Dispersal and behavior of Pacific halibut *Hippoglossus stenolepis* in the Bering Sea and Aleutian Islands region

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ABSTRACT: Currently, it is assumed that eastern Pacific halibut *Hippoglossus stenolepis* belong to a single, fully mixed population extending from California through the Bering Sea, in which adult halibut disperse randomly throughout their range during their lifetime. However, we hypothesize that halibut dispersal is more complex than currently assumed and is not spatially random. To test this hypothesis, we studied the seasonal dispersal and behavior of Pacific halibut in the Bering Sea and Aleutian Islands (BSAI). Pop-up Archival Transmitting tags attached to halibut (82 to 154 cm fork length) during the summer provided no evidence that individuals moved out of the Bering Sea and Aleutian Islands region into the Gulf of Alaska during the mid-winter spawning season, supporting the concept that this region contains a separate spawning group of adult halibut. There was evidence for geographically localized groups of halibut along the Aleutian Island chain, as all of the individuals tagged there displayed residency, with their movements possibly impeded by tidal currents in the passes between islands. Mid-winter aggregation areas of halibut are assumed to be spawning grounds, of which 2 were previously unidentified and extend the species' presumed spawning range ~1000 km west and ~600 km north of the nearest documented spawning area. If there are indeed independent spawning groups of Pacific halibut in the BSAI, their dynamics may vary sufficiently from those of the Gulf of Alaska, so that specifically accounting for their relative segregation and unique dynamics within the larger population model will be necessary for correctly predicting how these components may respond to fishing pressure and changing environmental conditions.

KEY WORDS: Spawning component · Spawning dispersal · Pacific halibut · PSAT tag · PAT tag · Bering Sea · Aleutian Islands

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INTRODUCTION

Marine fish species may have complex population structures, and, in many cases, management units contain population complexes with several spawning components (Stephenson 1999). For example, several stocks of Atlantic herring *Clupea harengus* mingle in common feeding areas, yet they maintain genetic differentiation based on spatial and temporal differences in migratory behavior and homing to spawning locations (Ruzzante et al. 2006). Segregation of spawning into discrete components has the potential to generate internal population structures at scales not adequately captured in a single-unit-stock management approach

(Stephenson 1999, Frank & Brickman 2001). Therefore, knowledge of seasonal dispersal and spawning locations of a migratory fish species can aid in fishery management.

The Pacific halibut *Hippoglossus stenolepis* fishery is an important resource throughout western Alaska, with 3200 t (estimated value: US\$25 million ex-vessel) of dressed product (gutted and gilled) landed during 2009 in the Southeast Bering Sea and Aleutian Islands (BSAI) fishery¹ (Fig. 1). Little is known about the ecology of adult halibut in the Bering Sea and along the

¹Areas 4A to D in www.fakr.noaa.gov/ram/ifqreports.htm (accessed on 21 June 2010)

Fig. 1. Map of the North Pacific Ocean with a depth key. Dotted lines indicate the dominant circulation pattern in the Bering Sea (Stabeno et al. 1999)

Aleutian Islands. It is assumed that adult halibut feed in shallow, nearshore areas during the summer, undertake a spawning migration to deeper water during winter, and return to their summer grounds during spring (Dunlop et al. 1964, Best 1981). In the Southeast Bering Sea (SEBS), spawning appears to be concentrated in relatively discrete winter spawning grounds near the edge of the continental shelf in the Bering Canyon and the Pribilof Canyon (Fig. 1) (St-Pierre 1984). After spawning, egg and larval stages drift pelagically in the Bering Sea gyre for approximately 6 mo (Skud 1977, St. Pierre 1989) and then settle in nearshore areas (Thompson & Van Cleve 1936). After settling, it is thought that juvenile halibut conduct contranatal migrations to the area in which they were spawned to maintain population stationarity (Skud 1977, Hilborn et al. 1995).

From the 1930s through the 1950s, at least 3 stocks of halibut were recognized, 1 in the Bering Sea and 2 in the Gulf of Alaska (GOA) (Fukuda 1962, Skud 1977). After this period, research indicated extensive intermingling of halibut among areas, and it was assumed that there was only a single stock of halibut. This research was based, in part, on 2 lines of evidence: (1) conventional tagging experiments (Skud 1977, review in Kaimmer 2000), in which a portion of halibut tagged on the SEBS continental shelf dispersed to the GOA, and (2) surveys conducted during the winter spawning season that only identified major spawning grounds in the GOA and a small portion of the southeastern-most corner of the Bering Sea (St-Pierre 1984). More recently, the results of an extensive passive integrated transponder (PIT) tagging study (Kaimmer & Geernaert 2004) have suggested broad-scale dispersal throughout Alaska and British Columbia of halibut large enough (i.e. ≥ 82 cm fork length [FL]) to be legally retained by the commercial fishery (Clark & Hare 2007).

Because of this previous research, it is assumed that eastern halibut belong to a single, fully mixed population extending from California through the Bering Sea, in which adult halibut disperse randomly throughout their range during their lifetime. Therefore, since 2007, the total abundance of eastern halibut has been assessed on a coast-wide basis from California to the Bering Sea, treating the population as a single entity that is homogenized over time due to migration (Clark & Hare 2007). From the perspective of fishable biomass, the paradigm of a single fully mixed stock suggests that local processes are subordinate to those governing overall abundance and that local effects of harvest depletion will be ameliorated by subsequent immigration from adjacent areas. At the reproductive level, the paradigm of a fully mixed stock implies that halibut from several feeding areas, including halibut from the BSAI region and those from the GOA (Fig. 1), mingle on common spawning grounds or at least display some degree of migratory interlacing between adjacent regions (e.g. Koutsikopoulos et al. 1995) without clear geographic segregation in dispersal patterns.

