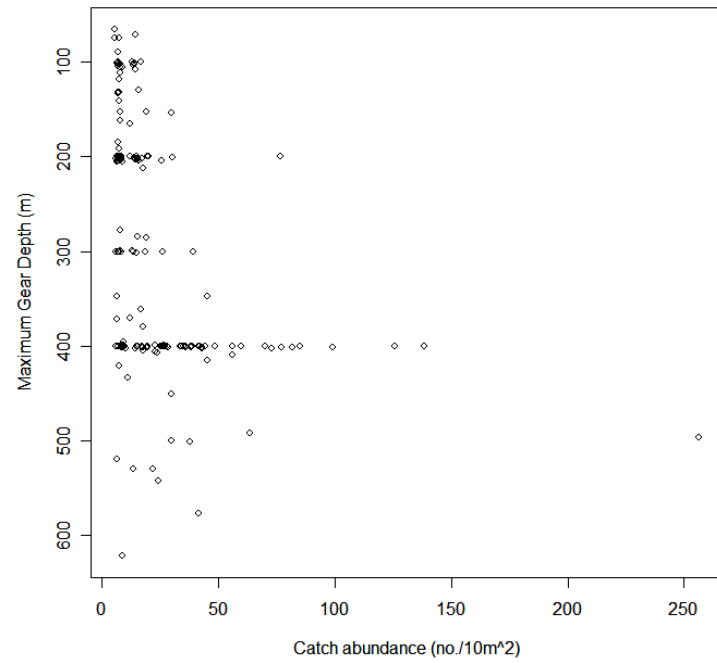
Figure 13. The relationships between larval abundance and maximum gear depth sampled with 60cm bongo nets (*p-value* <0.05).
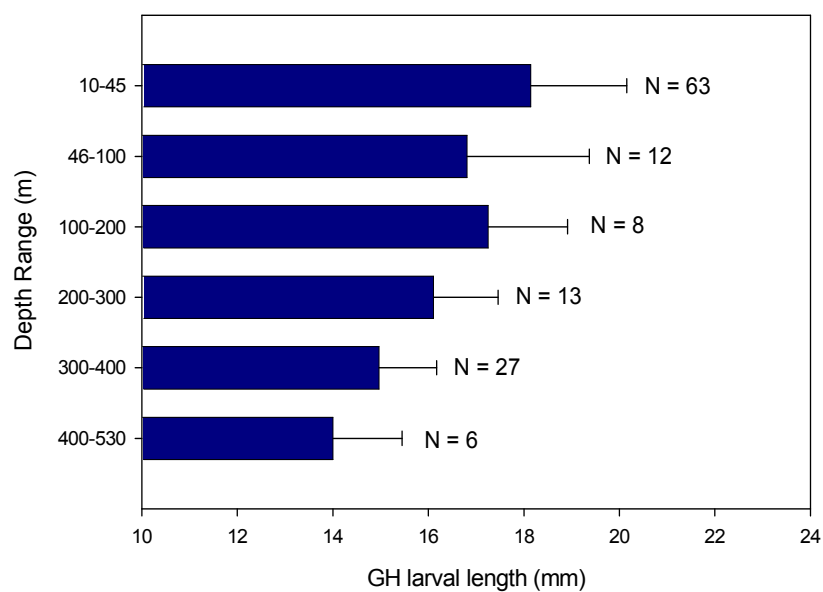
Figure 14. The vertical distribution of Greenland halibut larvae by larval length (mean ± standard deviation) and caught numbers collected in April from the Multiple Opening and Closing Net and Environmental Sampling System (MOCNESS; *p-value* <0.05).

Pelagic juvenile distribution

Pelagic juveniles were found over the middle and outer domains between 56°N and 58°N between July and September in MBT and MT samples (Fig. 15). The pattern of pelagic juvenile distribution was fairly consistent among years except for 2005 when larvae appeared in the inner domain north of 58°N from MBT sampling. Some juveniles were concentrated in Pribilof Canyon and near the Pribilof Islands, indicating that they likely crossed the continental slope through Pribilof Canyon. The length of pelagic juveniles ranged from 24.4 to 54 mm SL (mean = 35.57 mm, sd = 5.02 mm). Peak abundances occurred for fish between 30 and 40 mm. Mean abundances of Greenland halibut pelagic juveniles were significantly different among months and years (ANOVA, *p-value* < 0.05).

Newly settled juvenile distribution

Newly settled juveniles (60 mm - 90 mm FL) caught with BT gear were found over the continental middle domain in the vicinity of St. Matthew Island between 58°N and 62°N during late spring and summer (late May to early October, but primarily in June and July; Fig. 16). The smallest length of newly settled juveniles was 60 mm, occurring in July. Newly-settled juveniles ranged in length from 60 mm to 90 mm (mean = 88.38 mm, sd = 5.53 mm) (Table 5). No newly settled juveniles were collected south of the Pribilof Islands.
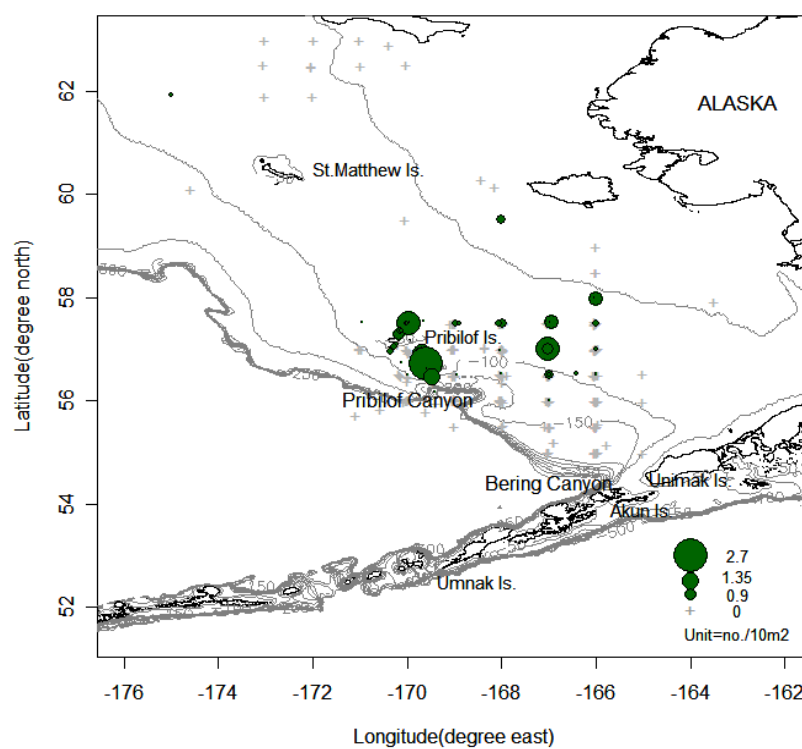
Figure 15. Pelagic juveniles during summer (July to August) collected from the modified beam trawl and Methot trawl. Bubble sizes indicate catch per unit effort, and plus signs represent non-catch stations.
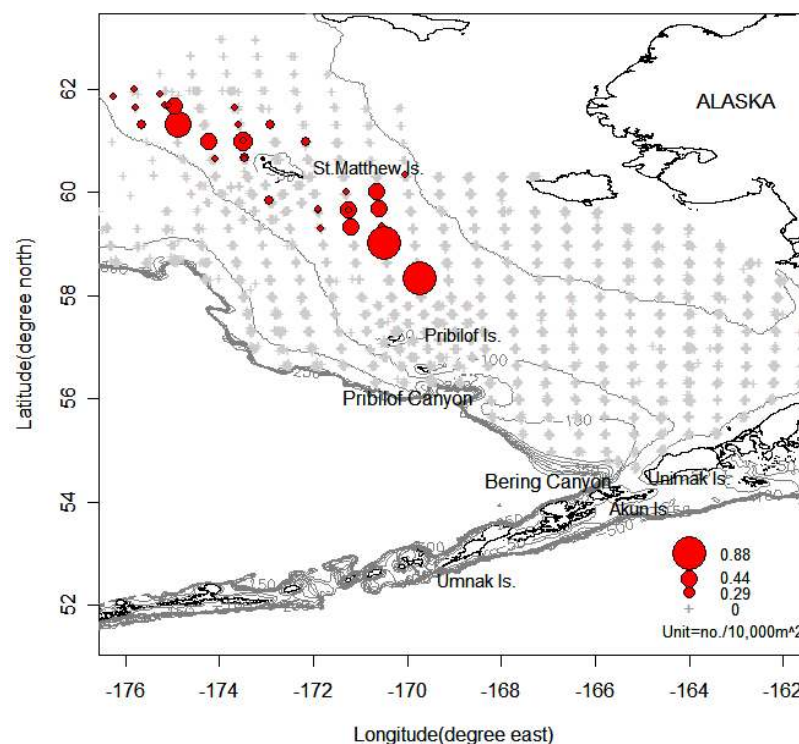
Figure 16. Newly settled juveniles (<100 mm) during summer (late May to early October) collected from the bottom trawl. Bubble sizes indicate catch per unit effort, and plus signs represent non-catch stations.

