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Further investigation of seasonal movements and environmental conditions experienced by Pacific halibut in the Bering Sea, examined by pop-up satellite tags

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Abstract

Currently, the commercial fishery for Pacific halibut (*Hippoglossus stenolepis*) in the eastern Pacific Ocean is managed within a series of regulatory areas within which differing harvest control rules are applied. We hypothesize that Pacific halibut in the Bering Sea and Aleutian Islands belong to a separate sub-population from those in the Gulf of Alaska, with respect to spawning structure. We studied the putative spawning locations and seasonal migration of Pacific halibut along the southeastern Bering Sea shelf-edge as indicators of population structure, building on prior research that characterized sites on the southeast Bering Sea shelf and in the Aleutian Islands. Pop-up Archival Transmitting tags provided no evidence that Pacific halibut moved out of the Bering Sea into the Gulf of Alaska during the mid-winter spawning season, supporting our hypothesis of separate sub-populations. Mid-winter aggregation patterns suggest that a spawning ground may be located in Middle Canyon, which is approximately 600 km northwest of the nearest documented spawning area in the Pribilof Canyon. The summarized depth data transmitted via satellites may be useful for identifying spawning behavior. If discrete acts of spawning are identified, they may be used to refine some assumptions of the spawning characteristics of Pacific halibut, including spawning frequency and season.

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Introduction

The Pacific halibut (*Hippoglossus stenolepis*) fishery is an important resource throughout western Alaska (Fig. 1), especially where it is harvested under the Community Development Quota (CDQ) program (NRC 1999). The CDQ program was established to provide income to coastal communities with access to Aleutian Island and Bering Sea marine resources. The program has been hailed by the National Research Council as a critical innovation for local economic development, and Pacific halibut represents one of the key species within the program. For stock assessments conducted on this species from 2006–2013, the eastern Bering Sea/Aleutian Island (BSAI) region was not assessed independently from the remainder of the Pacific Ocean stock, but rather as a component of a single coastwide population (Clark and Hare 2007, Stewart and Martell 2014) that is believed to be relatively well-mixed from Oregon to Alaska.

It is generally believed that throughout its range, this population of Pacific halibut feeds largely on the continental shelf during the summer, undertakes a spawning migration to deeper water during winter, and returns to summer feeding grounds during spring (Dunlop et al. 1964, Best 1981). Recent Passive Integrated Transponder (PIT) tag research has confirmed that ontogenetic migration may continue at sizes and ages that are recruited to the fishery, resulting in area-specific annual redistribution of harvestable biomass estimated to range between 7.8% net immigration and 21.3% net emigration, depending upon the region considered (Webster et al. 2013). These results are generally consistent with analyses of Pop-up Archival Transmitting (PAT) tag data suggesting that large (<100 cm) halibut display approximately 80% interannual fidelity to their summer feeding grounds, with about 60% of individuals homing to within 20 km of the previous year's location after having departed the continental shelf for the winter (Loher 2008).

Spawning appears to be concentrated in relatively discrete winter spawning grounds, although it is likely that spawning occurs along much of the continental shelf-edge within the spawning range, near the edge of the continental shelf from at least British Columbia, Canada through the Pribilof Canyon (Fig. 1) in the southeast Bering Sea (St. Pierre 1984). For purposes of stock assessment, the spawning stock is considered to comprise a single pool, and a single coastwide estimate of spawning stock biomass is calculated as one metric of current stock status (Stewart and Martell 2014). Similarly, catch limit reductions invoked to account for lost reproductive potential due to bycatch mortality are distributed to all areas in proportion to their current exploitable biomass (Stewart and Martell 2014); an approach that follows historical analyses which rested upon the assumption that reproductive losses from regional bycatch affect the reproductive potential of the entire population (Sullivan et al. 1994). Still, segregation of spawning into discrete units has the potential to generate internal population structure at scales not adequately captured in a single-unit-stock management approach (Stephenson 1999, Frank and Brickman 2001). At the adult level, the paradigm of a well-mixed stock implies that Pacific halibut from several feeding areas, including fish from the BSAI region and those from the Gulf of Alaska (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.