Evidence indicates that the single population paradigm for halibut is simplistic and that some level of either limited dispersal or reproductive isolation occurs in the BSAI region. Early genetic evidence (Grant et al. 1984, Bentzen et al. 1999) was consistent with the hypothesis of panmixia, but recent work suggests mixing of some stock components (Hauser et al. 2006, Nielsen et al. 2010). Accordingly, population dynamics in the SEBS, Aleutian Islands, and GOA have appeared somewhat decoupled from one another over the last decade. Indices of survey and commercial catch per unit effort (CPUE), and of exploitable biomass (i.e. that portion of the stock which is vulnerable to capture on longline gear), have remained relatively stable in the central GOA, whereas declines of 50 to 70% in all

indices have been observed in the BSAI region (Hare & Clark 2008). These indicators appear to have stabilized in the Aleutian Islands, where a lower exploitation rate has recently been adopted relative to the GOA (Hare 2006), but the downward trend has persisted in the SEBS. This prompted the International Halibut Commission (IPHC), to label the SEBS 'an area of concern' in 2007 (Hare & Clark 2008) and suggest that lower exploitation rates may need to be invoked throughout the Bering Sea. Differences between the dynamics of the BSAI region and GOA have been attributed to differential recruitment strength of important year classes (Hare 2006, Hare & Clark 2008), implying that the stock must be spatially structured in terms of pre-recruit abundance and distribution. At smaller spatial scales, local depletions, in which commercial CPUE steadily decreased over several years, have occurred in the Pribilof Islands region of the SEBS, as well as in the Aleutian Islands area (Hare 2005, 2006). In the case of the Pribilof Islands, commercial CPUE declined roughly 3-fold from 1995 through 2003, accompanied by harvest shortfalls that rose from a mean of around 10% of the annual regional quota to nearly 60% (Loher 2008). Each year's regional quota was established as a set proportion of estimated eastern Bering Sea abundance, and therefore no such shortfalls should have occurred in a fully mixed population where dispersal of post-recruit age classes is expected to have a homogenizing effect over timescales relevant to the fishery.

Previous conventional tagging studies (Kaimmer 2000, Kaimmer & Geernaert 2004) primarily examined summertime dispersal and ontogenetic migrations and therefore leave many questions regarding halibut movement and potential population structure unanswered. For example, conventional tags provide limited information on dispersal and behavior of individuals during time at liberty because no information regarding location or depth occupied by the halibut is obtained between tag deployments and recapture locations. Additionally, conventional tagging results can be influenced by fishing effort (Hilborn et al. 1995, Bolle et al. 2001) and for halibut, they tend to be restricted to analyses of feeding distributions rather than spawning distributions, as the commercial fishery is closed during the winter spawning season (IPHC 1998). From a demographic perspective, it is important to understand the structure of spawning components within the population, necessitating tagging methods that can reliably generate data during the winter spawning season, when actual genetic exchange occurs. In particular, no IPHC winter surveys have ever been conducted along the Aleutian Islands or farther north than the Pribilof Canyon in the Bering Sea (St-Pierre 1984). Therefore, it is possible that previously unidentified spawning grounds exist, which could

change our interpretation of population structure of halibut in the Northeast Pacific Ocean.

On an ocean-basin scale, we hypothesize that the BSAI region contains a discrete spawning component, defined as a region from which little or no emigration occurs for the purpose of spawning, of halibut in the eastern Pacific Ocean, because land masses and ocean currents partially separate the BSAI region from the GOA. If there is indeed a discrete spawning component of halibut in the BSAI region, this may have a substantial impact on local productivity and stock dynamics in the fisheries and may, in part, explain the apparent decoupling of BSAI abundance trends from those observed in the central GOA. Therefore, the goal of the present study was to investigate halibut that feed during the summer in the BSAI to determine the degree to which they remain there to spawn or move into the GOA. To accomplish this goal, we tagged adult halibut in the BSAI with pop-up archival transmitting (PAT) tags. This technology allows us to determine winter location of the tagged halibut and to infer behavioral patterns in a manner that is free of the recapture biases inherent in conventional tagging studies. For the analysis in this study, the area south of the Aleutian Islands will be considered part of the BSAI.

MATERIALS AND METHODS

Study area. The Bering Sea is a semi-enclosed, high-latitude sea that is 2 million km² in area and is bounded on the north and west by Russia, on the east by Alaska, and on the south by the Aleutian Islands (Fig. 1; Stabeno et al. 1999). It is divided almost equally between a deep basin (maximum depth: 3500 m) and the continental shelf (<200 m), which is broad in the eastern portion of the sea (>500 km). The dominant circulation in the Bering Sea basin is a cyclonic gyre, with southward flow forming the western boundary current and northward flow forming the eastern boundary current. The Aleutian Islands form a permeable barrier between the Bering Sea and the GOA. Unimak Pass, which is relatively shallow (<80 m) and narrow (30 km), forms the only significant conduit between the continental shelves of the GOA and the eastern Bering Sea. Of the 14 main Aleutian passes, only 3 are deeper than 700 m.

