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**Seasonal movements and
environmental conditions
experienced by Pacific halibut in
the Bering Sea, examined by
pop-up satellite tags**

by

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Contents

Abstract	4
Introduction	5
Methods	8
Results	10
Discussion	17
Acknowledgements	21
References	21

Abstract

Currently, Pacific halibut are managed as one population extending from California to the Bering Sea. However, we hypothesize that a spawning subpopulation of Pacific halibut exists in the Bering Sea. In this study, we examined the seasonal migration and depth-specific behavior of Pacific halibut in the Bering Sea, which serve as indicators of possible population structure. We tagged 12 adult halibut in August, 2002 near St. Paul Island with Pop-up Archival Transmitting (PAT) tags. Externally attached to the fish, PAT tags recorded depth, temperature, and ambient light intensity. The PAT tags released from the fish on either 15 February 2003 or 1 May 2003 and transmitted the historical data and location to Argos satellites. Data were recovered from nine tags: one fish was recaptured after 12 days at-liberty, seven tags released from the fish and reported to Argos satellites as scheduled, and one tag prematurely released from the fish after 42 days and then transmitted to the satellites as scheduled. The tagged fish ranged from 112 to 137 cm FL and were at-liberty from 12 to 258 days. Distance traveled from the release site ranged from 0–513 km. Fish visited a range of depths between 12 and 844 m where temperatures ranged from 1.4–9.4°C. Several halibut moved between International Pacific Halibut Commission regulatory areas during the course of the study, but there was no evidence that any of the halibut moved out of the Bering Sea. While sample size was small, the lack of movement into the Gulf of Alaska during the winter spawning season is consistent with the hypothesis that the Bering Sea supports a locally resident population.

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Introduction

The Pacific halibut (*Hippoglossus stenolepis*) fishery is an important resource throughout western Alaska, with just under nine million pounds (est. >\$20 million ex-vessel) of product landed during 2004 in the Aleutian Islands and southeast Bering Sea directed fishery. About 1.7 million pounds were harvested by local communities under their Community Development Quotas (CDQ). The CDQ program was first established by the North Pacific Fishery Management Council in 1992 to provide income to disadvantaged coastal communities with access to Bering Sea marine resources. The program has been hailed by the National Research Council as a critical innovation for local economic development (NRC 1999). Halibut represent one of the keystone species within the program, thus its sound management on regional scales represents an important management objective within the context of the Magnuson-Stevens Fishery Management and Conservation Act.

Adult halibut in the Bering Sea are found along the continental shelf off of North America and the Asiatic coast between Hokkaido Island and the Gulf of Anadyr, as well as in the Sea of Okhotsk (Fig. 1). Younger fish are found in relatively shallow inshore waters while adults have been captured as deep as 1,000 m and are regularly taken at depths of 300–500 m (Best 1981). The youngest halibut are usually found in the south-eastern Bering Sea while adults spread out on the continental shelf. Adult halibut in the Bering Sea feed on the continental shelf during the summer, undertake an offshore spawning migration to the continental slope during winter, and return to their summer grounds during spring (Dunlop et al. 1964, Best 1981). Spawning appears to be concentrated in relatively discrete winter spawning grounds near the edge of the continental shelf of the eastern Pacific, from at least British Columbia through the Pribilof Canyon (Fig. 1) in the southeast Bering Sea (St. Pierre 1984).

The distribution of spawning grounds relative to hydrographic features, especially those that influence larval advection and delivery to nursery areas, are important factors to consider in spatially-explicit management practices. If spawning grounds are reproductively isolated from one another, then important population substructure may exist that should be incorporated in stock definitions. The International Pacific Halibut Commission (IPHC) used this philosophy in conjunction with hydrographic and biological information known at the time to delineate the earliest Regulatory Areas (Thompson and Herrington 1930, Thompson et al. 1931). However, dynamics within the Bering Sea have never been fully understood. The most complete documentation of spawning distribution, based on winter research surveys (St. Pierre 1984),

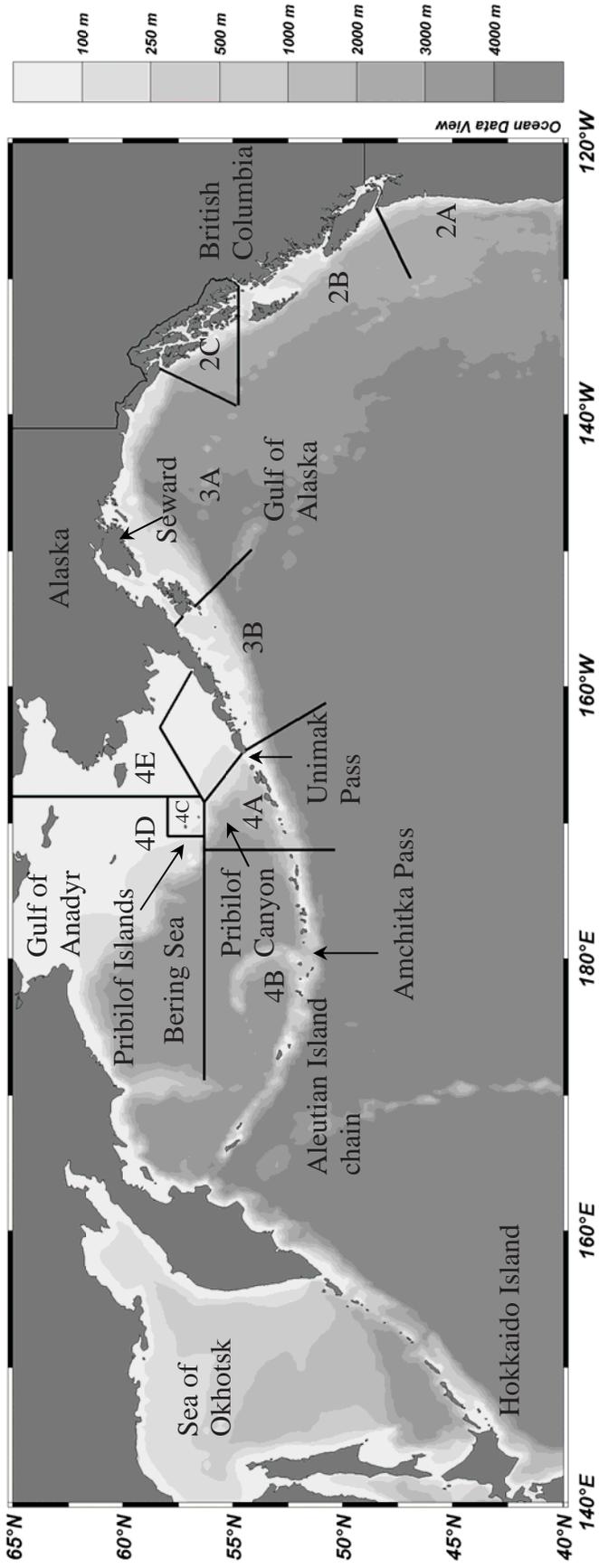


Figure 1. Map of North Pacific Ocean, Bering Sea and International Pacific Halibut Commission regulatory areas (delineated by black lines).

fails to report spawning north of the Pribilof Canyon nor west of Unimak Pass, largely due to a lack of information in these areas (Fig. 1). It is likely that spawning grounds exist outside of the documented range and any of these grounds might be relatively isolated and support independent subpopulations. Given its importance for defining population structure, additional study of Bering Sea halibut spawning distribution is clearly warranted.