However, because of land masses and ocean currents that partially separate the BSAI region from the GOA, we hypothesize that Pacific halibut from these regions do not intermingle on common spawning grounds, but rather that active spawners largely remain within their respective regions throughout the year. If Pacific halibut from the BSAI region do not commonly mix on the spawning grounds with individuals from the GOA, the BSAI region may support a separate spawning component of Pacific halibut (see review in Seitz et al. 2007). Hereafter, we will refer to such regionally-derived groups as "spawning sub-populations"; solely implying that the spawning-age halibut found on these grounds, regardless of their natal origin or earlier ontogenetic migration history, have predominantly remained in the same ocean basin to spawn as that in which they were found during the prior summer, as opposed to crossing ocean-basin boundaries to spawn. If there is indeed a spawning sub-population of Pacific halibut in the BSAI region, this may have a substantial impact on local productivity and population dynamics in the fisheries of western Alaska, especially considering past observations of regional declines in catch per unit effort (Hare 2005, 2006) and exploitable biomass (Clark and Hare 2002).

To address the BSAI sub-population hypothesis, we began an investigation to examine the winter locations, which are considered potential spawning areas, and migratory pathways of Pacific halibut in five locations that encircle the range of Pacific halibut in the Bering Sea and Aleutian Islands region (Seitz et al. 2007; Seitz et al. 2008). Prior to the experiment described in this paper, we tagged adult Pacific halibut with PAT tags (Seitz et al. 2003) in three locations: near St. Paul Island (Fig. 1), along the southeast Bering Sea shelf-edge, and near Attu and Atka Islands (Fig. 1) in the Aleutian chain. PAT tags allow us to determine winter location of the tagged fish and some aspects of their migration timing and routes, without depending upon winter fisheries to recapture the tagged individuals.

Figure 1. Map of Bering Sea and Aleutian Islands regions with release (●) and recovery sites (o) of Pacific halibut from previous PAT tag investigations.

Results from prior PAT-tag investigations conducted along the Aleutian Chain and around the Pribilof Islands indicated no movement of Pacific halibut out of the BSAI region into the Gulf of Alaska during the mid-winter spawning season, consistent with the hypothesis of spawning sub-populations (Fig. 1). Within the BSAI region, there was evidence for geographically-localized sub-populations as all of the Pacific halibut tagged near the Aleutian Islands displayed residency near the islands where they were tagged. In the southeastern Bering Sea, the Pacific halibut ranged farther from their tagging location than those from the Aleutian Islands, but did not display any evidence of having crossed the Aleutian Ridge. Although these investigations represent an advance in our knowledge of Pacific halibut biology in the BSAI region, completion of our original experimental design is imperative because three shortcomings prevent confident inference regarding population structure of these fish in the eastern Pacific Ocean. First, the sample size of tagged Pacific halibut on the southeastern Bering Sea continental shelf was very small (n=7). Second, the geographical distribution of PAT tag releases was highly localized around St. Paul Island; thus, a representative view of Pacific halibut behavior across the entire southeastern Bering Sea shelf was not obtained. Third, and arguably the most important, Pacific halibut were not PAT-tagged and released near the strait that connects the Bering Sea and the Gulf of Alaska: Unimak Pass (Fig. 1). One would hypothesize that interlacing between the Bering Sea and GOA should be most strongly detectable around Unimak Pass, and so this deficiency in the prior studies deserves greater attention.

The goal of the present study was to rectify the previously-described shortcomings by tagging Pacific halibut at two additional areas in the southeast Bering Sea with PAT tags to complete a five-site circum-BSAI experimental design. This report represents the third installment of a continuing investigation of spatial spawning stock structure using PAT tags on Pacific halibut in the BSAI region (see also Seitz et al. 2007, Seitz et al. 2008). Using these PAT tag data, we seek to determine winter locations of tagged Pacific halibut and infer migration timing and pathways used during their putative spawning migration. This information can be used to refine our understanding of regional spawning population structure and to infer whether BSAI Pacific halibut spawn locally and are likely to contribute primarily to western Alaskan recruitment potential, as well as the likelihood that summer Bering Sea residents contribute to Gulf of Alaska spawning groups and larval pools.