Age-1 distribution

Age-1 (length-size class: 140 mm – 220 mm FL) Greenland halibut were concentrated over the outer shelf domain, although they also appeared over the middle domain (Fig. 17). Data indicate that age-0 Greenland halibut moved westward and into deeper water with increasing size.

Larval and juvenile feeding habits

Ten yolk-sac larvae were found among sixty sampled larvae during stomach content analyses (11.72 to 17 mm SL). Body size of feeding larvae ranged from 17.5 to 24 mm SL (mean = 20.09 mm SL, sd = 2.07 mm). Size of pelagic juveniles ranged from 25 mm to 40 mm SL (mean = 30.94 mm SL, sd = 3.77 mm). Empty stomachs were found 31.67 % in larval samples, but none were found in juveniles samples. For non-empty stomachs of larvae, prey items include *Calanus sp.*, *Psudocalanus sp.,* *Oithona sp.,* nauplii, and unidentified crustacean eggs (Table 6). For non-empty stomachs of pelagic juveniles, *Calanus sp.*, *Psudocalanus sp., Thysanoessa sp.,* and fish larvae including a flathead sole (*Hippoglossoides elassodon*) and *Gadid sp.* were identified among the gut contents (Table. 6). Two pelagic juveniles had unidentified masses in their stomach due to digestion. Copepoda formed the major prey constituting 87.09 % in larvae and 50.00 % in pelagic juveniles of food items by occurrence. For pelagic juveniles, fish larvae comprised the second largest portion of the stomach contents, accounting for 47.06 % by occurrence. The third most important food item was euphausiids (*Thysanoessa sp.*), with 29.41 % by occurrence.

Otolith microstructure

The length of the Greenland halibut including larvae and pelagic juveniles from which otoliths were obtained ranged from 15.81 to 26.00 mm SL (mean = 21.77 mm SL, sd = 2.67 mm) in May 2007. It was difficult to interpret otolith microstructures of Greenland halibut larvae. Daily increment rings in otoliths were not discernible in all samples using the compound microscope, due to their small size. We were, however, able to measure four clear increment rings in each otolith (Fig. 18(a)). Otolith diameter is correlated with standard length, and the otolith diameter at each well-defined increment seems to be consistent between specimens (Fig. 18(b)).
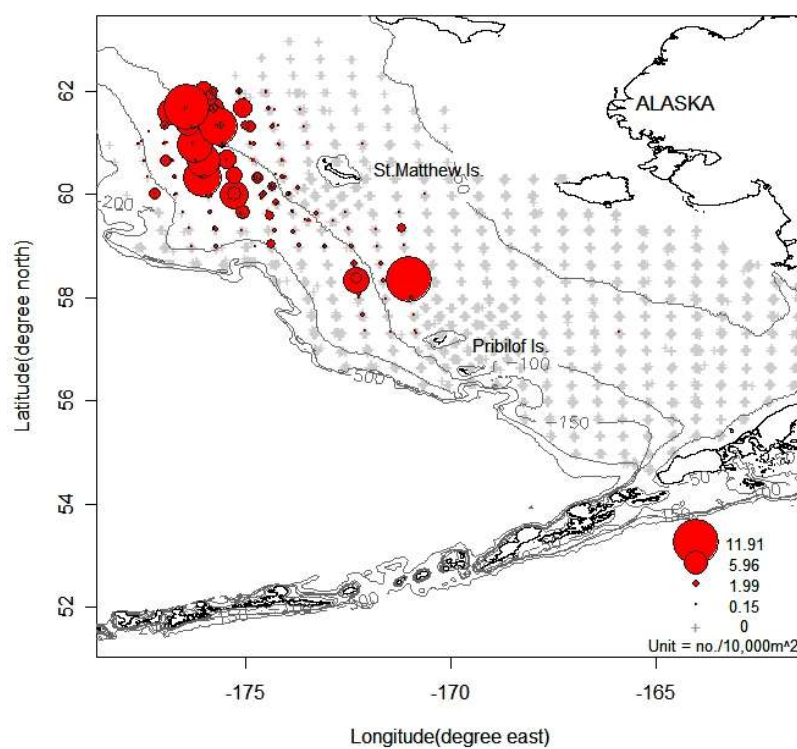
Figure 17. Age-1 juveniles (140 mm - 220 mm) during summer (late May to early October) from the bottom trawl. Bubble sizes indicate catch per unit effort, and plus signs represent non-catch stations.