PAT tag deployment. Four deployments of Wildlife Computers PAT tags were conducted from 2002 to 2008; these provided data on the dispersal of halibut from summer feeding areas (i.e. tag release locations) in the BSAI to their winter grounds (i.e. tag reporting and recovery locations). PAT tags were attached following a previous protocol (Seitz et al. 2003), adapted from similar deployments of pop-up tags on Atlantic bluefin

Table 1. *Hippoglossus stenolepis*. Deployment summary: pop-up archival transmitting (PAT) tags attached to halibut in the Bering Sea and Aleutian Islands region

Tagging location	Year	No. of fish tagged	No. of tag recoveries	Fork length (cm) Mean ± SD	No. of tags with winter locations	No. of days at liberty Mean ± SD	Longitude No. of tags No. of estimates		Displacement (km) Mean ±SE
Aleutian Islands									
Attu Island	2004	13	11	131.1 ± 16.4	11	204.3 ± 1.8	11	129	46.1 ± 9.8
Atka Island	2004	12	5	126.0 ± 13.7	5	195.2 ± 2.6	5	25	41.5 ± 31.4
Amchitka Pass	2008	4	1	119	1	195	1	98	102
Southeast Bering Sea									
Bering Canyon	2006	12	11	117.4 ± 4.7	9	156.4 ± 12.2	5	7	42.7 ± 19.4
Bering Canyon	2008	18	6	90.0 ± 8.0	6	218.0 ± 24.5	5	166	147.7 ± 36.3
St. Paul Island	2002	9	8	121.1 ± 8.9	6	184.3 ± 1.4	6	137	161.8 ± 72.4
Middle Canyon	2006	12	12	118.9 ± 8.0	10	240.9 ± 1.4	9	151	186.6 ± 104.2
Middle Canyon	2008	18	1	84	1	164	1	29	782

tuna *Thunnus thynnus* (Block et al. 1998). The halibut were captured by hook and line, using benthic longline gear rigged with 16/0 circle hooks on 0.7 to 1.3 m gangions with 5.5 m spacing, baited with chum salmon *Onchorhynchus keta*, and soaked during daylight for approximately 6 h prior to retrieval. From 2002 to 2006, the halibut were deemed appropriate for PAT tagging and released if they were >105 cm FL because they were likely to be sexually mature (Clark et al. 1999). In 2008, the tag tether configuration was modified to allow halibut of all commercially legal sizes (≥ 82 cm FL) to be tagged. The tags were connected to titanium darts with a tether that was 15 cm in length and constructed of 130 kg test monofilament fishing line wrapped in adhesive lined shrinkwrap. The darts were inserted through the dorsal musculature and pterygiophores, anchoring them in the bony fin ray supports of the body. The position of the darts was about 2.5 cm medial of the dorsal fin on the eyed side of the halibut where the body began to taper towards the tail.

A total of 98 halibut were tagged and released during 4 summers (Table 1, Fig. 2). Tagging from 2002 to 2006 was conducted at discrete tagging sites, while tagging in 2008 employed a broader release design, in which halibut were tagged in an approximately even spatial distribution along the entire length of the Aleutian Island chain and along the continental shelf edge from Bering Canyon to Middle Canyon.

Data collection and analyses. Each PAT tag contained 3 electronic sensors that measured ambient water temperature, depth of the tag, and ambient light intensity (Seitz et al. 2003, Teo et al. 2004). On a pre-programmed date, the PAT tags actively corroded the pin to which the tether was attached, thus releasing the tag from the animal. The tag then floated to the surface and transmitted summarized historical data records to the Argos satellite² system. Upon popping up, the tags' endpoint positions were determined from

the Doppler shift of the transmitted radio frequencies in successive uplinks received during 1 Argos satellite pass (Keating 1995). The transmitted data then were processed further by Wildlife Computers' PC-based software.

Two generations of tags were used: older PAT tags (serial numbers 00P####, 02P####, and 04P####) and newer PAT tags (serial numbers 06A####). The older PAT tags did not have a premature detachment detection function. Therefore, if they detached from the halibut before the scheduled pop-up date because of a connection malfunction, the tags would drift on the surface of the ocean until the programmed pop-up date and then report to Argos. Newer PAT tags had a premature detachment detection function, which was activated by 8 consecutive days of depth readings of 0 m. Upon activation of the premature detachment detection function, the tags reported to Argos. PAT tags deployed in 2002 and 2004 were programmed to detach on 15 February of the year following the fishes' tagging, and tags deployed in 2006 were programmed to detach on 1 February, to determine the fishes' winter grounds, as adult halibut are thought to spawn annually from approximately November through March (St-Pierre 1984). Tags deployed in 2008 were programmed to detach 365 d after deployment, during summer. However, given that the latter tags were equipped with detachment detection, tags that reported during the 2008 to 2009 mid-winter spawning season (defined as 1 December 2008 to 28 February 2009) were included in the present analysis of dispersal to winter grounds.

In all deployments, the tags collected environmental data at 30 s (MK-10 PAT tags) or 1 min (PAT4 tags) intervals, and the data were subsequently summarized into 12 h periods by software within the PAT tag. Satel-

²www.argosinc.com (accessed on 12 January 2008)

Fig. 2. *Hippoglossus stenolepis*. Release (solid symbols) and reporting sites (hollow symbols) of pop-up archival transmitting (PAT)-tagged halibut in the Bering Sea and Aleutian Islands. Circles: PAT tags programmed to study mid-winter locations by popping-up in February (primary tag deployment). Squares: PAT tags programmed to study interannual dispersal by popping-up during the subsequent summer, but prematurely detached during the winter spawning season. Doglegged trajectories have been bent to avoid drawing on top of other points and over land features. Dotted lines indicate passes between the Aleutian Islands