In addition to determining spawning locations, delineating temporal patterns in spawning and associated seasonal movement is also critical to identifying subpopulations. Do the majority of fish from any particular summer ground tend to spawn at a specific spawning site, providing a mechanism for local population structure, or do they tend to migrate large distances and disperse, suggesting reproductive mixing?

The IPHC currently manages eastern Pacific halibut as a single population, a paradigm that was largely established from three lines of evidence. The first line of evidence came from conventional tagging experiments (Skud 1977, review in Kaimmer 2000) in which the majority of halibut tagged in the Bering Sea remain there, but many halibut also migrate to the Gulf of Alaska. The second line of evidence supporting a well-mixed population came from analyses of egg and larval distribution. From the major spawning grounds in the Gulf of Alaska, the prevailing current carries eggs and larvae in a north then westerly direction along the Aleutian Islands and through passes to the Bering Sea. As juveniles (age 2-8 years), the halibut counter-migrate in a southeasterly direction towards British Columbia, thus providing an opportunity for mixing if they do not return to their parents' exact spawning site. The third line of evidence came from previous, limited genetic studies that have not identified separate populations within the range of Pacific halibut (Tsuyuki et al. 1969, Grant et al. 1984, Bentzen et al. 1999).

According to this conceptual model of multi-life-stage population mixing, the combination of adult and larval dispersal would provide a reliable, annual supply of halibut to all parts of the range thus ensuring a healthy fishery every year. If adults from a local area in the Bering Sea are all captured during the fishing season, the cross-basin advection of pelagic eggs and larvae from adults from several feeding areas that mix on the spawning grounds will resupply all areas. If the halibut population is not well mixed but managed as such, there is potential for local feeding or spawning groups to be overharvested and potentially lost through regional overexploitation.

Although some evidence points to a single population, there is other evidence including fisheries statistics, conventional tagging data, and hydrography that indicates that the population structure may be more complex and that some level of isolation occurs in the Bering Sea. Local depletions, in which commercial catch-per-unit-effort (CPUE) steadily decreases over several years on specific fishing grounds, are occurring in the southeast Bering Sea (Hare 2005). This phenomenon should not exist in a fully-mixed population. While conventional tagging experiments provide valuable life-history information, their use for understanding migrations is limited. No information on location is obtained between tag deployment and recapture locations, and results can be highly influenced by fishing effort (Bolle et al. 2001). Specifically for Pacific halibut, the vast majority of conventionally tagged fish in the Bering Sea have been released in the summer and the bulk of the recoveries occurred during the summer due to fishing restrictions (IPHC 1998). Thus, there are relatively few conventional tag recoveries from winter spawning grounds. For stock structure, it is more important to understand the structure of spawning populations than summer feeding distribution. If fish are faithful to their spawning grounds, then population structure will likely exist even if they visit different summer feeding grounds from year-to-year. For egg and larval distribution studies, bathymetric and oceanographic data suggest that larvae spawned in the southeast Bering Sea may become entrapped in the Bering Sea gyre, thus limiting mixing with the Gulf of Alaska (Stabeno et al. 1999). Finally, juvenile fish that migrate from southeast Bering Sea nursery grounds into the Gulf of Alaska may simply represent fish that were spawned south of the Alaska Peninsula, were transported into the Bering Sea as larvae, and are returning to their natal subpopulation.

While genetics has proven a useful tool for understanding stock structure in many species, previous genetic studies with Pacific halibut (Tsuyuki et al. 1969, Grant et al. 1984, Bentzen et al. 1999) have failed to sample the Bering Sea thoroughly and have used genetic markers that may have lacked the resolution required to identify subpopulations. Nor did these genetics studies analyze fish captured on the spawning grounds, the point in the annual movement cycle that actually defines the genetic stock unit.

Mesoscale population structure may exist within the range of Pacific halibut and have a substantial impact on landings. On an ocean-basin scale, we hypothesize that the eastern Bering Sea contains a discrete spawning subpopulation, defined as a region from which little or no emigration occurs for purposes of spawning. Alternatively stated, we hypothesize that eastern Bering Sea summer resident halibut remain in the eastern Bering Sea in winter and therefore do not contribute to Gulf of Alaska spawning groups nor the Gulf of Alaska larval pool. One method of testing this hypothesis is examining seasonal redistribution of halibut tagged in the Bering Sea during summer, serving as an indicator of possible population structure. If halibut spawn in the Bering Sea, their pelagically drifting eggs and larvae will most likely be retained in the Bering Sea by the prevailing currents that create a large retentive gyre (Stabeno et al. 1999). Furthermore, while significant genetic segregation indicates isolation over geographic and temporal scales relevant to defining management units, lack of significant genetic differentiation among spawning groups does not necessarily imply mixing at rates that will result in repopulation of depleted grounds over time-scales relevant to fishery management.

The goal of the present study was to determine winter locations of Pacific halibut tagged in the southeast Bering Sea. To accomplish this goal we tagged adult halibut along the southeast Bering Sea shelf-edge with Pop-up Archival Transmitting (PAT) tags. This new technology allows us to determine winter locations of the tagged fish and some aspects of their migration routes without depending upon winter fisheries to recapture the tagged individuals. By examining PAT tag data from fish tagged during summer with tags that release during the spawning season, we will be able to infer whether Bering Sea halibut spawn locally and are thus likely to contribute primarily to western Alaskan spawning biomass and recruitment potential.

Methods

Wildlife Computers¹ PAT tags were externally tethered to Pacific halibut in this study. Each tag contained three electronic sensors that recorded ambient water temperature, pressure indicating the depth of the tag, and ambient light (for PAT tag details, see Seitz et al. 2003). The PAT tag 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 frequency in successive uplinks received during one Argos satellite pass (Keating 1995). The transmitted data then were processed further by Wildlife Computers' PC-based software. If the fish was captured and the tag retrieved before the pop-up date, the complete, high-resolution archival data record could be obtained.

The environmental data were sampled at two minute intervals and were subsequently summarized into 12-hour periods onboard the tag providing four types of data: percentage of time spent within specific depth ranges; percentage of time spent within specific temperature ranges; depth-temperature profiles from which minimum and maximum depths and temperatures may be extracted; and daily geolocation estimates for the time the tag was attached to the fish. Light-based geolocation estimates were produced by Wildlife Computers' proprietary software, Global Position Estimator (GPE), using the recorded ambient light data (Seitz et al. 2006).

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² www.argosinc.com

The first phase of estimating daily geolocation was extracting daily sunrise and sunset times from the light intensity data. Two programs, Argos Message Processor (AMP) and Time Series Processor (TSP), were used to identify and format light level data in an intermediate file that contained encoded light level curves for location calculations. AMP extracted sunrise and sunset data from the daily sunrise and sunset data transmitted through Argos satellites. TSP was used to identify dawn and dusk curves from the complete archival light data available only from physically recovered tags with high-resolution archival data.

The second phase of estimating geolocation was the calculation of the tags' daily longitude and latitude using the GPE program. First, we rejected days with light level curves that did not exhibit smoothly sloping light levels. GPE was used to calculate longitude for the remaining data based on the local noon of the tag (mean of the sunrise and sunset times). Local noon was compared to 1200 UTC (Coordinated Universal Time). Estimated longitude values that were outside the published range of the Pacific halibut, i.e., to the west of Hokkaido, Japan (140° E) or to the east of northern Baja California, Mexico (117° W; Mecklenburg et al. 2002), were considered outliers and were rejected. Once longitude was calculated, latitude, which is a function of day-length, was calculated by GPE, which used the "Dawn and Dusk Symmetry Method" (Hill and Braun 2001).