In this respect, it is important to reiterate that our study was specifically limited to investigating seasonal migration of adult halibut for the purposes of spawning; i.e., attempting to identify dispersal and aggregation patterns that are established only after reaching reproductive maturity. Ontogenetic mixing of halibut among regions undoubtedly occurs over a broad range of ages and across life-history stages (e.g., see Best 1971, St-Pierre 1989, Hilborn et al. 1995, Webster et al 2013). However, the extent to which the migration of non-reproductive individuals constitutes homogenization of population structure (i.e., exchange of genetic material among distant regions) as opposed to evidence of mechanisms whereby strict population segregation might be maintained (e.g., faithful repatriation of individuals to their location(s) of parental origin) cannot be assessed by any single tagging study. Rather, such inferences must be drawn through multidisciplinary means conducted over intergenerational time-scales. Here, we address questions of population structure established over shorter periods, with implications for shorter-period management actions. As such, an appropriate question to frame the processes under study might be “if a given group of spawners were eliminated through catastrophic action, how reasonable would it be to expect a spawning group to be re-established on the same spawning ground, composed of individuals from the same cohorts, within a few years?” At this spatiotemporal scale, evidence of seasonal migration between the BSAI and the GOA would imply spawning stock structure relatively consistent with the IPHC’s convention of viewing the coastwide spawning stock as a single pool (Sullivan et al. 1994); whereas very low levels of seasonal migration between the BSAI and the GOA might imply persistent substructure worthy of closer attention.

Methods

Twenty-four adult Pacific halibut were tagged with PAT tags (Wildlife Computers: Redmond, Washington, USA) and released on the southeastern Bering Sea continental shelf/slope: 12 in Middle Canyon during June 2006 and 12 in Bering Canyon during August 2006 (Fig. 2). These two locations were chosen as tagging sites in our experimental design because Middle Canyon is the north-westernmost fishing location in the United States Exclusive Economic Zone, while Bering Canyon is adjacent to Unimak Pass, the primary bathymetric connection between the GOA and BSAI regions.

PAT tags were externally tethered to Pacific halibut following a previously-successful protocol (Seitz et al. 2003). Captured halibut were deemed appropriate for PAT tagging and release if they were in good condition (i.e., likely to survive) and were at least 110 cm fork length (FL), as this was the smallest size of Pacific halibut successfully tagged in a previous study (Seitz et al. 2003). Additionally, this study aimed to monitor spawning movements and the vast majority of Pacific halibut ≥110 cm FL are sexually mature (Clark et al. 1999).

Each PAT tag contained three electronic sensors that recorded ambient water temperature, depth of the tag, and ambient light intensity (for PAT-tag details, see Seitz et al. 2003). The PAT tags actively corroded the pin to which the tether was attached, thus releasing the tag from the animal (i.e., "pop-up"). The tag then floated to the surface and transmitted summarized historical data records to the Advanced Research and Global Observation Satellite (Argos) system. Upon popping up, each tag's endpoint position was determined from the Doppler shift of the transmitted radio frequency in successive uplinks received during one 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.