lite transmission was comprised of these summaries, thus providing 4 types of data: (1) percentage of time spent within specific depth ranges (not analyzed here), (2) percentage of time spent within specific temperature ranges (not analyzed here), (3) depth–temperature profiles containing minimum and maximum depths and temperatures, and (4) ambient light levels during sunrise and sunset events. Light-based longitude estimates for tags attached to demersal fishes may be produced in relatively shallow depths (<100 m) during spring, summer, and fall (Seitz et al. 2006), although obtaining such estimates is dependent upon water clarity and weather conditions. During winter and when halibut are at considerable depth (>200 m), light levels are typically too low to obtain estimates. For all days yielding sufficient light intensity data, longitude estimates were produced using Wildlife Computers' proprietary software, Global Position Estimator (GPE) (Seitz et al. 2006). In short, GPE was used to identify daily sunrise and sunset events. Next, days with sunrise/sunset data that did not exhibit smoothly sloping light levels from high to low or low to high were rejected. Finally, GPE calculated longitude for the remaining days by comparing the local noon of the tag (mean of the sunrise and sunset times) to 12:00 h UTC (Coordinated Universal Time). Estimated longitude values that were outside the published range of halibut, i.e. 140°E to 117°W (Mecklenburg et al. 2002), were discarded from analyses, as these would place the halibut on land. In Alaskan waters, the mean magnitude of longitude estimate errors is approximately $5 \pm 4^\circ$ at 150 m depth (Seitz et al. 2006).

Latitude estimates have been found to be highly variable in previous PAT tagging experiments for halibut (Seitz et al. 2006). Longitude estimates, being based upon time of local noon, are somewhat robust to the attenuation of light due to turbidity and cloud cover. In essence, as long as light attenuation has remained constant throughout the day and the halibut has not changed depth appreciably, apparent noon will be properly centered regardless of the absolute light values obtained. Latitude, on the other hand, is based upon unbiased daylength estimates (Teo et al. 2004). These are notoriously difficult to obtain at depth, in the turbid conditions normally associated with halibut habitat, especially at high latitudes typified by considerable cloud cover throughout the year. Daylength is nearly always estimated to be too short, translating into highly biased latitude estimates. The problem is only exacerbated in mid-winter, the time of year of greatest interest in the present study, when total irradiance is lowest and daylength is extremely short. Therefore, latitude estimates were not generated for determining movement of halibut in the present study.

Potential movement from Bering Sea summer feeding grounds to GOA potential winter spawning grounds was assessed by examining final reporting location, longitude estimates, and depth and temperature records of each halibut. In short, a halibut may have moved from the Bering Sea to the GOA if its final reporting location or any of its longitude estimates were located east of Unimak Pass (164.9°W), the easternmost connection between the Bering Sea and the GOA, and it inhabited depths >200 m, which do not exist east of 164.9°W in the Bering Sea. Relatively large and abrupt changes in temperature (>2°C) at a consistent depth also may provide additional evidence of dispersal from the Bering Sea to the GOA, as the bottom water in these areas contains relatively distinct hydrographic properties (Musgrave et al. 1992, Stabenot et al. 1999).

To assess the degree to which movements between tagging and reporting locations were likely to represent spawning migrations, the seasonal dispersal behaviors of individual halibut were classified into 5 behavior types based on pop-up locations and depth records (Fig. 3), similar to previous research on bigeye tuna *Thunnus obesus* (Schaefer & Fuller 2002):

(1) wintertime shelf residents were halibut that remained on the continental shelf and never experienced depths >200 m after October 1 according to conservative estimates of active spawning depth (Loher & Seitz 2008a) and initial onset of the fall offshore dispersal period (Loher & Seitz 2008b), respectively;

(2) slope dispersers were halibut that were located on the continental slope in water >200 m on the pop-up date;

(3) long-distance slope dispersers were halibut that were located in water >200 m depth on the pop-up date and also had moved >200 km from their release site and changed general areas, i.e. from the southeastern Bering Sea to the Aleutian Islands;

(4) long-distance shelf dispersers were located in water ≤200 m on the pop-up date and had moved >200 km from their release site and changed general areas;

(5) feeding-site returnees were halibut whose pop-up locations were on the shelf and in close proximity to the location at which the halibut were tagged and released (Loher 2008), but could not have remained near their tagging locations for the duration of the experiment because they experienced maximum depths >200 m. Depths of this magnitude do not exist on the continental shelf, indicating that the halibut moved off the shelf to the slope during their time at liberty. Note that, in this sense, feeding-site returnees were also slope (Type 2 and 3) dispersers, but whose depth records allowed resolution of both their autumn offshore migration and their subsequent onshore return

Fig. 3. *Hippoglossus stenolepis*. Examples of 4 general behavior types of halibut, with pop-up locations (map), depth profiles, and longitude (lower graphs). Depth profile for the long-distance shelf disperser is not depicted, but is similar to those for other shelf residents, with the exception of larger geographic displacement between tagging and pop-up. O: location at which the tag reported to Argos; ●: estimated daily longitude. The feeding-site returnee at bottom left was not included in the analysis because its tag popped-up on 1 May; it is included here because its longer period at liberty more clearly illustrates this behavior type

migration. Given the nature of the available data, their ultimate offshore destination was unknown, and so it was not possible to determine whether these halibut had exhibited Type 2 or 3 dispersal prior to returning to the shelf.

To identify possible spawning activity, short-period (diel) variability in depth was examined for each individual on the basis of the total range in depths visited over 12 h summary periods. High-resolution (i.e. over minutes) depth data have been used to identify behav-

ior believed to represent active spawning in bluefin tuna (Teo et al. 2007) and in halibut (Seitz et al. 2005). Putative halibut spawning behavior consists of a conspicuous routine in which an individual conducts 6 to 10 regularly spaced (92 ± 1.8 h) abrupt ascents (34 ± 2.0 m min^{-1}) or 'spawning rises' during mid-winter. These abrupt ascents closely parallel the actions of other spawning flatfish observed *in situ* (Carvalho et al. 2003), and the regular spacing is consistent with ovulatory intervals observed in Atlantic halibut *Hip-*

poglossus hippoglossus during which each new batch of eggs is hydrated (Finn et al. 2002). Although such high-resolution data were not available here, the coarse-scale data were investigated for the possibility that they might contain similar indication of spawning activity.