Geolocation estimates were qualitatively examined. The number of days with geolocation estimates was defined as the days that produced longitude and latitude estimates, after outliers were removed. Daily error magnitude was estimated as the absolute value of the true position minus the estimated position. For each comparison, we calculated the mean error and bias assuming the fish was stationary (or nearly so) during this time. Daily positional bias was estimated as the true position minus the estimated position. If positions were accurate, they should have a bias of zero. A negative bias meant that a position estimate was either north or east of the known positions, and a positive bias meant that a position estimate was either south or west of the known position. It was impossible to know the true daily position of each fish for the duration of the experiment, thus we were unable to calculate error and bias estimates for the duration of the track. However, we compared the estimated positions of the tags for the six days immediately following release and the six days previous to either recapture or reporting to Argos satellites to the respective known positions (Seitz et al. 2006).

For all tagged fish, we report fish size, release and recovery locations, number of days with geolocation estimates, estimated daily position, and the minimum and maximum depths and temperatures recorded for each 12-hour period. The minimum and maximum depths and temperatures for the 12 hours immediately following release were excluded. The percentage of time spent in specific depth and temperature ranges, as well as the full depth-temperature profiles, are not reported here because only one of the Pacific halibut undertook drastic depth changes within a 12 hour summary period. Because of the coarse resolution of depth and temperature ranges (100-250 m), the percentage of time spent in each range was not as informative as absolute maximum and minimum depths.

We followed a previously successful protocol for attaching the PAT tags to halibut (Seitz et al. 2003). PAT tags were tethered to titanium darts using 130 kg test monofilament fishing line wrapped in adhesive-lined shrink-wrap. The darts were inserted through the dorsal musculature and pterygiophores, anchoring them in the bony fin-ray supports of the halibut. The position of the darts was about 2.5 cm medial of the halibuts' dorsal fin on the eyed-side of the fish where the body began to taper towards the tail. The fish were pulled to the surface while hooked and brought onto the vessel in a net. They were placed on the pre-wetted, smooth metal deck of the vessel, and blindfolded to keep them calm. The scientist and captain assessed the halibuts' condition for post-release viability by examining their opercular movement, muscle strength, and gammarid sand flea infestation. Captured halibut were deemed appropriate for PAT tagging and release if they were in good condition (ie. likely to survive) and were at least 110 cm fork length

(FL), as this was the smallest size of halibut successfully tagged in a previous study (Seitz et al. 2003). Additionally, this study aims to monitor spawning movements and the vast majority of halibut ≥ 110 cm FL are sexually mature (Clark et al. 1999).

Twelve adult halibut were tagged and released around St. Paul Island in the Pribilof Islands during August 2002 (Fig. 1; Table 1). Three groups of four fish were captured and released at three different locations. This allowed examination of whether fish separated by small distances on summer feeding grounds might be members of separate groups that migrate to different winter spawning grounds. Three tags from each four-fish group were programmed to release on 15 February 2003 to determine the halibuts' winter grounds, as adult halibut are known to spawn annually and inhabit their spawning areas in mid-February (St. Pierre 1984). Because an Argos-determined location was provided on pop-up, spawning ground location could be obtained with a winter pop-up date even if the tagged fish were too deep to estimate geolocation with the GPE program. To test site fidelity to summer feeding grounds, one tag from each group of fish was programmed to release on 1 May 2003.

Results

Of the 12 halibut released with PAT tags, data were recovered from nine, a recovery rate of 75%. One fish was recaptured by a commercial longline vessel after 12 days at-liberty, while seven tags popped off the fish and reported to Argos satellites as scheduled (Table 1; Fig. 2). The last tag prematurely released from the fish after 42 days, drifted on the surface of the ocean for the next 142 days and then transmitted to the satellites as scheduled. Three tags did not transmit.

The tagged fish ranged from 112 to 137 cm FL and were at-liberty from 12 to 258 days. The maximum distance traveled from the release site was 513 km while the minimum was 0 km (Table 1; Fig. 2). Of the four fish released west of St. Paul Island, one swam south to the continental slope in the Pribilof Canyon and one swam to Yunaska Island in the Aleutian chain. The only tag that was physically recovered, also released west of St. Paul Island, was captured at the release location. Of the four fish released north of St. Paul Island whose tags remained attached for the duration of the experiment, both swam to the west of the island and stayed in relatively shallow water on the continental shelf. Tag 00-0822, also released north of St. Paul Island, reported to Argos above the Shirshov Ridge in Russian waters, but was not attached to the fish for the duration of the experiment. Of the four fish released off of Otter Island, two swam south to the continental slope, with one tag popping-up in the Pribilof Canyon. The only tag that reported in May 2003, also released near Otter Island, reported to Argos in close proximity to the release location.

Vertical movement and behavior of the halibut varied among release groups (Fig. 3). With the exception of the fish whose tag was physically recovered, the fish released west of St. Paul Island and near Otter Island displayed a wide range of depths during their time at-liberty. All of these fish ranged in depth from less than 65 m to greater than 650 m. Two fish tagged south and west of St. Paul Island, 02P0328 and 00-0824, had a depth range of over 800 m, and the shallowest and deepest depths of all fish were 12 and 844 m (Table 1). The time at which the fish moved from the continental shelf (<200 m) to the continental slope (>200 m) varied from late September (00-0824) to mid-January (02P0322). When on the continental shelf, these fish generally remained at relatively constant depths (65-125 m). However, once these fish moved to the continental slope, with the exception of fish 02P0323, their depths fluctuated more (250-800 m). The three fish released north of St. Paul Island displayed different vertical movement than the six fish released west of St. Paul Island and near Otter Island. They remained in depths between 40 and 92 m for the duration of the experiment.