Table 6. The frequency (%) of occurrence of prey items in Greenland halibut larvae and pelagic juveniles.
Larvae = 60, Empty stomach in larvae = 19, yolk-sac larvae = 10
Pelagic juveniles = 36, digested = 2

Prey items	Larvae		Pelagic juveniles	
	N_i	%	N_i	%
Crustaceans				
Calanoida			7	20.1
Calanus sp.			5	14.71
Pseudocalanus sp.	1	3.23	2	5.88
Cyclopoida				
Oithona sp.	2	6.45		
Copepoda nauplli	6	19.35		
Unidentified copepoda	14	45.16	10	29.41
Euphausiacea			10	29.41
Thysanoessa sp.			9	26.47
Unidentified Euphausiacea			1	2.94
Crustaceans eggs	4	12.90		
Fish larvae			16	47.06
Flathead sole			1	2.94
Gadid sp.			5	14.71
Unidentified fish larvae			10	29.41

(a)

Larvae: 26 mm and diameter: 110 *u*m   Larvae: 24 mm and diameter: 88um

The first ring

The second ring   The third ring

The forth ring
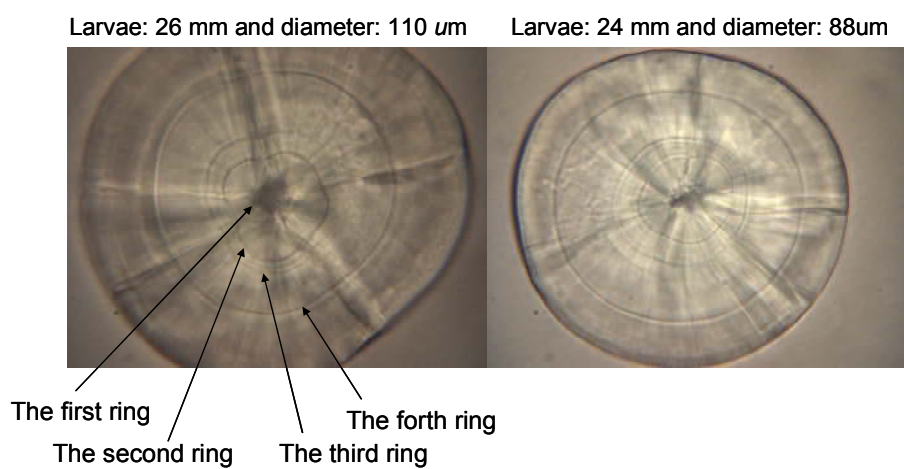
(b)
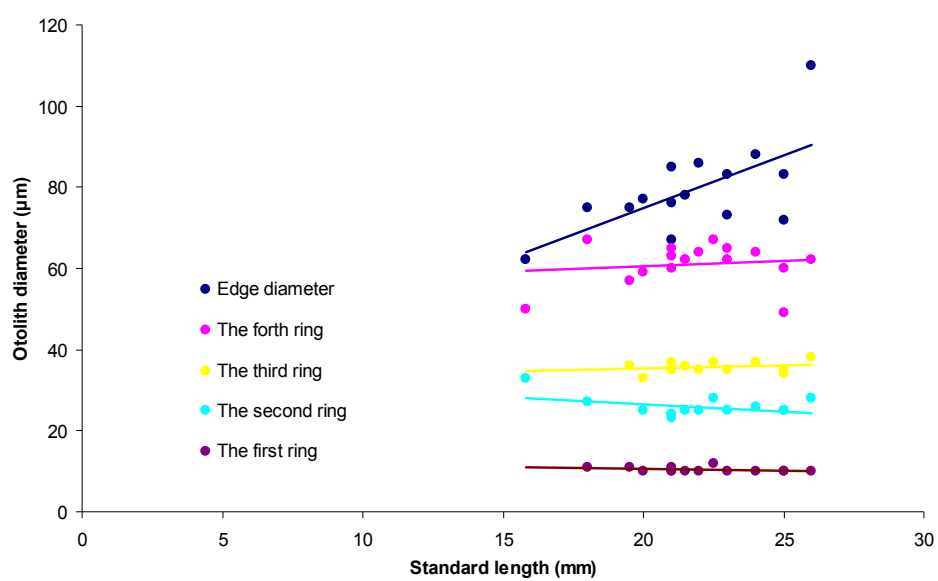
Figure 18. (a) Otolith microstructure of larvae and pelagic juveniles and (b) Relationship between standard length (SL; mm) and otolith diameter (µm).

CHAPTER 4: DISCUSSION

Spawning location and timing

The spawning time and locations of Greenland halibut in the EBS are still poorly defined, and the little that 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, though Bulatov (1983) noted spawning along the continental slope off Unimak Pass during winter from February to March. Alton *et al*. (1989) inferred that Greenland halibut mainly spawn over the slope area between Unimak Pass and the Pribilof Islands, and he also considered the AI a spawning area based on trawl surveys. Based on my analyses of eggs and larval distributions, I suggest spawning locations along the AI and the EBS slope, particularly Bering Canyon region, as evidenced by eggs and early stage larvae collected along the eastern most AI (Umnak and Unalaska Islands), and along the southern EBS slope (south of the Pribilof Islands) during winter. Our findings are consistent with the assertions of Alton *et al*. (1989) that most Greenland halibut adults are found in the central and southern slope regions of the EBS, as we found that the spatial distribution of eggs and larvae had centers of abundance along the slope and over the basin (below 3000 m) between Akun Island and the Pribilof Islands.

With regard to spawning time, we found that the smallest Greenland halibut larvae (8.8 mm) were collected in March. In the Atlantic, Stene *et al*. (1983) reported that egg development time of Greenland halibut was around 50 days after fertilization between 4 °C and 5 °C. Most eggs were in 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 and 2009 near Bering Canyon as the late stages of development indicating that spawning had likely commenced 1-2 months prior. From horizontal eggs and larval distribution patterns, we hypothesize the existence of three spawning - population structure scenarios in the EBS and western AI. The first possibility is that there is a single spawning group occurring in both the EBS and eastern AI slope that 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.

Spawning depth and vertical egg distribution through ontogeny

Based on previous work in the Atlantic, the specific gravity of eggs has been shown to be positively correlated with development (Stene *et al*. 1983). The change in egg density with ontogeny may affect vertical egg distribution; denser eggs could be concentrated in the deeper water. Given the results of vertical larval distribution, eggs must hatch at deeper depths (below 500 m). Collectively, it seems that older eggs have a greater specific gravity than younger eggs even though I found no relationship between egg density and egg stage.

In my study, eggs were found from 50 m to 400 m depth in February 2008. Previous studies reported Greenland halibut eggs are located in the mesopelagic, not the epipelagic. Interestingly, however, my results showed that eggs are located in both the epipelagic and mesopelagic zones. Initial distribution of eggs may be a

consequence of spawning depth. In the eastern Norwegian and Barents Seas of the Atlantic Ocean, it is known that Greenland halibut spawn in deeper water (between 600 m and 700 m) (Fedorov 1971, Godo and Haug 1989). However, recently, Vollen and Albert (2008) reported that pelagic behavior of adult Greenland halibut is related to spawning season (August-October) between northern Norway and Bear Island in the Atlantic Ocean. Furthermore, according to preliminary archival tag research (James Ianelli, personal communication), it seems that adult Greenland halibut have strong vertical movement and pelagic behavior during their spawning season in the Bering Sea. These results may suggest that Greenland halibut spawn in the epipelagic zone.