RESULTS

Hippoglossus stenolepis tagged from 2002 to 2006 ranged from 110 to 154 cm FL, and each individual was at liberty for 165 to 240 d (Table 1). Data were recovered from 47 of 58 tags (81%), of which 41 tags provided Argos-determined winter locations. The remainder of the tags was recovered during summer or fall in the commercial fishery ($n = 2$), prematurely detached ($n = 4$), or did not report ($n = 11$). In addition, 8 tags from the 2008 deployment reported during the winter on dates ranging from 18 December to 23 February, consistent with documented dates of active spawning (Loher & Seitz 2008a). These halibut ranged from 82 to 119 cm FL and were at liberty for 164 to 251 d; 6 had been tagged in the vicinity of Bering Canyon, 1 at Middle Canyon, and 1 to the north of Amchikta Pass (Fig. 2).

For halibut whose tags remained attached through winter, horizontal displacements (great-circle distance between release and reporting locations) ranged between 0 and 815 km (Fig. 2, Table 1). On average ($\pm$ SE), the horizontal displacement of halibut tagged near the Aleutian Islands was smaller (47.6 ± 11.1 km; range: 1 to 167 km; Table 1) than that of halibut tagged elsewhere in the SEBS (224.4 ± 65.7 km; range: 4 to 815 km; Table 1). Furthermore, all pop-up locations of halibut tagged near the Aleutian Islands were within the group of islands where they were released (Fig. 2A,B).

A total of 748 longitude estimates were produced by the tags that remained attached through winter, of which 6 were outside of the published range of Pacific halibut and were discarded from analyses (Table 1). For 37 of the halibut, all light-based longitudes were west of Unimak Pass (164.9° W), the easternmost connection between the Bering Sea and GOA through which Pacific halibut are likely to move (Table 2). Of the remaining individuals, 6 had longitude estimates that were east of the pass and 6 did not report any longitude estimates. Thus, maximum detectable short-period dispersal to the GOA, based on the assumption that all longitude values $<164.9^\circ$ W indicated transient dispersal from the Bering Sea, would be 14%. However, an alternative must be considered: movement to areas within the Bering Sea located east of the given reference. Pacific halibut habitat extends eastward to 161° W in Norton Sound and to 157° W in Bristol Bay

(Fig. 1); no individual produced a combination of light-based geolocation estimate and depth readings that allows a definitive conclusion of movement out of the Bering Sea (Table 2).

Overall, 6 halibut had longitude estimates east of Unimak Pass (Table 2); 4 of these were tagged in the vicinity of Bering Canyon, and all of their longitude estimates that were east of Unimak Pass ($n = 29$; 1 to 22 halibut $^{-1}$; range: 158.3 to 164.9° W), as well as their endpoint locations (163.3 , 163.9 , 162.3 , and 162.3° W), were consistent with residence in Bristol Bay (Fig. 2C). The fifth individual was also tagged at Bering Canyon. It produced 46 of 48 longitude estimates consistent with either the GOA or Bristol Bay (range: 161.3 to 164.4° W), but produced a Bering Sea endpoint location that was not in Bristol Bay (166.4° W). The sixth halibut was tagged near St. Paul Island and produced 2 of 27 longitude estimates east of 164.9° W (162.1 and 162.8° W). No depths (16 to 150 m) associated with longitude estimates for any of these 6 individuals when east of 164.9° W were sufficiently deep (>200 m) to unequivocally place them in GOA waters.

The halibut occupied depths from 0 to 844 m. In all, 85% of the tagged halibut displayed movement to slope habitat in autumn or winter, consistent with off-shore dispersal for the purpose of spawning (Fig. 2, Table 3). As such, the majority of halibut tagged in the present study were likely to have represented spawning individuals, and their movements, to be reflective of regional spatial stock structure. Short-distance slope dispersal was the most common behavior type in both the Aleutian Islands and SEBS (Table 3). Halibut in the SEBS displayed all other behavior types as well. In contrast, halibut near the Aleutian Islands showed only short-distance movements, with no evidence of long-distance dispersals (Table 3).

A total of 32 halibut showed appreciable fluctuations in depth on a diel basis, in which the minimum and maximum depths within a 12 h summary period did not closely correspond (Fig. 4A). The other 9 individuals did not conform to this pattern and only showed appreciable fluctuations in depth on a diel basis on isolated occasions during mid-winter, when minimum depths were from 100 to 400 m shallower than maximum depths in the same 12 h summary period (Fig. 4B).

Table 2. *Hippoglossus stenolepis*. Number of halibut occupying various depth and location combinations during their spawning season (results are only from PAT tags that enabled longitude estimates)

	<200 m	>200 m
West of Unimak Pass	4	33
East of Unimak Pass	6	0

These large depth deviations occurred as early as 21 December 2006 and as late as 27 January 2007. These 9 individuals exhibited between 2 and 6 depth deviations each, with nearly regular time intervals between them of 3 to 6 d. The exact time intervals between depth deviations were specific to the individual.

Halibut in the present study experienced ambient water temperatures from 0.2 to 10.0°C. When they occupied the continental shelf (<200 m), there appeared to be gradual warming and cooling trends of ambient temperatures associated with the change of seasons (Fig. 5A). When halibut occupied the continental slope (>200 m), there were no trends in ambient water temperature, likely because they were located at a depth that isolated them from seasonal temperature fluctuations (Fig. 5B). Several halibut experienced more abrupt shifts in ambient temperatures (~2 to 6.0°C) within 12 h summary periods that occurred concurrently with rapid changes in depth during the same time periods (Fig. 5C). There were no abrupt changes in water temperature for halibut whose depth did not change considerably within a 12 h summary period, indicating that it is unlikely that any individual changed water masses while dispersing, such as from the Bering Sea to the GOA.