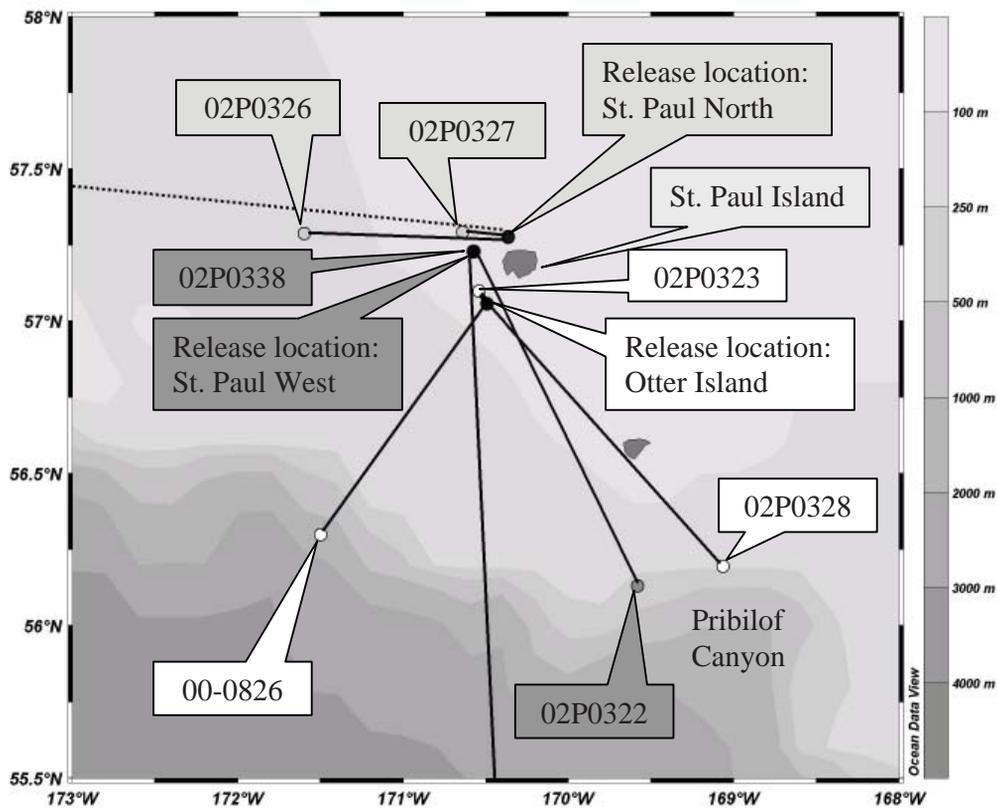
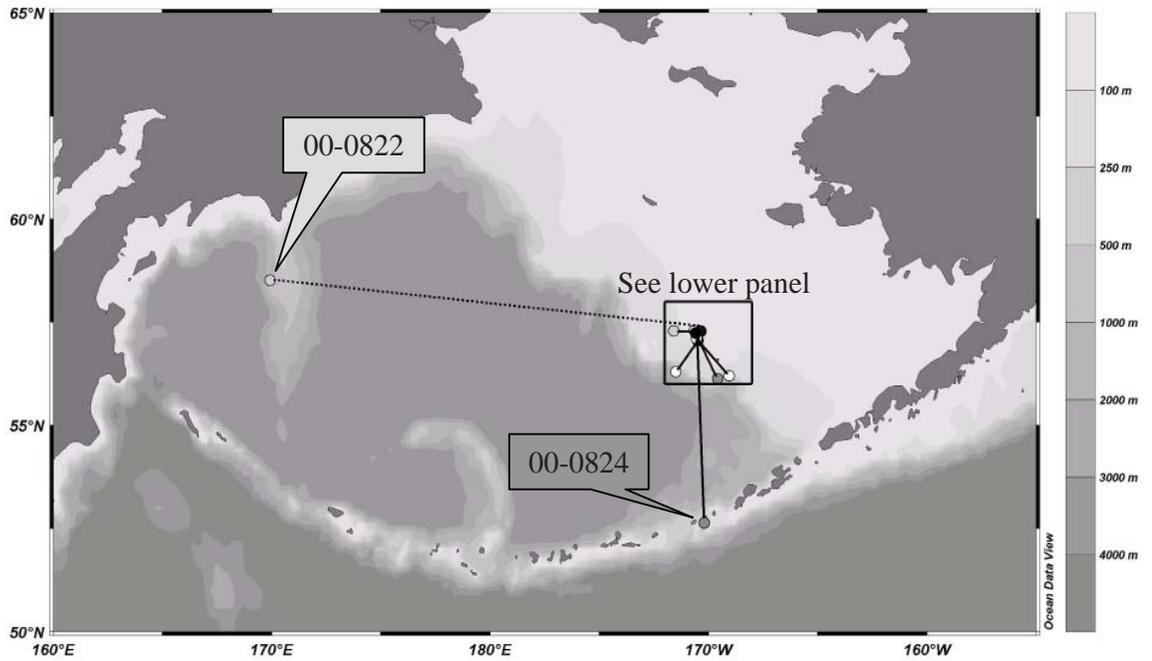
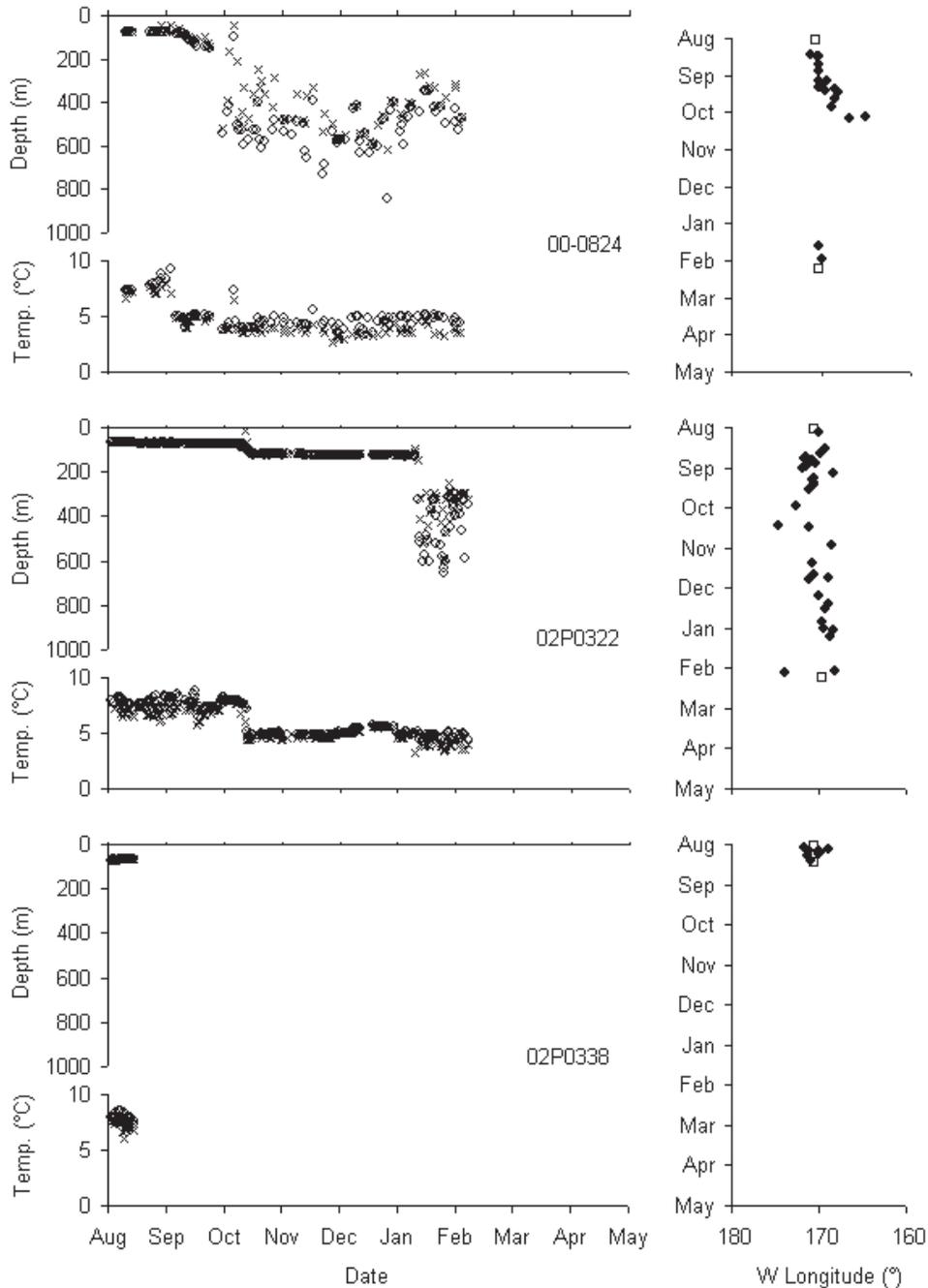
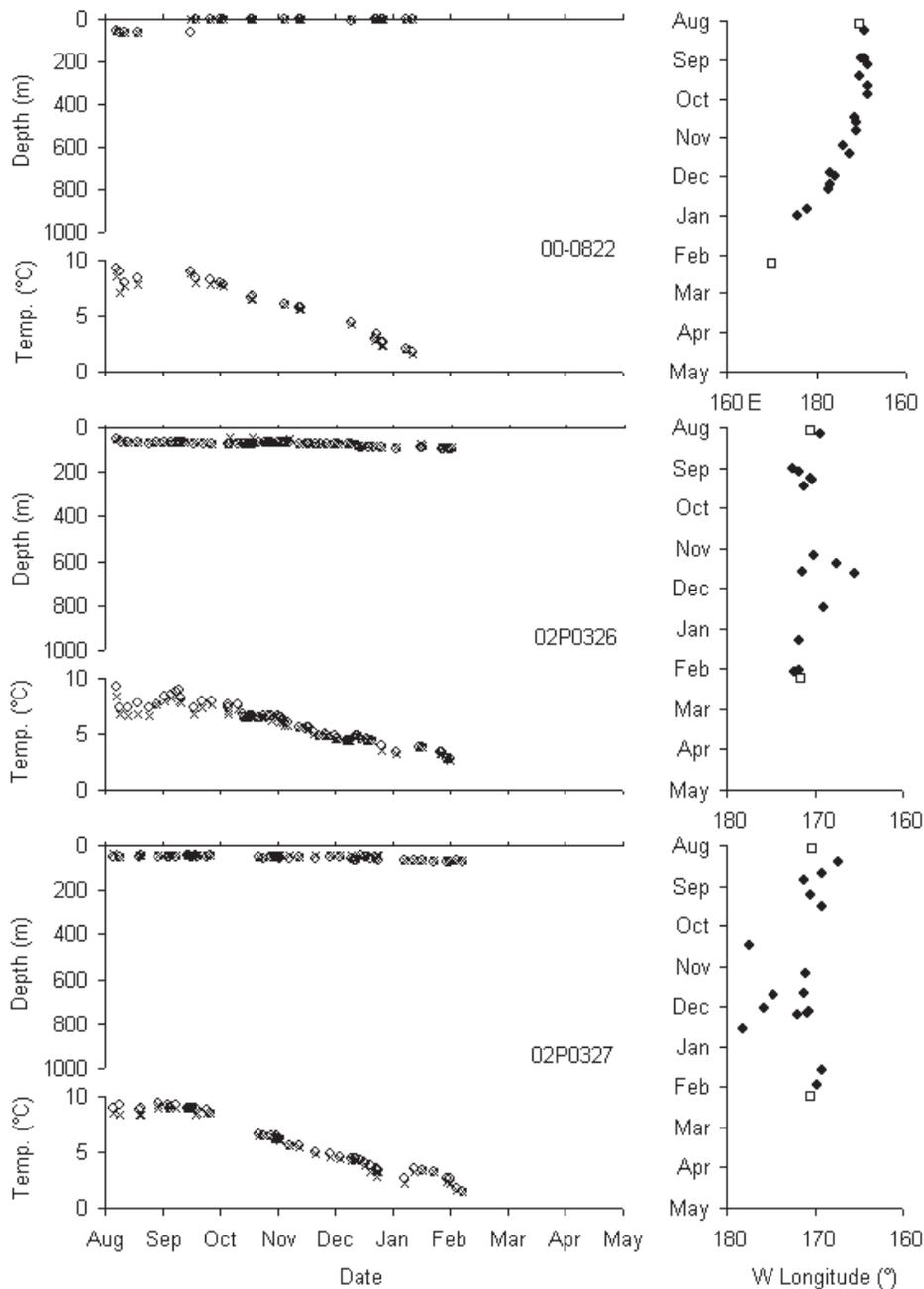