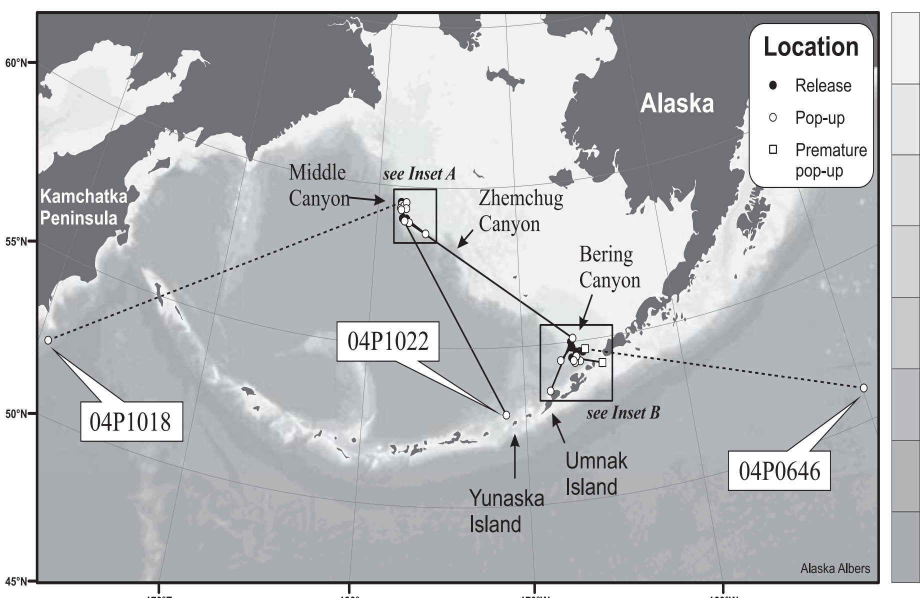
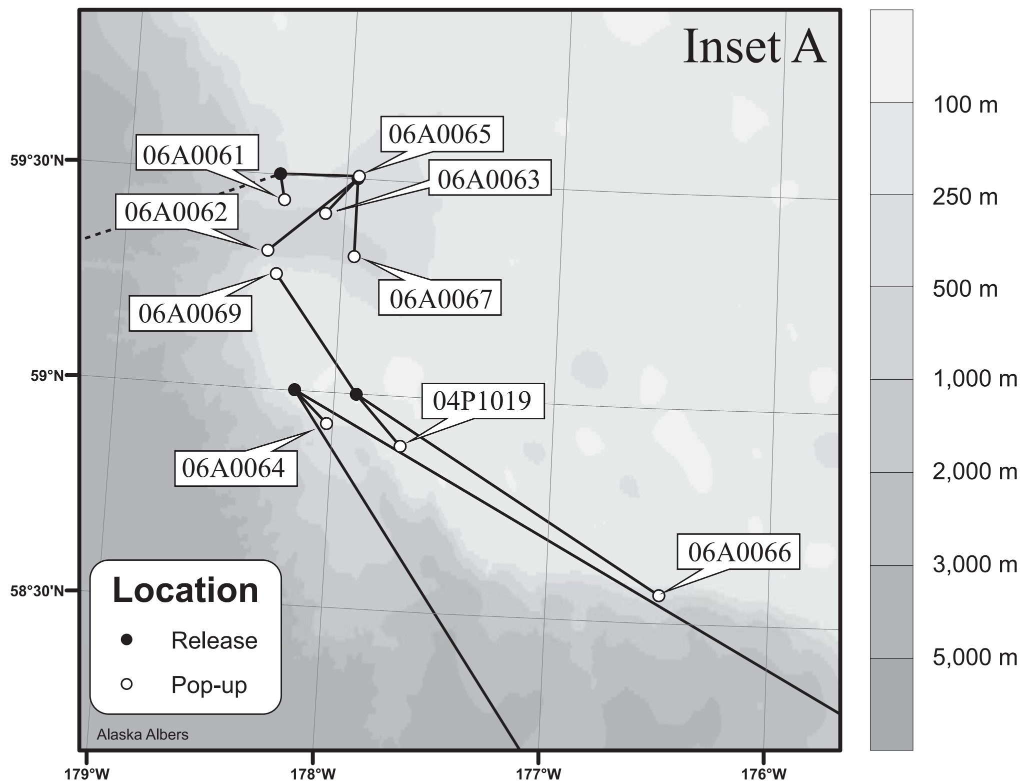


Figure 2. Release (●) and recovery sites (o = tags that transmitted on 1 February 2007, □ = tags that prematurely released from the fish and transmitted after drifting on the surface of the ocean for eight days) of PAT-tagged halibut in the Bering Sea, summer 2006. Solid lines indicate the straight-line path between release and recovery positions of tags that remained attached for the duration of the experiment or transmitted eight days after prematurely releasing from the fish, while dashed lines indicate the straight-line path between release and recovery positions for tags that prematurely released and drifted on the surface of the ocean until the scheduled pop-up date. Numbers are equivalent to the PAT tag numbers given in Tables 1 and 2.



