Combining field observations and modeling approaches to examine Greenland halibut (*Reinhardtius hippoglossoides*) early life ecology in the southeastern Bering Sea

J.T. Duffy-Anderson [a,*], D.M. Blood [a], W. Cheng [b], L. Ciannelli [c], A.C. Matarese [a], D. Sohn [c], T.C. Vance [a], C. Vestfals [c]

[a] Recruitment Processes Program, Resource Assessment and Conservation Engineering Division, Alaska Fisheries Science Center, NOAA Fisheries, 7600 Sand Point Way NE, Seattle, WA 98115, USA
[b] Joint Institute for the Study of the Atmosphere and Ocean, P.O. Box 354235, University of Washington, Seattle, WA 98195, USA
[c] College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis, OR 97331, USA

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ABSTRACT

Spawning in Greenland halibut (*Reinhardtius hippoglossoides*) occurs along the continental slope and in submarine canyons in the eastern Bering Sea. It is assumed that these bathymetric features and their associated circulation patterns deliver eggs and larvae to suitable nursery habitats over the continental shelf. However, there have been no directed field studies examining spawning areas or transport of Greenland halibut early life stages in the Bering Sea, nor is it known how large-scale oceanographic forcing modulates specific physical mechanisms of delivery. The present study was undertaken to: better define spawning areas of Greenland halibut, examine development and distribution of larvae, and understand the influence of climate variations on interannual patterns of transport, distribution and abundance. Eggs were found in Bering and Pribilof Canyons and over the adjacent slope in February and early March, confirming that spawning occurs in these regions. Larvae were present over the slope, outer shelf and middle shelf in winter and spring, and settled juveniles were collected over the shelf in September. Oceanographic modeling approaches that simulate larval advection from spawning to nursery habitats indicate that depth-discrete variations in transport pathways from submarine canyons to the adjacent shelf contribute to interannual variability in transport trajectories. Overall, our results highlight specific physical mechanisms of delivery that are modulated by large-scale atmospheric and oceanographic forcing, potentially varying the degree of slope–shelf connectivity for Greenland halibut and other slope-spawning species.

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1. Introduction

The role of oceanographic features in structuring marine habitat use has long been an area of intense scientific interest and research effort. Fundamental theories espouse that on evolutionary time scales, fishes spawn in areas with existing bathymetric features and persistent circulation patterns that deliver larvae to suitable nursery habitats. Deep water (>400 m), slope-spawning species that have juveniles that recruit to nursery habitats over the continental shelf (<200 m) must contend with the necessity of spawning in areas that afford vertical connectivity in addition to horizontal connectivity. For these species, propagules must be reliably advected up the slope margin and then across the continental shelf to target nursery habitats. Deepwater flatfishes are particularly well-adapted to this unique combination of criteria (e.g., Bailey et al., 2008; Minami and Tanaka, 1992). However, though species may be well-adapted to make use

of environmental features that promote directed transport of offspring, it is likely that the specific physical mechanisms of delivery are modulated by large-scale atmospheric and oceanographic forcing, potentially varying the degree of slope–shelf connectivity.

The southeastern Bering Sea (Fig. 1) is characterized by a deep basin (depth range 200–3500 m) and a wide continental shelf (>500 km) which is further subdivided by bathymetry into three major domains: the inner continental shelf (<50 m), the middle shelf (50 m–100 m), and the outer shelf (100 m–200 m). General circulation in the basin is in the form of a cyclonic gyre, with the Kamchatka Current forming the western boundary, the Aleutian North Slope Current flowing eastward along the Aleutian Islands, and the Bering Slope Current forming the eastern boundary (Stabeno et al., 1999). Several submarine canyons traverse the slope margin, Zhemchug Canyon to the north, followed by Pribilof, and Bering Canyons to the south (Fig. 1). Pribilof and Zhemchug Canyons have trough shaped basins while Bering Canyon has a wide slope valley (>400 km). These canyons and adjacent slopes form important spawning grounds for a number of marine fish and elasmobranch species including skates (Hoff, 2010), rockfishes (Love et al.,

2002), smoothtongues (Sinclair and Stabeno, 2002), and flatfishes (Sohn et al., 2010; St-Pierre, 1984), and are hypothesized to facilitate flux of water and entrained particles from the basin to the shelf (Normark and Carlson, 2003).

Spawning in the circumpolar deepwater flatfish, Greenland halibut (*Reinhardtius hippoglossoides*), also known as Greenland turbot (Ianelli et al., 2011), in the Bering Sea is believed to occur over the slope and in large submarine canyons, with larvae and juveniles recruiting to the middle and outer domains of the continental shelf (Sohn et al., 2010). Spawning has generally been inferred from observations of distribution of larval stages, as published reports of egg distributions for this species in the Pacific are few (Bulatov, 1983; Mikawa, 1963; Pertseva-Ostroumova, 1961). The lack of data has been based, in part, from the inability to conclusively identify Greenland halibut eggs based on morphology alone. Moreover, a comprehensive morphological description is lacking for Greenland halibut early life stages collected in the North Pacific, though some information for the species in the North Atlantic has been published (Stene et al., 1999).