Transport mechanisms

Hydrographic features such as slope currents, submarine canyons, and baroclinic eddies are important 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 larvae suggest that their dispersal and transport could be physically influenced by both the ANSC and BSC. The ANSC may transport larvae eastward, while the BSC may transport larvae northward. In particular, the flow in the upper 45 m of the water column is probably directly associated with dispersal of Greenland halibut larvae once they get at shallower depths. The flow of a portion of the Alaska Coastal Current that enters the eastern Bering Sea through the Unimak Pass may be related to northward shallow flow of the Bering Sea. Results indicate ontogenetic changes in vertical

distribution of Greenland halibut larvae; the largest larvae were most abundant in the upper 45 m. Changes of larval vertical distribution could facilitate their transport and shelf-slope 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 self-slope exchange are processes influenced by the structure of BSC.

Submarine canyons

The spatial distribution of pelagic juveniles 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 deep-water flatfishes, and similar mechanisms are hypothesized here for slope-spawning species in the EBS. Data from this research suggest that Greenland halibut larvae spawned in the western AI or in Bering Canyon likely cross from the slope to the shelf via flows through Bering Canyon. Results show that those larvae that remain entrained in the BSC are advected northwards towards Pribilof Canyon. I hypothesize that larvae that do not cross to the shelf through either Bering or Pribilof Canyons are swept northwards towards the largest canyon, Zhemchug Canyon. Bering, Pribilof, and Zhemchug Canyons are known to be important conduits of slope-shelf exchange, transporting nutrients and biological particles from the basin to the shelf (Stabeno *et al*. 1999, Mizobata and Saitoh 2004, Stabeno *et al.* 2008). I propose that these canyons also serve as important conduits for ingress of the 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 appear to be advected eastward towards settlement areas over the middle domain. Evidence from satellite-tracked drifters deployed by the Fisheries Oceanography Coordinated Investigations program at the AFSC over 15 years (Janet Duffy-Anderson, personal communication) suggests 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.* in review). 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 the wind is primarily from the northeast from December – March (~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 strengthen somewhat in the fall (Stabeno *et al.* 2002), which could serve to enhance advection of those remaining pelagic juveniles 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 van Meurs 1999). In the Gulf of Alaska, it has been also reported that eddies are among the main physical mechanisms for cross-shelf transport (Bailey *et al.* 2008). However, it should be noted that in the EBS 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, age-0 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 this dataset (60 mm) was on the middle shelf near St. Matthew Island. My observations indicate a preferred settling location on the middle shelf near St. Matthew Island. Such location is usually surrounded by a cold water pool, with an average summer bottom temperature less than 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 juveniles over the outer shelf indicates that they move into deeper water with increasing age (or size). Results confirmed observations of size-related variability of Greenland halibut spatial

distribution between newly settled juveniles and age-1. In the EBS, some studies have shown 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.

Greenland halibut have a limited nursery area compared with other abundant flatfish species that reside in the Bering Sea, such as Pacific halibut (*Hippoglossus stenolepis*). Interestingly, Greenland and Pacific halibut have similar patterns of horizontal larval distributions; however, they show different nursery habitat preferences for settlement. Settlement of Greenland halibut age-0 is only found on the middle shelf around the St. Matthew Island. In contrast, Pacific halibut appear to have three primary nursery grounds in the EBS: 1) along the northern Alaska Peninsula from the Black Hills to Port Moller, 2) near the Pribilof Islands, especially around St. Paul Island, and 3) near St. Matthew Island. Differences in depth preference, spawning area, larval dispersal, and/or duration likely give rise to the observed differences in settlement for these two species (Bailey 2008). Rijnsdorp *et al*. (1992) suggested the "nursery size hypothesis" – that there is a positive relationship between size of nursery ground and recruitment success in sole (*Solea solea*) stocks of the Irish Sea and North Sea. Also, the hypothesis has been valid for European plaice (*Pleuronectes platessa*) stock; bigger surface area of the nursery grounds yields

stronger year-class strength in the North Sea (Van der Veer *et al*. 2000). My study found no evidence to indicate that size of nursery ground has been changed over 25 years. However, it seems that newly settled juveniles in some years were found south of St. Matthew Island, while the juveniles in others years were found north of the Island. It may be possible that size variability of nursery ground which is caused by environmental change (i.e. warm temperature in the bottom) also generate variations of year-class strength on Greenland halibut.

Larval and pelagic juveniles feeding habits

The observation of a yolk-sac larvae of 17 mm in length in my study suggest that larvae have a long period from hatching until the first feeding, indicating that the yolk-sac supports required nourishment for the larvae survival and growth for long time. Vertically, the larvae start to feed in the upper 300 m, based on the size and vertical distribution in April. Therefore, food availability between the surface and 300 m may affect their survival successes. The results indicate that pelagic juveniles are vigorous piscivorous. Larger prey types were mostly found in stomachs of larger size fish, which may be related to mouth or gape size as well as energy requirements for growth. Also, different spatial distributions could influence different prey items consumed. Given that I found both small (*Pseudoclanus sp.*) and big (*Clanus sp. and Thyssanoessa sp.*) mesozooplankton, and fish larvae in the stomach of pelagic juveniles, it seems that they have a broad size preference in prey items. It is possible that variations of food patch conditions in time and space influence their survival as stated in the match-mismatch hypothesis by Cushing (1975). Most empty-stomach larvae, which were found along the slope near Pribilof Canyon, were observed in 2007.

If cross-shelf transport is poor such that larvae are retained over the slope instead of being advected over the shelf, this situation may result in unsuccessful feeding and cause vulnerability in growth and survival. In the eastern Norwegian and Barents Seas, Haug *et al*. (1989) reported that Greenland halibut feed on copepods, amphipods, decapods, and unidentified fish larvae (Greenland halibut larval range: 17 - 69 mm of which 85% falls within 25 - 45 mm). Also, Haug *et al*. (1989) reported that more than half of the larvae sampled had empty stomachs.

Biological transition marks in otoliths

The clearly defined rings observed in the otoliths might be biological transition marks. In the Atlantic Ocean, Stenberg (2007) reported that two check marks in otoliths of Greenland halibut pelagic juveniles using a scanning electron microscope. One check mark indicates the hatching in otolith (from core to approximately 27 μm). Another is the first feeding or change of temperature-associated with change of vertical depth distribution from deeper to shallower (from core to approximately 66.7 μm). For other flatfish, Lagardere and Troadec (1997) reported that common sole larvae (*Solea solea*; size range: 4 - 12 mm) had three well-defined rings. They determined that the first ring in the otolith indicates a hatching check mark, the second ring corresponds to mouth opening, and third ring reveals the first intake of food. From the Greenland halibut otoliths examined in this study, the first ring may be the hatch check mark, the second ring may be the mouth opening check mark, third ring may be the first feeding check mark, but the significance of the fourth ring is unclear. Use of a scanning electron microscope may help to resolve some of these outstanding questions.