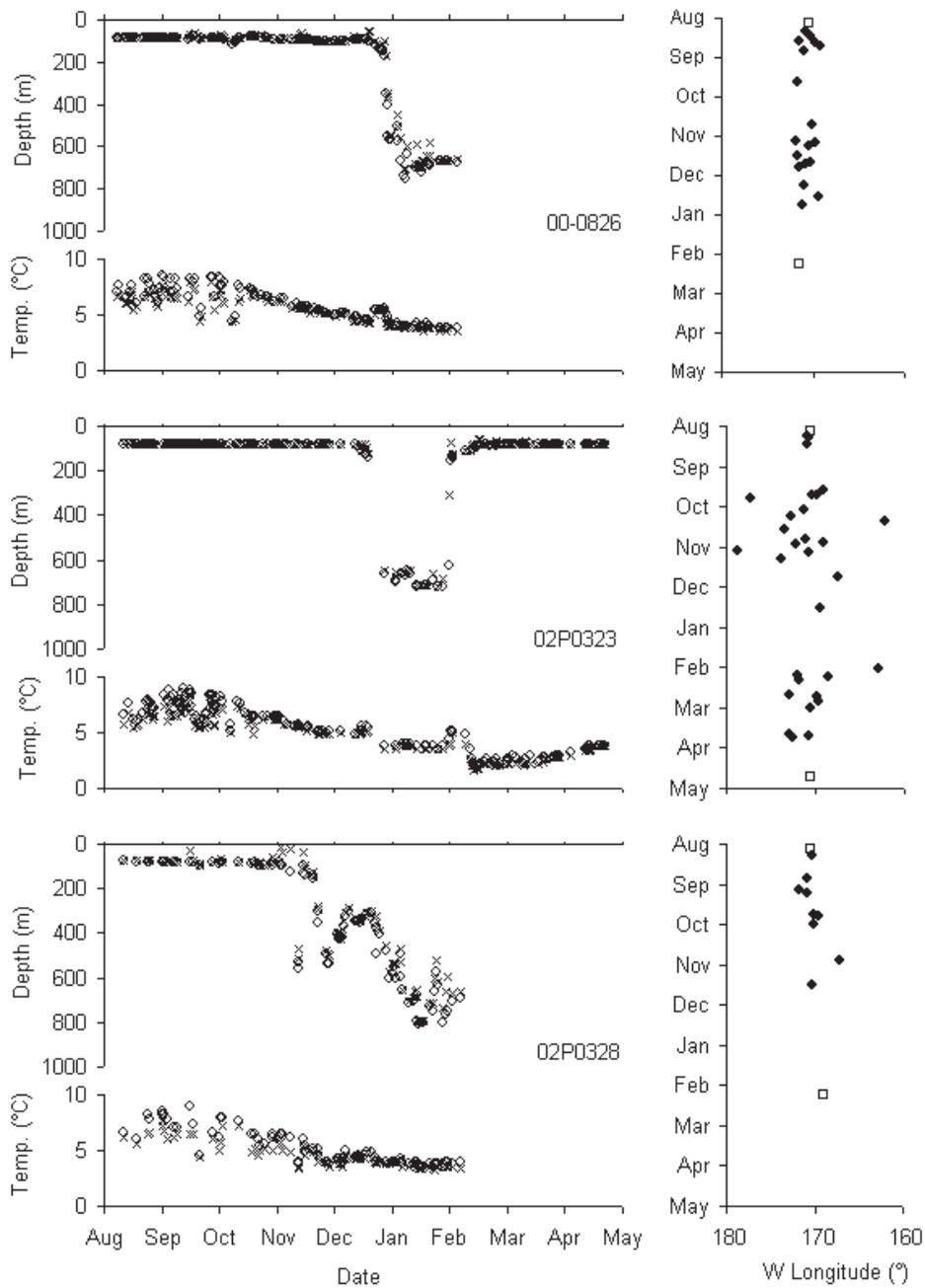
Figure 2. Release (●) and recovery sites (○) of halibut PAT-tagged in the Bering Sea, August 2002. Numbers are equivalent to the PAT tag numbers given in Table 1. Gray shades of the tags correspond to those of their respective release areas.