DISCUSSION

Spawning group spatial structure

The results of the present study are inconsistent with the hypothesis that Pacific halibut that feed during the summer in the Bering Sea and near the Aleutian Islands are likely to contribute substantially to the GOA spawning group. Although PAT tags on ~14 % of halibut in this study generated longitude estimates that could have placed them in the GOA prior to the end of their tagging periods, no such locations were consistent with known spawning depths for the species

Table 3. *Hippoglossus stenolepis*. Behavior types of halibut in the Bering Sea and Aleutian Islands. Note that 1 tag attached to a halibut in Bering Canyon did not transmit depth data; therefore, its behavior type is unknown

	Shelf resident	Short- distance slope dispenser	Long- distance slope dispenser	Long- distance shelf dispenser	Feeding- site returnee
Attu Island	2	7	0	0	2
Atka Island	0	2	0	0	3
Amchitka Pass	0	1	0	0	0
Bering Canyon	3	9	0	0	2
St. Paul Island	2	3	1	0	0
Middle Canyon	0	8	2	1	0

Fig. 4. *Hippoglossus stenolepis*. Maximum (solid lines) and minimum (broken lines) depths for each 12 h summary period of a halibut PAT tagged in the Bering Sea. Panel A is representative of halibut that displayed considerable fluctuations in depth on a diel basis. Panel B is representative of halibut that did not show appreciable fluctuations in depth on a diel basis, except for isolated occasions during mid-winter when minimum depths were much shallower than maximum depths in the same 12 h summary period

(Loher & Seitz 2008a), and all individuals ultimately produced mid-winter endpoints in the Bering Sea. If any movement to the GOA occurred, it was relatively transient and there is no evidence to support the hypothesis that it was associated with spawning. We are unable to speculate about the population differentiation of Pacific halibut throughout its range, but the apparently high rates of retention of a BSAI region spawning group suggests that there was some merit to the multiple stock concept used by the IPHC from the 1930s to the 1950s (Thompson & Herrington 1930, Van Cleve & Seymour 1953), which was further supported by parasite data in later studies (Blaylock et al. 2003).

While our results suggest that halibut that feed in the BSAI region during summer are unlikely to mix into the GOA spawning group, they say nothing about whether mixing might occur via the reverse phenomenon: halibut that feed in the GOA joining BSAI spawning groups. However, halibut have also been PAT tagged in the GOA during the summer with winter pop-up dates (Seitz et al. 2003, Loher & Seitz 2006), thereby providing a complement to the present study. In the

Fig. 5. *Hippoglossus stenolepis*. Examples of ambient water temperatures (lower panels in A, B, C) experienced at depth (upper panels in A, B, C) by halibut for each 12 h summary period (solid lines: maximum; broken lines: minimum). (A) Halibut that occupied the continental shelf (<200 m), where gradual cooling of ambient temperatures was associated with the change of seasons. (B) Halibut that occupied the continental slope (>200 m) where ambient temperatures showed no warming or cooling trends. (C) Halibut that experienced more abrupt shifts in ambient temperatures within 12 h periods that occurred concurrent to rapid changes in depth

above-mentioned studies, halibut tagged in the Southeast and Southwest GOA demonstrated a northward dispersal towards major spawning grounds in the central GOA, but not to the BSAI region. The GOA studies were of more limited scope than the current work, but further support our present hypothesis that the Bering Sea contains a local, resident spawning group, poten-

tially independent of that in the GOA. To fully test this hypothesis, more tagging of a similar nature is warranted in the western GOA to examine the possibility that seasonal cross-basin mixing of adults could be invoked by GOA summer residents dispersing northward into the BSAI region.

In contrast to the results of the present study, conventional tagging (Skud 1977, Kaimmer 2000) and recent PIT tag analyses (Webster et al. 2008) have documented movement of halibut from the Bering Sea into the GOA. These results have supported the paradigm of the fully mixed stock and may seem contradictory to the present results, but the observed dispersal processes are likely incomparable. Using offshore dispersal and putative spawning rises as evidence of sexual maturity, we infer that most of the observed movement represents dispersal of adult halibut (Seitz et al. 2005). In contrast, previous conventional tag studies reported migration rates of 'tagged adult halibut' (Skud 1977), but all halibut >65 cm FL were considered adults, a distinction that the author considered 'an arbitrary division consistent with the size limit', made in the absence of maturity information for any of the tagged individuals. Considering that female maturity in the Bering Sea presently begins at ~75 cm FL and size at 100% maturity does not occur until at least 130 cm FL (T. Loher unpubl. data), it is likely that a larger proportion of the conventional tag releases were comprised of immature individuals than in the present study. As such, it is likely that our study addresses seasonal inter-basin dispersal for the presumed purpose of spawning, whereas prior tagging has focused on interannual summer-to-summer dispersal, consistent with the notion of ontogenetic redistribution of juvenile Pacific halibut. Similar conclusions may be drawn from PIT tag results, in which halibut ($n = 12$) observed moving from the Bering Sea to the GOA ranged from 81 to 123 cm FL (T. Loher unpubl. data). Further investigation of the influence of size and age on dispersal patterns in the PIT tag data is warranted and ongoing, as size-dependent dispersal has been demonstrated in a variety of taxa, from fishes (Dorazio et al. 1994, Imbert et al. 2010) to arthropods (Etherington & Eggleston 2003, Okada et al. 2007). In the meantime, the likely occurrence of ontogenetic redistribution indicated by conventional and PIT tag data does not preclude the establishment of spawning stock structure, indicated by PAT tag results, at scales relevant to fishery management.