Oceanographic modeling has been previously used to examine dispersal and transport pathways of Greenland halibut in Greenland waters and in the north-east arctic (Ådlandsvik, 2000; Ådlandsvik et al., 2004). This approach revealed that transport of Greenland halibut early life stages in these systems is dependent upon spawning location, transport depth, and interannual variability in dominant flow regime. The present study aimed to continue and extend the published work on Greenland halibut to the Bering Sea by: 1) using directed field sampling (2006–2010) to more completely describe early life ecology in Bering Sea, 2) providing a more complete taxonomic description of the morphology and development of the early life stages, and 3) employing an oceanographic circulation model to better understand how climate variations may affect interannual patterns of transport, distribution and connectivity of this species between spawning and nursery areas.

2. Materials and methods

2.1. Study area and biological sampling

The geographic regions of sampling were the eastern Bering Sea (EBS) slope and adjacent shelf in the vicinity of Bering and Pribilof Canyons (Fig. 1). Multiple field surveys (February, May, September) were conducted over a period of four years (2006–2010) aboard the NOAA Ships *Miller Freeman* and *Oscar Dyson* (Table 1). All months were not sampled in all years because cruise timing was opportunistic and occasionally constrained by logistical factors. The primary objective of Greenland halibut work on all cruises was to examine the abundance and distribution of Greenland halibut eggs, larvae, and juveniles in the EBS. Depth-integrated egg and larval samples were collected using 60 cm bongo nets strung with 0.505 mm mesh. Tows were to 10 m off-bottom over the continental shelf, and to 500 m or 600 m over the slope and basin as determined in real time. Vertically stratified tows were conducted at selected stations when eggs were observed in bongo collections. Depth intervals sampled were: 0–20 m, 20–30 m, 30–40 m, 40–50 m, 50–100 m, 100–200 m, 200–300 m, and 300–400 m. Depth-discrete sampling was accomplished using the Multiple Opening and Closing Net and Environmental Sensing System (MOCNESS; Wiebe et al., 1976). The volume of water filtered by both types of nets was estimated using calibrated flow meters. The ship's speed was adjusted to maintain a tow wire angle of 45°. Upon net retrieval, ichthyoplankton samples were immediately preserved in 5% buffered formalin. Preserved samples were sorted and larvae were identified and measured (standard length in mm, SL) at the Plankton Sorting and Identification Center in Szczecin, Poland. Verification of all larval identifications and egg measurements was done at either Oregon State University in Corvallis, OR, USA or at the Alaska Fisheries Science Center (AFSC), in Seattle, WA, USA.

Settled juvenile Greenland halibut were collected in autumn using a 3.05 m plum staff beam trawl rigged with 7 mm mesh, a 4 mm cod end liner, and tickler chains (Gunderson and Ellis, 1986). Towing speeds ranged from 1.5 to 3 knots. The towed area was calculated and data were standardized to CPUE for an area of 1000 m². Juvenile Greenland halibut were identified, separated from the main catch, and immediately frozen at −20 °C. In the laboratory, samples were thawed, identifications were verified, and individuals were measured (total length in mm, TL).

2.2. Physical environment

Physical data were collected simultaneously with biological samples using either SeaBird[1] SBE 911 plus Conductivity Temperature Depth (CTD) casts, a SeaBird[1] SEACAT profiler SBE 19 Plus attached in-line with plankton net arrays, or a net-mounted SeaBird[1] SBE-39 temperature and depth profiler attached to the beam trawl (juveniles).

2.3. Egg and larval taxonomy and development

Taxonomic and morphological data were obtained from eggs and larvae collected during the above ichthyoplankton surveys and from historical surveys conducted from 1979 to 2009 by the Recruitment Processes Program at the AFSC.[2]

Marine teleost eggs are typically identified by their size if they are in the early stage of development and the embryo has not formed, or if distinctive characters are not visible from the developing embryo. Conclusive identification of early-stage Greenland halibut eggs in the Bering Sea has been confounded by the presence of Pacific halibut (*Hippoglossus stenolepis*) eggs, which spatially and temporally co-occur with Greenland halibut eggs (Matarese et al., 1989; 2003). Late-stage Greenland halibut eggs can be identified by the 60–65 myomeres visible in the embryo as compared to Pacific halibut that have a maximum of 51 myomeres. To determine whether Greenland halibut eggs could be identified from the Bering Sea, we conducted an extensive examination of historical collections of Pacific halibut eggs collected in the Gulf of Alaska, where Greenland halibut do not occur. We reasoned that if we could determine a maximum size for Pacific halibut eggs from the Gulf of Alaska collections (193 eggs), we could assume that early-stage eggs collected in the Bering Sea that exceeded the maximum size of Pacific halibut eggs were probably Greenland halibut. Using this approach we determined that all Pacific halibut eggs from the Gulf of Alaska were <3.5 mm diameter, and assumed that all eggs ≥3.5 mm diameter in the Bering Sea were those of Greenland halibut. The smallest late-stage egg that could be positively identified as Greenland halibut was 3.54 mm, which was close to our threshold size. It should be noted that we do not know the minimum size of Greenland halibut eggs, and eggs smaller than 3.5 mm diameter in our collections may have been erroneously identified as Pacific halibut. Thus our approach may have underestimated abundances of Greenland halibut eggs collected from our surveys, and the values should be considered conservative.

2.4. Egg developmental staging

Greenland halibut eggs were staged according to developmental criteria described by Blood et al. (1994) according to a 21-stage schedule developed and standardized for walleye pollock (*Theragra chalcogramma*). Staging criteria for walleye pollock are the standards to which northern marine teleost egg development are compared and were easily adapted to egg development in Greenland halibut. Eggs

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