Figures 3a. Release location: St. Paul west. Maximum (o) and minimum (x) depths and temperatures occupied by nine Pacific halibut within each 12-hour period and daily longitude estimates after outliers were removed. Though the same time, depth, temperature and longitude scales are used to allow comparisons among fish, data are only shown for the time period each PAT tag was at large. For all tags that reported to Argos satellites, AMP was used to estimate daily longitude. For tag 02P0338 which was physically recovered, Time Series Processor (TSP) was used to estimate daily longitude. For longitude plots, □ = beginning position (release) and end location (recapture position or position at which the tag reported to Argos) and ● = estimated position.



Figures 3b. Release location: St. Paul north. Maximum (o) and minimum (x) depths and temperatures occupied by nine Pacific halibut within each 12-hour period and daily longitude estimates after outliers were removed. Though the same time, depth, temperature and longitude scales are used to allow comparisons among fish, data are only shown for the time period each PAT tag was at large. Tag 00-0822 prematurely released from the fish on 26 September 2002, thus subsequent recordings do not represent depths, temperatures and longitude experienced by the fish, but rather by the drifting tag. For all tags that reported to Argos satellites, AMP was used to estimate daily longitude. For longitude plots, □ = beginning position (release) and end location (recapture position or position at which the tag reported to Argos) and ● = estimated position. Note the different longitude scale for tag 00-0822 that was used because the tag prematurely released from the fish on 26 September 2002 and drifted into the eastern hemisphere.



Figures 3c. Release location: Otter Island. Maximum (o) and minimum (x) depths and temperatures occupied by nine Pacific halibut within each 12-hour period and daily longitude estimates after outliers were removed. Though the same time, depth, temperature and longitude scales are used to allow comparisons among fish, data are only shown for the time period each PAT tag was at large. For all tags that reported to Argos satellites, AMP was used to estimate daily longitude. For longitude plots, □ = beginning position (release) and end location (recapture position or position at which the tag reported to Argos) and ● = estimated position.

Daily temperature minima and maxima did not show large variation among fish (Fig. 3). The smallest temperature range experienced by an individual halibut was 5°C (00-0826) while the maximum was 8°C (02P0327). Fish 02P0327 experienced both the minimum and maximum temperatures observed for any fish: 1.4°C and 9.4°C. For fish released near Otter Island and west of St. Paul Island, water temperatures experienced by the fish generally declined during the experiment. When these fish moved to the continental slope, there were abrupt changes associated with the change in depth. In particular, 00-0826 and 02P0323 experienced temperature increases of approximately 2°C in December when they traveled below 100-200 m, and re-entered cooler water upon descending below 500-700 m. Fish 02P0323 experienced a similar short-term temperature increase as it moved back upslope in early February. For fish released north of St. Paul Island, there were no large daily fluctuations of temperature. These fish that stayed on the continental shelf generally experienced a gradual cooling trend in water temperature during the experiment. The fish that was recaptured after 12 days experienced a much smaller range in temperature (<3°C).

We recovered light data from all nine of the tags and examined their geolocation estimates. For the eight tags that transmitted their data to satellite, the percentage of days with longitude and latitude estimates ranged from 5.5% to just over 18% (Table 1). For the tag that was physically recovered, the percentage of days with geolocation estimates was 66.7%.

Geolocation estimates were produced for the six day period after release and the six day period before recovery for six of the eight tags (Table 1). Mean longitude error magnitude ranged from 0.2° to 2.1° (~12–130 km), but most were approximately 1° (approximately 60 km) or less while mean longitude biases ranged from -1.1° to 0.7° (approximately -67–42 km). Latitude estimates were found to be highly variable (Table 1) and therefore were not used for determining movement of halibut. The number of individual geolocation estimates from which mean longitude bias was calculated was insufficient to determine if bias was significantly different from a hypothetical value of zero.

Because individual longitude estimates may be subject to occasional large errors, one must practice caution when using these estimates to represent the true position of the fish (A. Seitz³ unpublished data.). However, examining trends in estimates may be useful for determining the direction of movement. For all but one fish (02P0323), every light-based longitude was west of Unimak Pass (165° W longitude), therefore there is no supporting evidence that the halibut may have spent time in the Gulf of Alaska and then returned to the Bering Sea between the release and pop-up dates (Fig. 3). For 02P0323, there are two points east of 165° W longitude, but all of the longitude estimates were highly varied and the pop-up location was close to the release location. Therefore, claiming that the fish traveled to the Gulf of Alaska is tenuous because there is no trend in longitude estimates to support such a claim. With the exception of 00-0824, there did not appear to be any obvious trends indicating mesoscale (>150 km; A. Seitz³ unpublished) movement of fish whose tags remained attached for the duration of the experiment (Fig. 3). Most of the longitude estimates were scattered around a hypothetical line connecting the release and recovery locations. Occasionally, longitude estimates for individual fish showed a large fluctuation over short time periods, which did not appear to be related to depth fluctuations, but the true positions of the fish were probably a function of an average of a series of adjacent longitude estimates (A. Seitz³ unpublished data). In contrast to the other fish, the longitude estimates of fish 00-0824 showed an obvious trend of movement away from the tagging area towards the east, beginning in September. Once the fish reached approximately 166° W longitude, the tag stopped producing longitude estimates, which coincided with the fish

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moving into deeper water (>165 m; Fig. 3). Tag 00-0822 also produced longitude estimates with an obvious trend of movement, in this case westward. This most likely occurred after the tag prematurely detached from the fish and was advected in the prevailing surface currents.

Discussion

Identifying adult spawning locations, movement patterns and associated levels of mixing will help determine the population structure of Pacific halibut in the Bering Sea and the Gulf of Alaska. The movements of Pacific halibut are poorly understood and previous studies are limited. Long-term movements were first examined from 1913 to 1924 using conventional tags, when the IPHC allowed a winter fishery during which fishers were able to recover fish tagged during the summer feeding season. This allowed a brief assessment of spawning locations and seasonal movements from summer feeding grounds to winter spawning grounds. After 1924, this winter fishery was closed as a protective measure and only sparse winter distribution data have been collected since.

PAT tags are a fisheries-independent tool for studying fish and have proven to be an effective method for studying halibut biology and ecology in the Gulf of Alaska (Seitz et al. 2002, 2003) and now the Bering Sea as well. By using PAT tags, we are able to avoid artifacts associated with conventional tagging experiments such as imbalance in fishing effort among areas, as well as ensuring tag returns during winter. With data recovery from 9 out of 12 tags, this is among the best success rates for PAT tag experiments for any fish species (Gunn and Block 2001), is better than a previous PAT tag experiment for halibut in the Gulf of Alaska (Seitz et al. 2003) and roughly equivalent to our concurrent work (Loher and Seitz 2006).

The tags that functioned properly provided a first *in situ* observation into the seasonal movements and conditions of the environment of halibut in the southeast Bering Sea. From these data, we can theorize about the life history of halibut in the Bering Sea. Like halibut in the Gulf of Alaska (Seitz et al. 2003), the fish in the Bering Sea demonstrated variability in migration patterns among groups of fish tagged at geographically proximate locations. In the northern Gulf of Alaska, fish released in Resurrection Bay near Seward, AK, swam east to known spawning grounds on the continental shelf edge while fish released off Cape Aialik, only 15 km from Resurrection Bay, either migrated southwest or remained in the vicinity of their release location (Seitz et al. 2003). Similarly, halibut released off of the north side of St. Paul Island moved west and remained north of the island while fish released off the western and southern sides of the island moved south or stayed in their vicinity of release.