Several of the halibut at various locations displayed homing to feeding locations, as evidenced by emigration to deep water while at liberty, followed by a return to within <1 km of their tagging locations (Fig. 3, Table 3). The frequent occurrence of homing to sum-

mer feeding sites in the current study and high rates of interannual homing demonstrated in a previous study in the GOA (Loher 2008) demonstrate that a large proportion of adults may return to the same area annually, throughout the geographic range, making them vulnerable to local depletions in areas with intensive commercial fisheries. St. Paul Island is an example where harvest shortfalls from 2000 to 2004 were from 14 to 56% of the annual catch limits, suggesting sensitivity of the population to locally concentrated exploitation (Hare 2005). This indicates that the movement of individual halibut may be relatively limited in the BSAI, in contrast to the assumption of complete mixing within the population of Pacific halibut.

Aleutian stock sub-structure

In addition to relative spawning segregation between the BSAI and GOA, the present results also suggest the possibility of finer scale population structure within the BSAI. All of the halibut tagged near Attu and Atka Islands, as well as those tagged at Petrel Bank, appear to have remained in the vicinity of the island near which they were released, with no evidence that the halibut crossed any passes along the Aleutian Island chain. The halibut released near Attu Island displayed no evidence of having crossed Near Strait (depth = 2000 m) to the west or Buldir Strait (depth = 640 m) to the east (Fig. 2). The halibut released near Atka Island did not appear to cross Amchitka Pass (depth = 1155 m) to the west or Amukta Pass (depth = 430 m) to the east (Fig. 2). The long-distance slope dispersers tagged near Middle Canyon and St. Paul Island swam to the eastern side of Amukta Pass, but, like the halibut tagged near Atka Island, there was no evidence that they swam across that pass. Although only the depths of Amchitka Pass and Near Strait exceed the maximum depth recorded by a halibut in the BSAI region (844 m), the halibut in the present study apparently did not cross shallower passes either. In this context, it is important to note that we are not suggesting that such passes present complete barriers to dispersal. On the contrary, recent PIT tagging (Webster et al. 2008) has demonstrated that halibut tagged near the Aleutian Islands may be recaptured to the east, and, because halibut are found in depths greater than those of both Buldir Strait and Amukta Pass, the depths of these passes do not appear to be an impediment to movement. Rather, we propose that factors such as swift currents and strong turbulence in the passes may deter movement (Hunt & Stabeno 2005), relative to the rates that would be observed in the absence of such features.

Another line of evidence that corroborates the hypothesis that movement across Aleutian passes may be limited is recent genetics results (Hauser et al. 2006, Nielsen et al. 2010). Using a variety of nuclear microsatellite loci, statistically significant ($p < 0.10$) permutation test results suggest that segregation occurs between halibut collected near Adak Island and those collected near both St. Paul Island and the US Pacific Northwest (Hauser et al. 2006). In another study, significant ($p < 0.05$) heterogeneity was detected between halibut from the Aleutian Islands and those from the GOA and the SEBS (F_{ST} range: 0.007 to 0.008; Nielsen et al. 2010). Significant F_{ST} values represent the first genetic evidence of divergent groups of Pacific halibut in the central and western Aleutian Archipelago. Previous studies have also reported Aleutian oceanographic conditions at deep inter-island passes, leading to ecological discontinuity and unique community structure east and west of Aleutian passes (Ladd et al. 2005, Logerwell et al. 2005). Aleutian Pacific halibut genetic structure may result from oceanographic transport mechanisms acting as partial barriers to gene flow with conspecifics from other areas of their range.

The mid-winter aggregations of halibut near Attu Island and Middle Canyon (Fig. 2) suggest that locally important spawning grounds extend as far as 1000 km westward and 600 km northward, respectively, of the nearest previously confirmed spawning areas. Previous to this study, there have been no spawning surveys west of the Bering Canyon or north of the Pribilof Canyon, both of which were previously identified as spawning grounds (St-Pierre 1984). Unfortunately, it is impossible to know whether halibut actively spawn at Attu Island or Middle Canyon, unless future research is conducted to assess spawning condition and/or egg and larval presence in the overlying water column. However, local aggregation of large individuals with high maturity probability, coupled with seasonal and diel vertical migration that is temporally consistent with known spawning behavior, strongly indicate the presence of spawning grounds at these locations.

Utility of broadcast data in identifying active spawning

For the first time, summarized depth data transmitted via satellites have proven useful for identifying putative spawning behavior in this species (Fig. 4). Putative spawning in Pacific halibut has been previously described using minute-by-minute archival records from physically recovered tags (Seitz et al. 2005, Loher & Seitz 2008a), but never from summarized data, because halibut typically undertake diel depth

changes throughout the year (Fig. 4A), masking potential spawning rises that might otherwise be visible. However, there were several individuals in the present study that did not undertake large diel migrations on a daily basis, but rather on only a few occasions. These isolated depth deviations all occurred during mid-winter and had nearly regular time intervals between them, similar to the previously described purported spawning rises. Therefore, these instances may represent spawning rises with the relatively shallow minimum depth representing the apex of the rise (Fig. 4B).

If large mid-winter diel depth deviations are indeed associated with active spawning, they may be used to refine some assumptions of spawning characteristics of Pacific halibut.