Data limitations

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 AI and northern portion of the EBS slope region. Adult distributions of Greenland halibut are known from catch by trawl, longline, and pot gears to occur 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 larvae are predominantly found in the eastern AI and southern EBS slope. However, eggs and 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 late stages (Ann Matarese, personal communication). To accurately identify spawning location and timing, samples of earlier stage eggs are needed, which requires the addition of early sampling periods in December and January. In the field, it is difficult to identify and quantify mortality caused by predation (Bailey and Houde 1989). The study of predation effect on mortality during early life stages was limited in my research.

Sampling and experimental issues

During the egg surveys of February 2008 and 2009 we found 111 and 6 eggs, respectively. More eggs collected in 2008 could be the results of different environmental conditions and/or variable sampling strategies between the two years. In 2008, 44 bongo tows were successfully completed, while in 2009 only 30 bongo tows were conducted. Also, 2009 survey mostly focused on sampling adult stages, rather than eggs and larvae.

The specific gravity of eggs can be affected by experimental conditions, particularly with regard to temperature at which the experiments were run and the water density at which the eggs were stored prior to the experiment. For example, facilities (i.e. a Controlled Environment Room) on the R/V Miller Freeman were not able to keep consistent temperature in 2008. Indicate a temperature range during the experiments. Also, some eggs that may have been collected from the deeper water (denser water) were preserved in the jar with the surface water (less denser water) before measuring their specific gravity, resulting in measuring very broad range of egg specific gravity in 2008. In 2009, only six eggs were collected although facilities allowed consistent thermal conditions on the R/V Oscar Dyson. The lack of a relationship between specific gravity of egg and developmental stage may have been influenced by logistical constraints of the experimental set up. For resolving this issue, I recommend to keep consistent conditions during the experiment.

Future works

Climate change in the North Pacific has significantly impacted many fish stocks (Hollowed *et al*. 2001, Hunt *et al*. 2002, and Wilderbuer *et al*. 2002). It is likely that variations in dispersal pathways induced by changes in BSC direction and strength play an important role in Greenland halibut year-class strength and recruitment success. For example, Wilderbuer *et al*. (2002), using an ocean surface current simulation model, found that 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. To identify drift pathways and successful settler, future research efforts might need model simulations considering both local and basin scales index of physical variations such as sea-ice coverage, wind (direction and strength), and sea-surface temperature and basin-scale such as the North Pacific Index (Trenberth and Hurrell, 1994), Arctic Oscillation Index, Pacific Decadal Oscillation Index, and El Niño-Southern Oscillation Index. Furthermore, size variations of suitable nursery locations for settled juveniles could affect recruitment variability on Greenland halibut in the EBS. Therefore, future study efforts may need to investigate size variability of nursery locations associated with environmental conditions such as bottom temperature and sediment type using historical survey data.

CHAPTER 5: CONCLUSION

Prior to this study, little was known about the spatial distribution and connectivity between spawning and potential nursery locations during the ontogeny of Greenland halibut in the EBS. Also, there was a general lack of knowledge regarding larval Greenland halibut feeding habits, growth, and overall ecology. Our results indicate that Greenland halibut larvae have a long pelagic duration and are subject to extended drift pathways before juvenile settlement. The distance of probable drift from spawning (near Bering Canyon) to nursery locations (near St. Matthew Island) in the Bering Sea is approximately 1,000 km, taking place over a six-month period and a vertical excursion of over 400 m. Greenland halibut occupy a variety of habitats for spawning, nursery, and settlement over this six-month period, and appear to utilize large swaths of the EBS shelf as nursery areas for immature stages. Also, their feeding ecology changes as they grow. The combined eggs and larval vertical distribution data from MOCNESS sampling indicate that Greenland halibut eggs hatch deep in water below 530 m, and then larvae rise to shallower depths as they develop and become more buoyant.

Based on these findings, I provide a schematic representation of horizontal and vertical distribution of Greenland halibut, and of connectivity between spawning areas and juvenile habitat during the first years of life (Fig. 19). The data provides evidence for spawning near Umnak and Unalaska islands, for spawning in Bering Canyon and entrainment in the BSC, for transport through Bering and Pribilof Canyons, and for nursery areas over the middle and inner domains.

I suggest that transport also occurs in Zhemchug Canyons, with slope-shelf connections similar as that described above for Bering and Pribilof Canyon. From these observations I hypothesize that recruitment in Greenland halibut may be highly vulnerable to the effects of hydrographical variations associated to meteorological forcing during larval advection. Furthermore, it is possible that size change of nursery locations could influence recruitment variability of Greenland halibut in the EBS, but further studies are needed to better clarify the role of settlement and nursery on Greenland halibut survival.
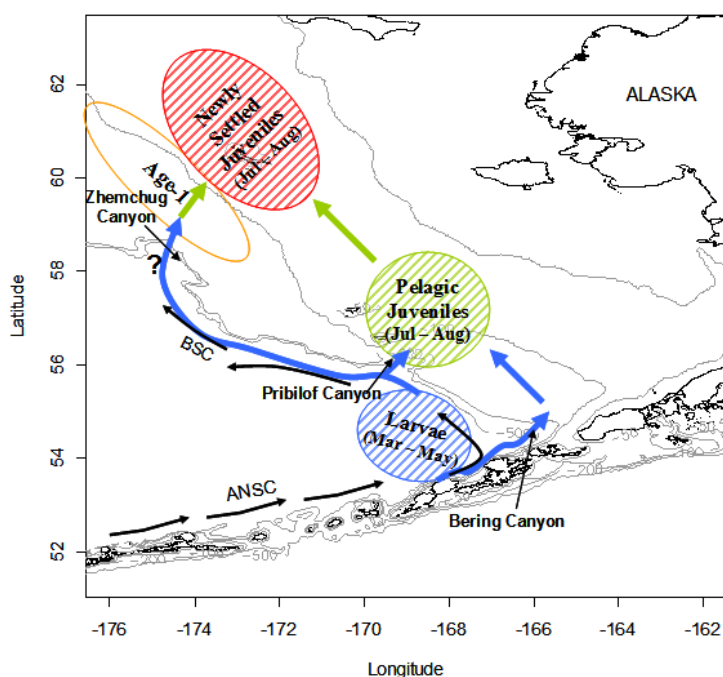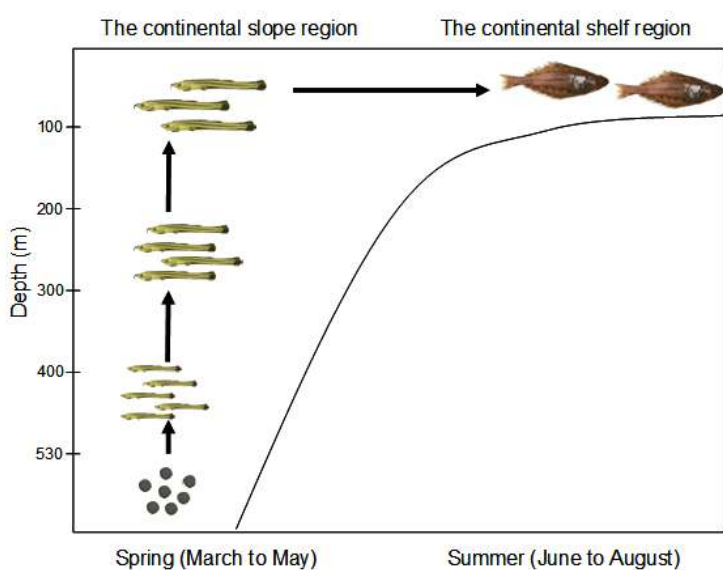
Figure 19. Schematic representations of Greenland halibut distribution and connectivity from larvae to settled juveniles. A. Horizontal distributions through different life history stages (Blue circle: larvae, Green circle: pelagic juveniles, Red circle: newly settled juveniles, Orange circle: age-1 fish, Blue arrows: possible larval transport routes from slope to shelf, Green arrows: possible movement routes of pelagic juveniles, BSC: Bering Slope Current, and ANSC: Aleutian North Slope Current. B. Vertical shifts also occurred with development.