Not only did the halibut in this study show variability in migration direction, but they also migrated to different locations on the ocean floor. Using the depth record as a proxy of the approximate location of the halibut on the ocean floor (Seitz et al. 2003), the halibut released north of St. Paul Island remained on the continental shelf, while the halibut released west and south of the island all visited the continental slope in the winter. We assume that the halibut on the continental slope are at their winter spawning locations (Seitz et al. 2003) because virtually all halibut in the size range of this study are mature (Clark et al. 1999). These adults are thought to migrate annually from shallow summer feeding grounds to deeper areas to spawn from November to March (St-Pierre 1984, IPHC 1998). Peak spawning is expected during January and February (Thompson and Van Cleve 1936), thus the mid February pop-up date that we used should maximize the likelihood that tagged fish will have completed their seasonal spawning migrations and will be located at or close to their winter grounds on the pop-up date.

The fish (00-0826) that swam to the continental slope northwest of the Pribilof Canyon added to our knowledge of spawning locations of halibut in the Bering Sea. Spawning is known to occur in the southeast Bering Sea as far north as the Pribilof Canyon (Thompson and Van Cleve 1936). Spawning may take place farther north in the Bering Sea, but winter spawning surveys

have never been conducted north of the Pribilof Canyon. We assume this fish was spawning because it moved to deeper water, which is consistent with presumed spawning migration. This suggests that spawning grounds may extend along the shelf-edge north of the Pribilof Canyon, which would represent an extension of the known winter spawning range of halibut relative to that previously reported (St. Pierre 1984).

One halibut, 00-0824, did not remain in the vicinity of St. Paul Island, but rather moved to the Aleutian Islands. This fish began its migration by swimming off the continental shelf onto the continental slope two months earlier than any of the other halibut. This fish could have taken two separate routes from the beginning to the endpoint: it may have taken a circuitous route by swimming southeast then southwest while hugging the continental slope between approximately 400 and 800 m (Fig. 3), or it may have swam straight from the tagging location to the pop-up location across the Bering Basin while swimming in the pelagic realm in the same depth range. The light-based longitude record clearly demonstrates that the fish swam to the east and was at approximately 165° W longitude by early October. This supports the hypothesis that the fish hugged the continental slope and took the circuitous route to its winter location. If this is indeed true, then the fish traveled farther than the straight-line distance between the tagging and pop-up locations. Taking the more circuitous route changes the distance traveled from 512.5 km to approximately 775 km. This interpretation may apply to all halibut and may be useful for interpreting the path of travel for halibut in previous (Seitz et al. 2003) and concurrent (Loher and Seitz 2006) halibut tagging experiments.

The timing of movement for the fish that left the continental shelf supports the hypothesis that halibut that migrate longer distances to the spawning grounds leave their summer feeding site earlier (Loher and Seitz 2006). In this study, the fish that swam to the continental slope in and near the Pribilof Canyon, whose horizontal displacement was 70–140 km, arrived on the slope from mid-November to early January. The fish that swam to the Aleutian Islands, whose horizontal displacement was much larger, arrived on the slope at the end of September and appears to have made most of its migration on the slope rather than the shelf. For comparison, in the Gulf of Alaska, one fish whose horizontal displacement was 190 km, arrived on the slope in late November while two fish whose horizontal displacement was 330 and 360 km, arrived on the slope in early November (Seitz et al. 2003). Similar results were also found in a concurrent study in the Gulf of Alaska where halibut on summer feeding grounds at the southern edges of the GOA began their migrations earlier than fish that spend the summer in the northern Gulf of Alaska (Loher and Seitz 2006). This pattern is likely due to the longer distances traveled between their seasonal grounds.

The movement of one fish confirms homing to its summer feeding site for this individual. IPHC scientists believe that halibut show fidelity to summer feeding sites (IPHC 1998). This conclusion is based upon conventional tag experiments where most fish are released during the summer and recaptured near the release location during following summers. However, with conventional tags, there is no way of ascertaining that the fish actually moved to the continental slope during the winter to spawn, as opposed to simply having remained near the tagging site throughout time-at-liberty. Thus, homing cannot be resolved from interannual site fidelity using conventional tags. One halibut PAT tagged in the Gulf of Alaska was recaptured just 2.5 km from its tagging site two years after tagging, after having spent its first winter on the continental slope (Seitz et al. 2003). This fish provided the first documented evidence of true homing following migration to alternate winter grounds. In the present study, fish 02P0323 provided further documentation of the same; its PAT tag reported to Argos near its tagging site. However, it could not have remained near the tagging location during the winter because the fish experienced maximum depths of approximately 650–700 m from mid-December to early February. Depths of this magnitude do not exist on the continental shelf, indicating that the fish moved off the shelf to the slope. After spending the winter in deep water on the slope, the fish moved back

to its summer feeding ground south of St. Paul Island. Although the distance between tagging and reporting location was 5.4 km, the fish may have been even closer to its tagging location. The lag between the tag releasing from the fish and reporting to Argos was just over four hours, in which time the tag may have drifted due to tides, wind or currents. Additionally, the error estimate of the reporting location by Argos was ± 1.0 km, therefore, the fish could have been even closer than the reported distance to its tagging site.

Two fish tagged north of St. Paul Island did not travel to the continental slope by mid-February. There are several possible explanations for this behavior. The fish may have foregone a trip to the continental slope and spawned on the continental shelf. Although major spawning grounds are typically in deeper water on the shelf edge, spawning activity is not limited to the slope, and may occur in depressions in the continental shelf (St-Pierre 1984, IPHC 1998). Alternatively, the fish may not have spawned. It is possible that these two fish, which displayed different behavior than the fish released south and west of the island, would have spawned later in the year and a February pop-up date was too early to capture their spawning migration. Another possibility is that halibut may skip spawning during some winters (Novikov 1964, Seitz et al. 2005, Loher and Seitz 2006).

The PAT tags can be used to examine the water temperature that the halibut inhabit. It is traditionally thought that few halibut live in temperatures of 2°C or less in the Bering Sea. Furthermore, catches are largest at temperature of 4–5°C (Best 1981). Soviet research in the southeastern Bering Sea reported the highest juvenile catch rates at 3.5–5.5°C (Novikov 1964). The water temperature data from this investigation generally corroborate the previous descriptions, but additionally quantifies the range of temperatures experienced by individuals. We are also able to examine regional differences of ambient conditions experienced by halibut in the Bering Sea and Gulf of Alaska. In general, the Bering Sea halibut inhabited colder and deeper water. The minimum and maximum temperatures experienced by any fish in the Bering Sea (1.4 and 9.4°C) were 2.4 and 2.8°C colder, respectively, than any fish in the Gulf of Alaska (3.8 and 12.2°C) (Seitz et al. 2003, Loher and Seitz 2006).