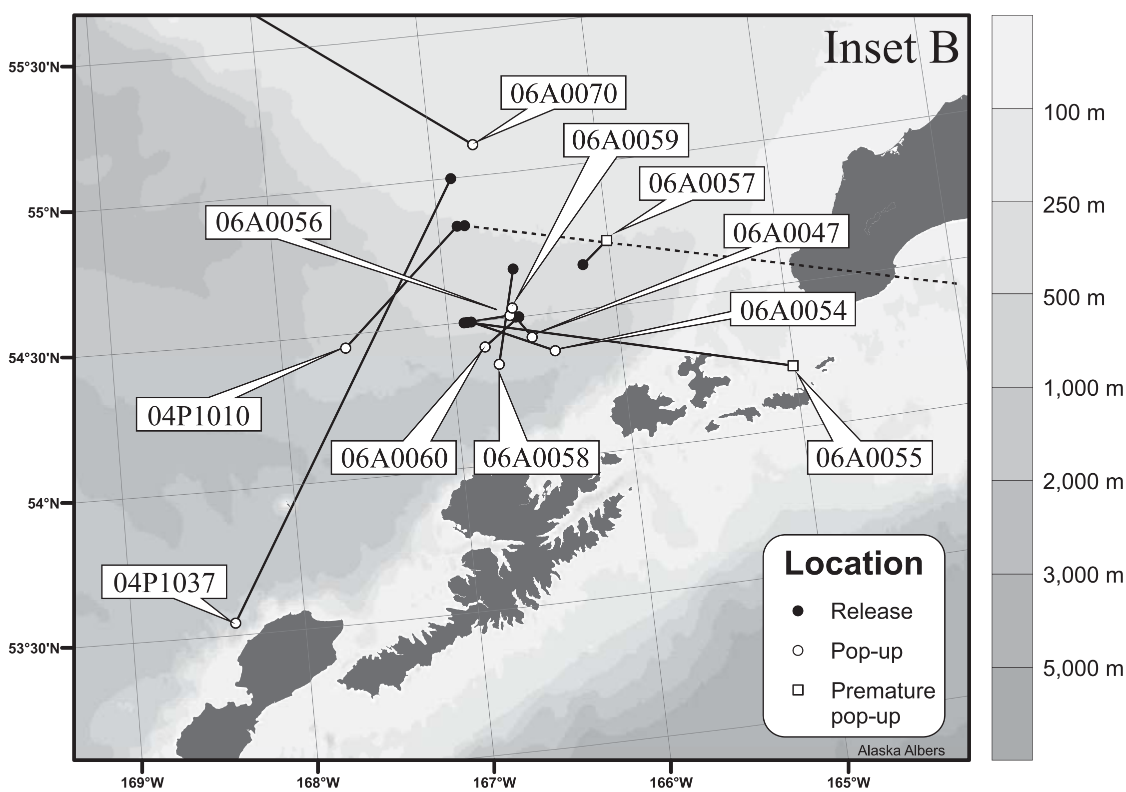


Figure 2. Concluded.

Two generations of tags were used: older PAT4 tags (serial numbers 04P####) and newer MK-10 PAT tags (serial numbers 06A####). The premature release function was not activated in PAT4 tags. Therefore, if PAT4 tags detached from the fish 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. MK-10 PAT tags had a premature release detection function which was activated by eight consecutive days of depth readings of 0 m. After the premature release detection function was activated, the MK-10 PAT tags reported to Argos. All tags were programmed to release on 1 February 2007 to determine the fishes' winter grounds, as adult Pacific halibut are thought to spawn annually from approximately November through March (St. Pierre 1984).

The environmental data were sampled at one minute intervals and were subsequently summarized into 12-hour periods by software within the PAT tag thus providing four types of data: 1) percentage of time spent within specific depth ranges, 2) percentage of time spent within specific temperature ranges, 3) depth-temperature profiles from which minimum and maximum depths and temperatures could be extracted and, 4) daily geoposition estimates for the time the tag was attached to the fish.

Light-based longitude estimates were produced by Wildlife Computers' proprietary software suite, Global Position Estimator (GPE, version 1.02.0004), using the ambient light data (Seitz et al. 2006). The GPE software suite estimated the times of sunrise and sunset from the light intensity data. Daily light level curves that did not exhibit smoothly sloping light levels from high to low or low to high were rejected (Seitz et al. 2006). The GPE suite then calculated longitude for the remaining data based on the difference between the local noon of the tag (mean of the sunrise and sunset times) and Coordinated Universal Time (UTC). Estimated longitude values that were not possible for a fish released in the North Pacific Ocean were rejected from the data set. For example, an impossible longitude was one that placed the tag on land or outside the published range of the Pacific halibut (i.e., to the west of Hokkaido, Japan (140ºE) or to the east of Santa Barbara, CA, USA (117ºW); Mecklenburg et al., 2002). Latitude estimates have been found to be highly variable in previous PAT-tagging experiments (Seitz et al. 2006) and therefore were not used for determining movement of Pacific halibut.