BIBLIOGRAPHY

Ådlandsvik, B., Gundersen, A.C., Nedreaas, K.H., Stene, A. and Albert, O.T. (2004) Modelling the advection and diffusion of eggs and larvae of Greenland halibut (*Reinhardtius hippoglossoides*) in the north-east Arctic. *Fish. Oceanogr.* **13(6):** 403–415.

Albert, O.T., Nilssen, E.M., Nedreaas, K.H. and Gundersen, A.C. (2001a) Distribution and abundance of juvenile Northeast Arctic Greenland halibut (*Reinhardtius hippoglossoides*) in relation to survey coverage and the physical environment. *ICES J. Mar. Sci.* **58:**1053-1062.

Albert, O.T., Nilssen, E.M., Sten, A, and Gundersen, A.C. (2001b) Maturity classes and spawning behaviour of Greenland halibut (*Reinhardtius hippoglossoides*). *Fish. Res.* **51:**217-228.

Alton, M.S., Bakkala, R.G., Walters, G.E. and Munro, P.T. (1988) Greenland turbot *Reinhardtius hippoglossoides* of the East Bering Sea and the Aleutian Islands Region. NOAA Tech. Rep. NMFS 71, U.S. Dept. of Commerce: 31p.

Bailey, K.M. and Picquelle, S.J. (2002) Larval distribution patterns of offshore spawning flatfish in the Gulf of Alaska: sea valleys as transport pathways and enhanced inshore transport during ENSO events. *Mar. Ecol. Prog. Ser.* **236:** 205-217.

Bailey, K.M., Nakata, H. and Van der Veer, H. (2005) The planktonic stages of flatfish: physical and biological interactions in transport processes. pp. 94-119. In Gibson, R. (Ed.). Flatfishes: Biology and Exploitation. Blackwell Science Ltd, Oxford, UK, pp. 94-119.

Bailey, K.M., Abookire, A.A. and Duffy-Anderson, J.T. (2008) Pathways in the sea: A comparison of spawning areas, larval advection patterns and juvenile nurseries of offshore spawning flatfishes in the Gulf of Alaska. *Fish and Fisheries.* **9:**44-66.

Boje, J. and Hareide, N.R. (1993) Trial deepwater longline fishery in the Davis Strait, May–June, 1992. NAFO SCR Doc. 93/53, Serial No. N2236, p. 6

Boyra, G., Rueda, L., Coombs, S. H., Sundby, S., Adlandsvisk, B., Santos, M. and Uriarte, A. (2003) Modelling the vertical distribution of eggs of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*). *Fish. Oceanogr.* **12:**381-395.

Bowen, S. H. (1983) Quantitative description of the diet. In: NIELSEN, L. A.; JOHNSON, D. L. (Ed.) *Fisheries techniques.* Maryland: American Fisheries Society p. 325-336.

Brown, A.L. and K.M. Bailey (1992) Otolith analysis of juvenile walleye pollock *Theragra chalcogramma* from the western Gulf of Alaska, *Mar. Biol.* **112:**23–30.

Bulatov, D.A. (1983) Distribution of eggs and larvae of Greenland halibut (*Reinhardtius hippoglossoides*) (Pleuronectidae) in the eastern Bering Sea. *J. Ichthyol.* **23(1):**157-159.

Chiperzak, D.B., Saurette, F., and Raddi, P. (1995) First Record of Greenland Halibut (*Reinhardtius hippoglossoides*) in the Beaufort Sea (Arctic Ocean). *ARCTIC.* **48(4):** 368– 371.

Ciannelli, L. and Bailey, K.M. (2005) Landscape dynamics and resulting species interactions: the cod-capelin system in the southeastern Bering Sea. *Mar. Ecol. Prog. Ser.* **291:**227–236.

Coachman, L.K. (1986) Circulation, water masses, and fluxes on the southeastern Bering Sea shelf. *Cont. Shelf Res.* **5:**23-108.

Campana, S.E. and Neilson, J.D. (1985) Microstructure of fish otoliths. *Can J Fish Aquat Sci.* **42:**1014-1032.

Coombs, S.H. (1981) A density-gradient column for determining the specific gravity of fish eggs, with particular reference to eggs of the mackerel *Scomber scombrus. Mar. Biol.* **63**:101-106.

Coombs, S.H., Nicholsa, J.H. and Fosh, N.A. (1991) Plaice eggs (*Pleuronectes platessa L.*) in the southern North Sea: Abundance, spawning area, vertical distribution, and buoyancy. *J. Cons. Int. Explor. Mer.* **47:**133-139

Cushing, D.H. (1975) Marine ecology and fisheries. Cambridge, UK: Cambridge Univ. Press, 278 pp.

Cushing, D.H. (1982) Climate and Fisheries. London: Academic Press, 363 pp.

D'yakov, Y.P. (1982) The fecundity of the Greenland halibut, *Reinhardtius hippoglossoides* (Pleuronectidae), from the Bering Sea. *J. Ichthyol.* [Engl. Transl. Vopr. [khtiol.] **22(5):**59-64.

Duffy-Anderson, J.T., Busby, M., Mier, K.L., Deliyanides, C.M. and Stabeno, P. (2006) Spatial and temporal patterns in summer ichthyoplankton assemblages on the eastern Bering Sea shelf 1996-2000. *Fish. Oceanogr.* **15:**80-94.

Fargo, J. (1994) Examining recruitment relationships for Hecate Strait English sole (*Parophrys vetulus*). *Neth. J. Sea Res.* **32**:385–397.