The present data also provide some indication of travel among water masses of different origin during seasonal migration. The Bering Slope Current (BSC) forms the eastern boundary of the Bering Sea gyre, flowing from southeast to northwest offshore of the Pribilofs. The eastern band of the BSC creates a sub-surface layer of maximum temperature that impinges upon the slope at depths of 250–500 m (Kinder et al. 1975). A temperature minimum layer is found at depths <200 m, probably representing the cool subthermocline water of the Middle Domain (Stabeno et al. 1999, Flint et al. 2002). Temperature decreases uniformly with depth below 500 m (Kinder et al. 1975). The relatively warm temperatures experienced by two fish (00-0826 and 02P0323) at depths of roughly 200–600 m, during downslope migration in December and upslope migration in February, is consistent with movement across the BSC's temperature maximum layer. PAT tags could be used similarly to identify travel into the Gulf of Alaska where Pacific halibut experience a bottom temperature of approximately 6°C throughout the year (Seitz et al. 2003, Loher and Seitz 2006).

PAT tags can be used to compare depth ranges of halibut in the Bering Sea and Gulf of Alaska. The minimum and maximum depths experienced by any fish in the Bering Sea (16 and 844 m) were 16 and 108 m deeper, respectively, than any fish in the Gulf of Alaska (0 and 736 m; Loher and Seitz 2006). Whether these differences in depths and temperatures are due to regional differences in oceanographic conditions or differences in the biology of the species in the Bering Sea and the Gulf of Alaska will remain unknown until more tags are deployed in the future.

By combining pop-up location, geolocation by light estimates, depth, and temperature data, we hypothesize that Bering Sea halibut may constitute a separate spawning subpopulation of halibut from those in the Gulf of Alaska. There was no evidence of any fish tagged on summer

feeding grounds near St. Paul Island migrating to the Gulf of Alaska in the winter spawning season. Winter spawning location of halibut serves as an indicator of population structure because if adult halibut migrate out of the Bering Sea to the Gulf of Alaska to spawn, their eggs and larvae will drift in a westerly direction in the Alaska Stream or Alaska Coastal Current, depending on how far offshore they spawn (Reed and Schumacher 1986). The eggs and larvae may travel through one of the numerous passes through the Aleutian Island chain into the Bering Sea, or they may become entrapped in the counter-clockwise Gulf of Alaska gyre and remain there. Either way, if Bering Sea summer residents migrate to the Gulf of Alaska to spawn they will contribute to southern spawning assemblages, larval supply, and potentially to Gulf of Alaska nursery production, providing a mechanism for replenishment of potentially depleted grounds in the Gulf of Alaska. On the other hand, if these adult halibut remain in the Bering Sea to spawn, their eggs and larvae will likely become entrapped in the Bering Sea gyre or one of the smaller sub-gyres within the Bering Sea (Stabeno et al. 1999), contributing only to Bering Sea nursery production and providing far less opportunity for cross-basin mixing. If this pattern is continued for many generations in the absence of either migration by Gulf of Alaska summer residents into the Bering Sea to spawn or substantial dispersal of juveniles away from local nursery grounds, the result can be reproductive isolation of the Bering Sea relative to the Gulf of Alaska.

Three additional lines of evidence support the hypothesis of population substructure between the Bering Sea and the Gulf of Alaska in Pacific halibut. First, halibut PAT tagged on summer feeding grounds in the Gulf of Alaska have shown no evidence of migration into the Bering Sea (Seitz et al. 2003, Loher and Seitz 2006), further suggesting isolation of spawning groups. Second, the IPHC has been confronted with a number of local depletions in the Bering Sea in recent years, such as the halibut fishery near St. Paul Island. Harvest shortfalls from 2000–04 in Area 4C were 14, 15, 41, 56, and 45%, respectively, of the combined CDQ-IFQ quotas. Recovery in 2004 largely represented a decrease in quota relative to the other four years. The Pribilof Island area local depletion and recent declines in apparent abundance along the Aleutian Chain suggest that movement of individual halibut may be relatively limited in the Bering Sea, in contrast to the complete mixing implied under a single-population management model. Finally, emerging genetic results using nuclear microsatellite loci (Hauser et al. 2007), which are often more powerful in differentiating populations than serum protein data (Tsuyuki et al. 1969, Grant et al. 1984), have found significant genetic differentiation between spawning halibut from the southeast Bering Sea (Pribilof Canyon; Fig 1) and those from the central Gulf of Alaska (Portlock Bank, near Kodiak Island).

Another question that remains to be answered is: to what extent do halibut along the Aleutian Islands intermingle with those from the southeast Bering Sea and/or Gulf of Alaska? It is commonly accepted that the Gulf of Alaska extends only as far west as the end of the Alaska Peninsula (i.e. to Unimak Pass). The fish that was tagged in the Bering Sea and swam to the Aleutians Islands (00-0824) suggests that the southeast Bering Sea and Aleutian Islands may be connected through normal seasonal migrations, as opposed to the southeast Bering Sea and Gulf of Alaska. To confuse the issue even more, genetic data using microsatellites (Hauser et al 2006) suggest that halibut from St. Paul Island may be more genetically similar to those from as far south as Oregon than they are to fish from the central Aleutians. In that report, a hypothesis was presented that deep water passes along the Aleutian Chain, Amchitka in particular (Fig. 1), may create a barrier to migration and generate reproductive isolation in the Aleutians. It is interesting to note that 00-0824 did not move west across Amchitka pass during its time-at-liberty. The puzzle of possible population structure will only be solved with future tag deployments combined with other spatial population structure research such as genetics and otolith microchemistry.

Although we are unable to draw definitive conclusions regarding population structure, we can examine the extent of movement among IPHC Regulatory Area. In this study, all but one fish left Area 4C at some point over the winter (Fig. 1). Three halibut swam to the Area

4A Edge, one swam to 4D Edge, and one left Area 4C, but we are unable to ascertain where it went. Obviously, the redistribution of halibut that feed near St. Paul in the summer could have serious consequences on the local St. Paul halibut fleet if a year-round fishery is enacted. Interceptions outside Area 4C during the winter may add to the apparent local depletion around St. Paul Island.

Two problems were experienced typical to PAT tagging experiments. Three of the tags did not transmit data which could have been caused by a variety of factors including: tag malfunction (Seitz et al. 2003); premature release and then drifting ashore (in which case the tag would not be electrically grounded and would not transmit); and fishery recapture and subsequent non-reporting. We were unable to ascertain the cause of missing tags in this experiment. Additionally, one tag prematurely released from the fish well before the scheduled pop-up date. This was the first documented case of premature release in Pacific halibut PAT tagging experiments out of a total of 38 tags from this and two previous studies (Seitz et al. 2003, Loher and Seitz 2006). This rate of premature release is well below those for other pelagic fish experiments (Domeier et al. 2003, Stokesbury et al. 2004). Although we were unable to determine the cause of premature release in this experiment, it may have been due to failure of the tag anchor, leader or pin. All of these components of the tag are subjected to stress as a fish moves through the water. We speculate that PAT tags on halibut tend to experience higher data recovery rates and fewer premature release events than those on pelagic fish because halibut live a more sedentary life and swim at slower speeds than pelagic fish such as tuna and marlin.

Sample sizes in the present study are far too small to quantitatively address questions of reproductive mixing rates between the Bering Sea and Gulf of Alaska. Continued deployments are necessary to gain greater insight regarding the potential for halibut resident on summer feeding grounds in the Bering Sea to visit Gulf of Alaska winter spawning grounds, and *vice versa*. However, this study represents a foundation upon which an expanded metapopulation analysis can be constructed in the future. If halibut are geographically separated and remain in the Bering Sea or Gulf of Alaska, either through their entire life history or for the purposes of spawning, these areas may need to be managed as separate subpopulations.

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