Light-based longitude estimates were qualitatively examined. The number of days with longitude estimates was defined as the days that produced longitude estimates, after outliers were removed. Daily absolute error was estimated as the absolute value of the fish's "true" position (defined subsequently) minus the estimated position. Daily positional error was estimated as the true position minus the estimated position. A negative error meant that a longitude estimate was east of the true position and a positive error meant that a longitude estimate was west of the true 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 estimates for the duration of the track. However, we did know each fish's true position on the days of tagging and recovery (either recapture or reporting to Argos satellites) and used these as true positions. We then compared the estimated positions of the tags for the six days immediately following release and the six days previous to recovery to the respective true positions (Seitz et al. 2006), giving a possible total of 14 positions per fish. For each comparison, we calculated the mean absolute error and estimated the bias by averaging over the 14 error estimates, assuming the fish was stationary during this time. 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. However, examining trends in estimates has proven useful for determining the direction of movement (Loher and Seitz 2006), which is the approach used in this study.

For all tagged fish, we reported fish size, release and recovery locations, number of days with geolocation estimates, estimated daily longitude, and the minimum and maximum depths and temperatures recorded for each 12-hour period that the tag was attached to the fish. The minimum and maximum depths and temperatures for the 5 days immediately following release were not reported to exclude the possibility of reporting unrepresentative behavior of Pacific halibut caused by the stress of a tagging event. The percentage of time spent in specific depth and temperature ranges, as well as the full depth-temperature profiles are not reported here because of the coarse resolution of depth and temperature ranges (100–250 m and 1–10° C, respectively). Large, abrupt changes in maximum depth above or below 200 m were defined as the inshore or offshore dispersal between the continental slope (>200 m) and continental shelf (<200 m) and *vice versa* (Seitz et al. 2003).

Results

Middle Canyon tagging site

Data were recovered from 12 tags (100%) that were attached to fish 110–139 cm FL (Table 1; Figs. 2 and 3). One tag, 06A0061, was physically recovered in the commercial fishery on 3 October 2006 after 120 days at-liberty. Another tag, 04P1018, prematurely released sometime during the first two weeks of July 2006, drifted on the surface of the ocean for approximately 210 days and transmitted to Argos satellites as scheduled. The rest of the tags remained attached to fish for the duration of the experiment (~240 days) and reported to Argos as scheduled.

The maximum horizontal displacement (straight-line distance between release and recovery locations) of the tags that reported on 1 Feb 2007 was 815 km while the minimum was 12 km (median = 21 km; Table 1; Fig. 2). Eight fish, including the tag that was physically recovered (06A0061), were located close (<40 km) to their release locations: six in Middle Canyon and two (06A0064 and 04P1019) on the continental slope between Middle and Zhemchug Canyons. One fish (06A0066) was located in northern Zhemchug Canyon approximately 95 km from its tagging location, and two fish were located over 800 km from their release locations: one in northern Bering Canyon (06A0070) and one off of Yunaska Island in the Aleutian Chain (04P1022). The remaining tag (04P1018), which prematurely released, was located over 1500 km from its release site, off the east coast of the Kamchatka Peninsula.

The fish released in Middle Canyon displayed a wide range of depths during their time at-liberty (Fig. 3). The shallowest and deepest depths of all fish, excluding the five days after release, were 8 m and 752 m (Table 1); all fish experienced depths between 160 m and 472 m. Several fish showed appreciable fluctuations in depth on both a diel and a seasonal basis. There were two fish that did not conform to this pattern. Fish 06A0062 showed very few diel depth changes, except during three isolated occasions in late December 2006 and early January 2007 when its minimum depths were much shallower than its maximum depths. Similarly, fish 06A0063 showed very little diel depth change after early November, except for five isolated occasions during the same time period (December-January) as displayed by 06A0062.