(1) Historical survey data indicate that the spawning season lasts from November through March (St-Pierre 1984). The halibut in the present study ($n = 9$) did not commence putative spawning until mid-December, suggesting a potentially later peak in spawning than derived from survey data. The timing of commencement of putative spawning in the BSAI is consistent with that of halibut in the eastern GOA inferred from detailed archival tag data (Loher & Seitz 2008a). It is not possible to infer when the spring spawning season ends in the BSAI region because the tags popped-up in early February, which is likely the peak of spawning.

(2) It is assumed that individuals may protract spawning events through the entire winter season (St-Pierre 1984). In contrast, the halibut in the present study had putative spawning seasons lasting no longer than 21 d.

(3) In previous investigations, it was assumed that mere occupation of the continental slope during the winter may be indicative of active spawning (Seitz et al. 2003). However, from this study, it appears that inhabitation of the continental slope may not be a valid indicator of active spawning, because several halibut spent much of their time at liberty on the continental slope and dispersal times to and from this area varied widely, but putative spawning was observed only in December and January. Therefore, halibut may use the continental slope as habitat for activities other than spawning, such as feeding, or they may arrive on the slope well in advance of active spawning and use the initial period to form spawning aggregations and locate suitable mates.

Definitive conclusions about spawning are not possible at this time, because these spawning behavior observations are based on a small number of putative spawners ($n = 7$) and these individuals are unusual in that they did not perform diel vertical migrations; therefore, we are unable to ascertain whether the timing and length of reproductive activity of these halibut are typical or exceptional.

Logistical considerations

We experienced 2 problems typical to PAT tagging experiments: premature detachment and non-reporting. The rate of premature detachment in the present study (7%) was well below those reported for other experiments on pelagic fishes (Domeier et al. 2003, Stokesbury et al. 2004). We speculate that PAT tags on halibut tend to experience fewer premature detachment events than those on pelagic fishes, because halibut live a more sedentary life and swim at slower speeds. Another problem was non-reporting, mainly from the tags released near Atka Island ($n = 7$). Considering that all of the tags in the current study were deployed under similar conditions, we suspect that a portion of the Atka Island batch of tags had faulty batteries. This claim is evidenced by a halibut that was recaptured more than a year after being released with the tag still attached. This tag was diagnosed by its manufacturer as having a dead battery.

Limitations and broader ecological considerations

The present study was subject to limitations that prevent us from drawing conclusions regarding long-term population structure within the range of Pacific halibut.

(1) We received <1 yr of data from a fish species that may live up to 50 yr. While the present data demonstrate a clear mechanism whereby spawning structure may be established, these tag deployments are unable to capture observations necessary for maintaining that population structure over time, such as inter-annual regional fidelity to spawning areas.

(2) We observed only a small demographic component of halibut. Early deployments were conducted on large individuals due to the large size of the tags and concern for the health of the fish, and protocols were only recently modified to accommodate smaller individuals. As such, the present results are likely to have been biased toward females, given that Pacific halibut display marked sexual dimorphism— with considerably larger size-at-maturity in females (Clark et al. 1999). Sex-specific differences in site fidelity are common in birds (Ward & Weatherhead 2005, Williams & Rabenold 2005), and biased dispersal has been reported in several fish species, including striped bass *Morone saxatilis* (Dorazio et al. 1994) and brown trout *Salmo trutta* (Bekkevold et al. 2004). Given differential energy requirements associated with spawning, dispersal patterns and fidelity to spawning sites may well differ among population components. In particular, male halibut might represent a more dispersive population component than the female demographic, and their underrepresentation in the present data might bias our conceptual model of seasonal mixing.

(3) As discussed earlier, the present study was designed only to examine autumn spawning dispersal and only with respect to Bering Sea adult summer residents. Because we likely tagged only adults, we cannot eliminate the possibility that juveniles may change basins, thus introducing mixing among potential sub-populations. A thorough characterization of population structure in Pacific halibut will require integration of dispersal processes throughout all life-history stages, from advection of larvae by oceanic currents, to ontogenetic redistribution of pre-recruit ages, to site fidelity or straying of reproductive individuals over entire lifetimes. In this context, the present study provides evidence of regional population structure at 1 life stage and time scale important to fishery management: possible spawning components within the eastern halibut population, created by short-period reproductive separation of BSAI halibut from those in the GOA. Even if there is mixing of early life-history stages, this observed reproductive separation may lead to population sub-structure that is relevant to prosecution and management of a fishery.

Phylogeographical population structure has been found in other oceanic fishes, despite extended pelagic larval periods and apparent environmental continuity in adult habitats, including other flatfishes in the North-east Pacific Ocean, such as dover sole *Microstomus pacificus* (Stepien 1999) and other relatively large and mobile fishes, such as Atlantic bluefin tuna *Thunnus thynnus* (Boustany et al. 2008). Spatially structured populations have also been found in disparate aquatic taxa such as polar bears *Ursus maritimus* in the Arctic Ocean (Taylor et al. 2001) and northern fur seals *Callorhinus ursinus* in the North Pacific Ocean (Dickerson et al. 2010).

Identifying and preserving population structure has been declared an important goal of modern fishery science (Stephenson 1999, Frank & Brickman 2001). With respect to eastern Pacific halibut, an independent review of the IPHC's assessment process resulted in an unanimous call for increased treatment of local population dynamics, with 1 reviewer stating that 'future assessment modeling should be spatially structured' (Francis 2008) and the other suggesting attention to 'population mapping, so that in the longer term, a spatial model reflecting population structure as well as administrative areas might be developed' (Medley 2008). If there is indeed an independent spawning group of Pacific halibut in the BSAI, its dynamics may vary sufficiently from those of the GOA, so that specifically accounting for its relative segregation and unique dynamics within the larger population model will be necessary for correctly predicting how this component may respond to fishing pressure and changing environmental conditions.

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