Fedorov K.Y. (1971) Zoogeographic characteristics of the Greenland halibut (*Reinhardtius hippoglossoides* (Walbaum)). *J. Ichthyol.* **11(6):**971-976.

Gibson, R. N. (1994) Impact of habitat quality and quantity on the recruitment of flatfishes. *Neth. J. Sea Res.* **32:**191–206.

Godø, O.R. and Haug, T. (1989) A review of the natural history, fisheries, and management of Greenland halibut (*Reinhardtius hippoglossoides*) in the eastern Norwegian and Barents Seas. *J. Cons. Int. Explor. Mer.* **46:**62-75.

Gregg, M.C. (1998) Estimation and geography of diapycnal mixing in the stratified Ocean. In: Imberger, J. (Ed.) Physical processes in lakes and oceans. American geophysical Union, Washington DC, p.306-338.

Gregg, J.L., Anderl, D.M. and Kimura, D.K. (2006) Improving the precision of otolith-based age estimates for Greenland halibut (*Reinhardtius hippoglossoides*) with preparation methods adapted for fragile sagittae. *Fish. Bull.* **104:**643–648.

Haug, T., Bjørke, H. and Falk-Petersen, I.B. (1989) The distribution, size composition and feeding of larval Greenland halibut (*Reinhardtius hippoglossoides* Walbaum) in the eastern Norwegian and Barents Seas. Rapp. *P.-v- reun. Cons. Int. explor. Mer.* **191:**226-232.

Hjort, J. (1914) Fluctuations in the great fisheries of Northern Europe viewed in the light of biological research. Rapports et Proce`s-Verbaux des Re´unions du Conseil International pour l'Exploration de la Mer **20:** 1–228.

Hubbs, C.L. and Wilimovsky, N.J. (1964) Distribution and synonymy in the Pacific

Ocean and variation of the Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum). *Journal of the Fisheries Research Board of Canada* **21:**1129–1154.

Hunt Jr., G.L., Stabeno, P., Walters, G., Sinclair, E., Brodeur, R.D., Napp, J.M., Bond, N.A. (2002) Climate change and control of the southeastern Bering Sea pelagic ecosystem. *Deep-Sea Research Part II* **49:**5821–5853.

Hollowed, A.B., S.R. Hare, and Wooster, W.S. (2001) Pacific Basin climate variability and patterns of Northeast Pacific marine fish production. *Progr. Oceanogr.* **49:**257-282.

Houde, E.D. (1987) Fish early life dynamics and recruitment variability. *Am. Fish. Soc. Symp.* **2:** 17-29.

Houde, E. D. (1989) Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. Fishery Bulletin U.S. **87:** 471–495.

Hyslope, E. J. (1980) Stomach content analysis: a review of methods and their applications. *J. Fish Biol.,* Southampton, 17(4):411-429.

Ianelli, J.N. and Wilderbuer, T.K. (1995) Greenland turbot (*Reinhardtius hippoglossoides*) stock assessment and management in the Eastern Bering Sea. In: Proceedings of the International Symposium on North Pacific Flatfish. Alaska Sea Grant. AK-SG-95-04:407-441.

Ianelli, J.N., T.K. Wilderbuer, and Nichol, D. (2007). Stock assessment of Greenland turbot. In Stock assessment and fishery evaluation document for groundfish resources in the Bering Sea/Aleutian Islands region. Section 5. North Pacific Fishery Management Council, Anchorage, AK. http://www.afsc.noaa.gov/refm/docs/2007/BSAIturbot.pdf

Lasker, R. (1975) Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. *Fish. Bull.* US 73:453-462.

Jensen, A. (1935) The Greenland halibut (*Reinhardtius hippoglossoides*), its developement and migration. *K. Dan. Vidensk. Selsk. Skr.* **9:** 1-32.

Jørgensen, O. A. (1997) Movement patterns of Greenland halibut, Reinhardtius hippoglossoides, at West Greenland, as inferred from trawl survey distribution and size data. *Journal of Northwest Atlantic Fishery Science* **21:** 23–37.

Kendall AW, Jr, Kim S (1989) Buoyancy of walleye pollock (*Theragra chacogramma*) eggs in relation to water properties and movement in Shelikof Strait, Gulf of Alaska, p. 169-180. *In* R. J. Beamish and G. A. McFArlane [ed.] Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models. Can. Spec. Pub. Fish. Aquat. Sci. 108.

Lagardère, F. and Troadec, H. (1997) Age estimation in common sole *Solea solea* larvae: validation of daily increments and evaluation of a pattern recognition technique. *Mar. Ecol. Prog. Ser.* **155:**223-237.

Lanksbury, J.A., Duffy-Anderson, J.T., Busby, M., Stabeno, P.J. and Mier, K.L. (2007) Abundance and distribution of northern rock sole (*Lepidopsetta polyxystra*) larvae in relation to oceanographic conditions in the southeastern Bering Sea. *Prog. Oceanogr.* **72:** 39-62.

Leggett, W. C. and DeBlois, E. M. (1994) Recruitment in marine fishes: is it regulated by starvation and regulation in the egg and larval stages? *Neth. J. Sea Res.* **32:** 119–134.

Matarese, A.C., Blood, D.M., Picquelle, S.J., and Benson, J.L. (2003) Atlas of abundance and distribution patterns of ichthyoplankton from the northeast Pacific Ocean and Bering Sea ecosystems based on research conducted by the Alaska Fisheries Science Center (1972-1996). NOAA Prof. Paper NMFS vol. 1. 281pp.

Mayer, C.M. and Wahl, D.H. (1997) The relationship between prey selectivity and growth and survival in a larval fish. *Can. J. Fish. Aquat. Sci.* 54: 1504-1512.

McConnaughey, R.A. and Smith, K.R. (2000) Associations between flatfish abundance and surficial sediments in the eastern Bering Sea. *Can. J. Fish. Aquat. Sci.* **57:** 2410–2419

Methot, R.D. (1986) Frame trawl for sampling juvenile fish. *Calif. Coop. Oceanic Fish. Invest. Rep.* **27:**267-278.

Miller, J. M., Burke, J. S., and Fitzhugh, G. R. (1991) Early life history patterns of Atlantic North American flatfish: likely and (unlikely) factors controlling recruitment. *Neth. J. Sea Res.* **27:** 261–275.

Mizobata, K. and Saitoh, S. (2004) Variability of Bering Sea eddies and primary productivity along the shelf edge during 1998-2000 using satellite multisensor remote sensing. *J. Mar. Syst.* **50:** 101-111.

Mizobata, K., Saitoh, S.-I., Wang, J., 2008. Interannual variability of summer biochemical enhancement in relation to mesoscale eddies at the shelf break in the vicinity of the Pribilof Islands, Bering Sea. *Deep-Sea Research II* **50(16-17)**:1717-1728.