Seasonal dispersal and its timing varied considerably among individual fish (Fig. 3). Based on the 12-hourly maximum depths recorded by the tags, most fish undertook a clearly defined dispersal in which they moved from the continental slope to the continental shelf, and/or *vice versa*, and remained at their new location for longer than a month. Eight fish were released on the continental slope, of which five moved to the continental shelf with dispersal dates as early as 26 June 2006 (04P1019) and as late as 28 January 2007 (06A0070). Four of the fish that moved onto the continental shelf returned to the continental slope with dispersal dates ranging from 22 August 2006 (04P1019) to 1 December 2006 (06A0064). Only one fish (06A0070) was located on the continental shelf on the pop-up date. Three fish released on the continental slope remained there or only made very brief (<3 days) forays onto the continental shelf. The three remaining fish were released on the continental shelf and moved offshore to the continental slope within three weeks after release. Of these three fish, one (06A0067) remained on the slope until the pop-up date, one (00A0069) moved back to the shelf on 18 August 2006 where it remained for 3.5 months before it returned to the deeper waters of the continental slope, and one (04P1022) remained on the continental slope for approximately one month before showing large variations in depth for the remainder of its time at-liberty.

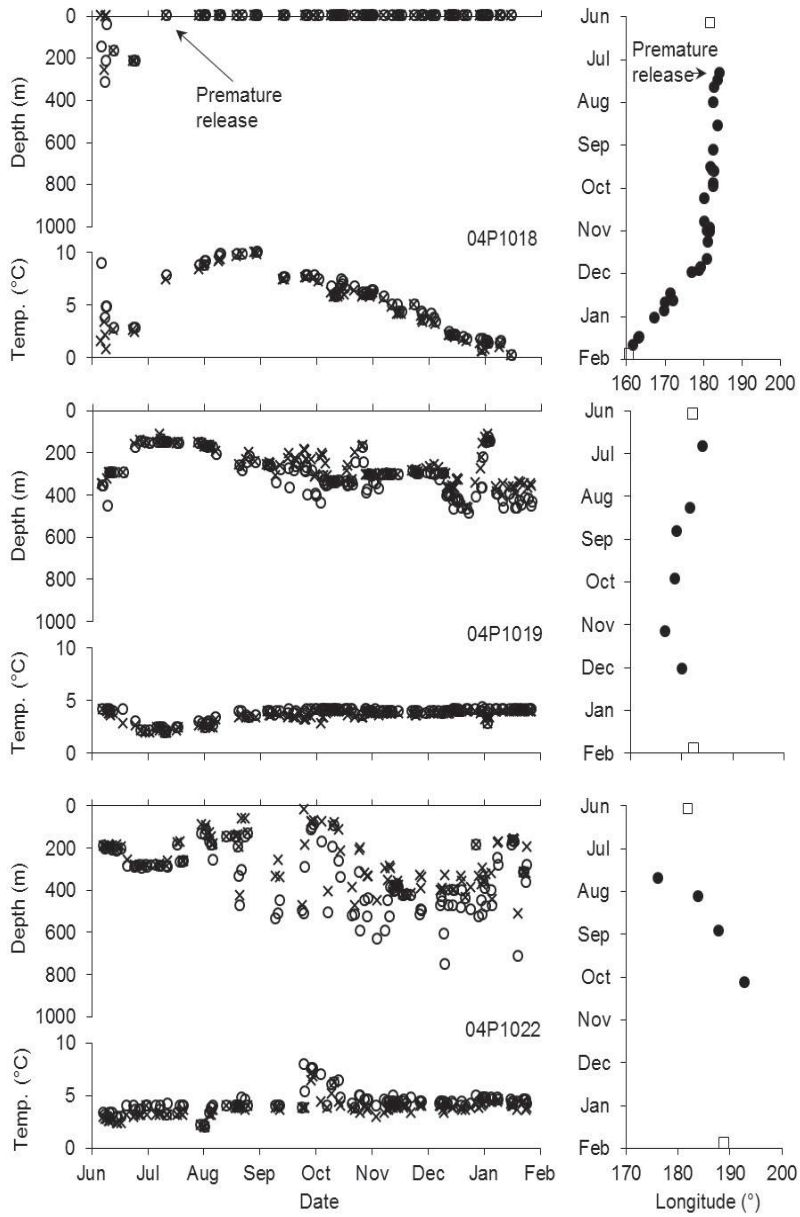


Figure 3. Maximum (o) and minimum (x) depths and temperatures for each 12-hour summary period, and daily longitude estimates after outliers were rejected for Pacific halibut tagged in Middle Canyon. For longitude plots, □ = release position and location at which the tag reported to Argos and ● = estimated position. 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-liberty. Note the different longitude scale for tag 04P1018 that was used because the tag prematurely released from the fish and drifted into the eastern hemisphere.