Musienko, L.N. 1970. Reproduction and development of Bering Sea fishes. Tr. Vses. Nachnoissled. Inst. Morsk. Rybn. Khoz. Okeanogr. 70 (Izv. Tikhookean. Nauchno-issled. Inst. Morsk. Rybn. Khoz. Okeanogr. 72:166-224) Transl. *In* Sov. Fish. Invest. Northeast Pac., pt. V:161-224. Isr. Program Sci. Transl., 1972.

Nielsen, E., Bagge, O., and MacKenzie, B. R. (1998) Windinduced transport of plaice (*Pleuronectes platessa*): early life-history stages in the Skagerrak-Kattegat. *Journal of Sea Research* **39:** 11–28.

Nikolenko, L.P. (1998) Distribution of eggs, larvae, and pelagic young of the Greenland turbot Reinhardtius hippoglossoides in the Sea of Okhotsk. *Russian Journal of Marine Biology.* **24(1)**:14-18.

Parada, C., Armstrong, D.A., Ernst, D., Hinckley, S. and Orensanz, J.M. (In review) Spatial dynamics of snow crab (*Chionoecetes opilio*) in the eastern Bering Sea. *Bull. Mar. Sci.*

Parrish, R. H., Nelson, C. S. and Bakun, A. (1981) Transport mechanisms and reproductive success of fishes in the California Current. *Biol. Oceanogr.* **1:** 175-203.

Schumacher, J.D. and Stabeno, P.J. (1998) The continental shelf of the Bering Sea. In: The Sea, Vol. XI. The Global Coastal Ocean: Regional Studies and Synthesis. New York: John Wiley, Inc., pp. 789-822.

Stenberg, C. (2007) Recruitment processes in West Greenland waters: with special

focus on Greenland halibut (Reinhardtius hippoglossoides, W.). PhD thesis. The University of Bergen.

Rijnsdorp, A. D., Van Beek, F. A., Flatman, S.,Millner, R. M., Riley, J. D., Giret, M., and De Clerck, R. (1992) Recruitment in sole stocks, *Solea solea* (L.) in the northeast Atlantic. *Neth. J. Sea Res.* **29:** 173–192.

Schott, J.W. (1966) A Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum) recorded in southern California. *California Fish and Game* **52(1)**:55–56.

Sinclair, M. (1988) Marine populations: an essay on population regulation and speciation.Washington Sea Grant, Univ. Washington Press, Seattle, 252p

Smidt, E.L.B. (1969) The Greenland halibut, *Reinhardtius gippoglossoides* (Walb.), biology and exploitation in Greenland waters. Meddr Danm.Fisk.-og Havunders., N.S., **6(4):**79-148.

Springer, A.M., McRoy, P.C. and Flint, M.V. (1996) The Bering Sea Green Belt: shelf-edge processes and ecosystem production. *Fish. Oceanogr.* **5:**205-223.

Stabeno, P.J., Kachel, N.B., Mordy, C.W., Righi, D. and Salo, S.A. (2008) An examination of the physical variability around the Pribilof Islands in 2004. *Deep- Sea Res*. **2(55):** 1701–1716.

Stabeno, P.J. and Meurs, P.V. (1999) Evidence of episodic on-shelf flow in the southeastern Bering Sea. *Journal of Geophysical Research* **104 (29):**715–720.

Stabeno, P.J., Schumacher, J.D. and Ohtani, K. (1999) The physical oceanography of the Bering Sea. In: *Dynamics of the Bering Sea.* T.R. Loughlin & K. Ohtani (eds) Fairbanks, AK: University of Alaska Sea Grant, Program Rep. 96-01, pp. 1-28.

Stabeno, P.J., Bond, N.A., and Salo, S.A. (2007) On the recent warming of the southeastern Bering Sea shelf. *Deep-Sea Res.* 2. **54:** 2599–2618.

Stene, A., Gundersen, A.C., Albert, O.T., Nedreaas, K.H. and Solemdal, P. (1999) Early development of Northeast Arctic Greenland halibut (*Reinhardtius hippoglossoides*). *J. Northw. Atl. Fish. Sci.* **25:** 171 – 177.

Shuntove, V.P. (1965) Distribution of the Greenland halibut and arrowtooth halibuts in the north Pacific. Vsesoyuznyi Nauchno-Issledovatel'skii Institut Morskogo Rybnogo Khozyaistva I Okeanografii 53:155–163. English translation, 1968. In: Soviet fisheries investigation in the northeastern Pacific, Part IV. 147– 156. Jerusaleum: Israel Program for Scientific Translations.

Sundby, S. (1983) A one-dimensional model for the vertical distribution of pelagic fish eggs in the mixed layer. *Deep Sea Res.* **30:**645–661.

Sundby, S. (1991) Factors affecting the vertical distribution of eggs. *ICES Mar. Sci. Symp.* **192:**33–38.

Swartzman, G., Huang, C., and Kaluzny, S. (1992) Spatial analysis of Bering Sea groundfish survey data using generalized additive models. *Can. J. Fish. Aquat. Sci.* **49**: 1366–1378.

Templeman, W. 1973. Distribution and abundance of the Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum) in the northwest Atlantic. *ICNAF Res. Bull.* **10:**83-98.

Trenberth. K.E. and Hurrell, J.W. (1994) Decadal Atmosphere-Ocean Variations in the Pacifc. *Climate Dynamics* **9:** 303-319.

Van der Veer, H.W., Ruardij, P., Van den Berg, A.J. and Ridderinkho, H. (1998)

Impact of interannual variability in hydrodynamic circulation on egg and larval transport of plaice *Pleuronectes platessa* L. in the southern. *North. Sea. J. Sea. Res.* **39:** 29-40.

Van der Veer, H.W., A.J. Geffen and J.I.J. Witte (2000) Exceptionally strong year classes in plaice *Pleuronectes platessa*: are they generated during the pelagic stage only, or also in the juvenile stage? *Mar. Ecol. Prog. Ser. 199:*255-262.

Van der Veer, H.W. and Leggett, W.C. (2005) Recruitment. In: Gibson, R.N. (Ed.) Flatfishes. Biology and exploitation. Blackwell Fish and Aquatic Resources Ser 9, Blackwell Oxford, London, 120-137.

Westrheim, S.J., and Pletcher, F.T. (1966) First records of the twoline eelpout, *Bothrocara brunneum*, Greenland halibut, *Reinhardtius hippoglossoides*, and shortbelly rockfish, *Sebastodes jordani*, in British Columbia waters. Journal of the Fisheries Research Board of Canada **23(2):**309– 312.

Wiebe, P.H., Burt, K.H. Boyd, S.H. and Morton, A.W. (1976) A multiple opening/closing net and environmental sensing system for sampling zooplankton. *Journal of Marine Research* **34:** 313-326.

Wilderbuer, T.K., Hollowed, A.B., Ingraham, W.J., Spencer, P.D., Conners, M.E., Bond, N.A. and Walters, G.E. (2002) Flatfish recruitment response to decadal climate variability and ocean conditions in the eastern Bering Sea. *Prog. Oceanogr.* **55:** 235-248.