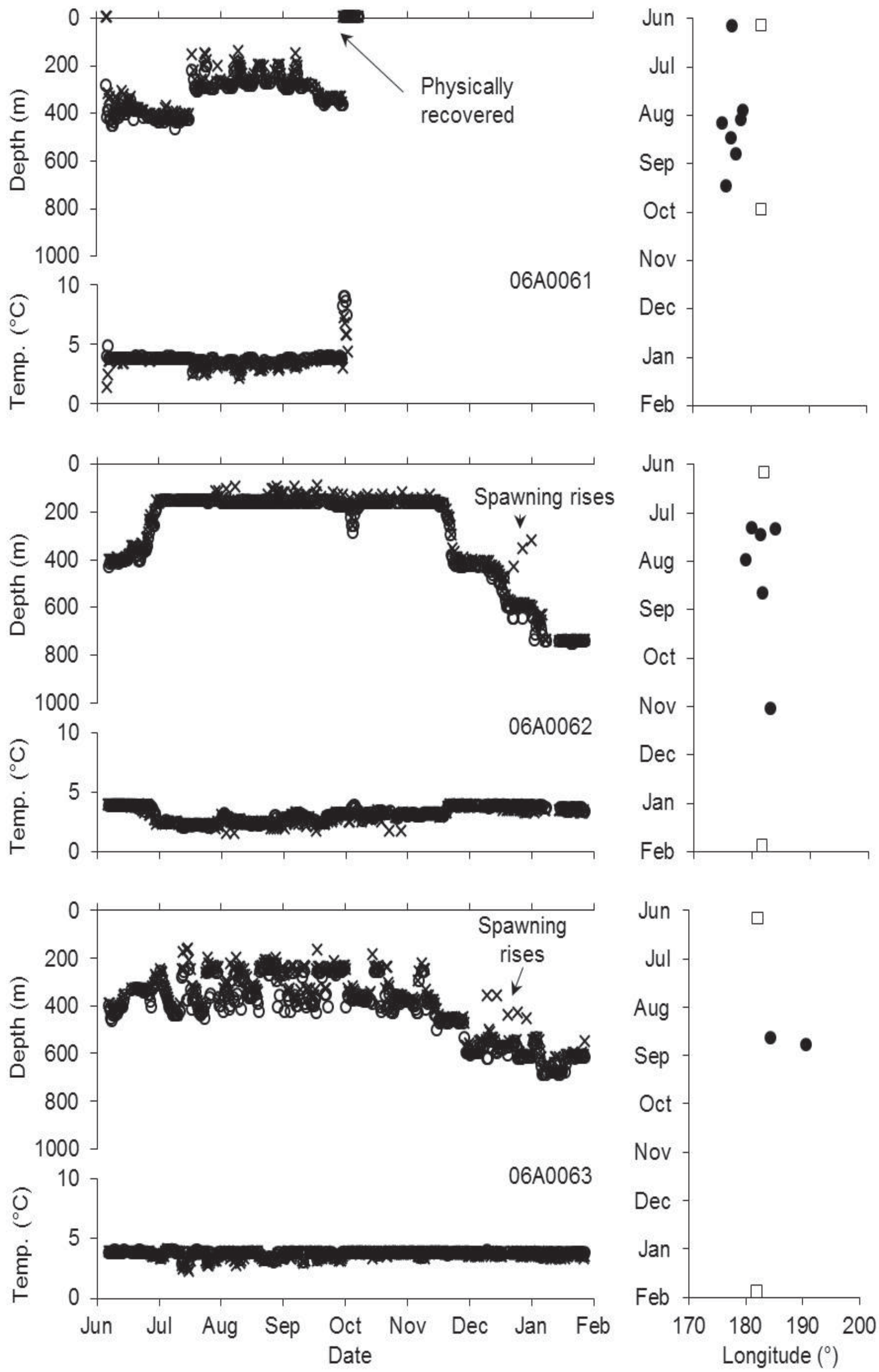
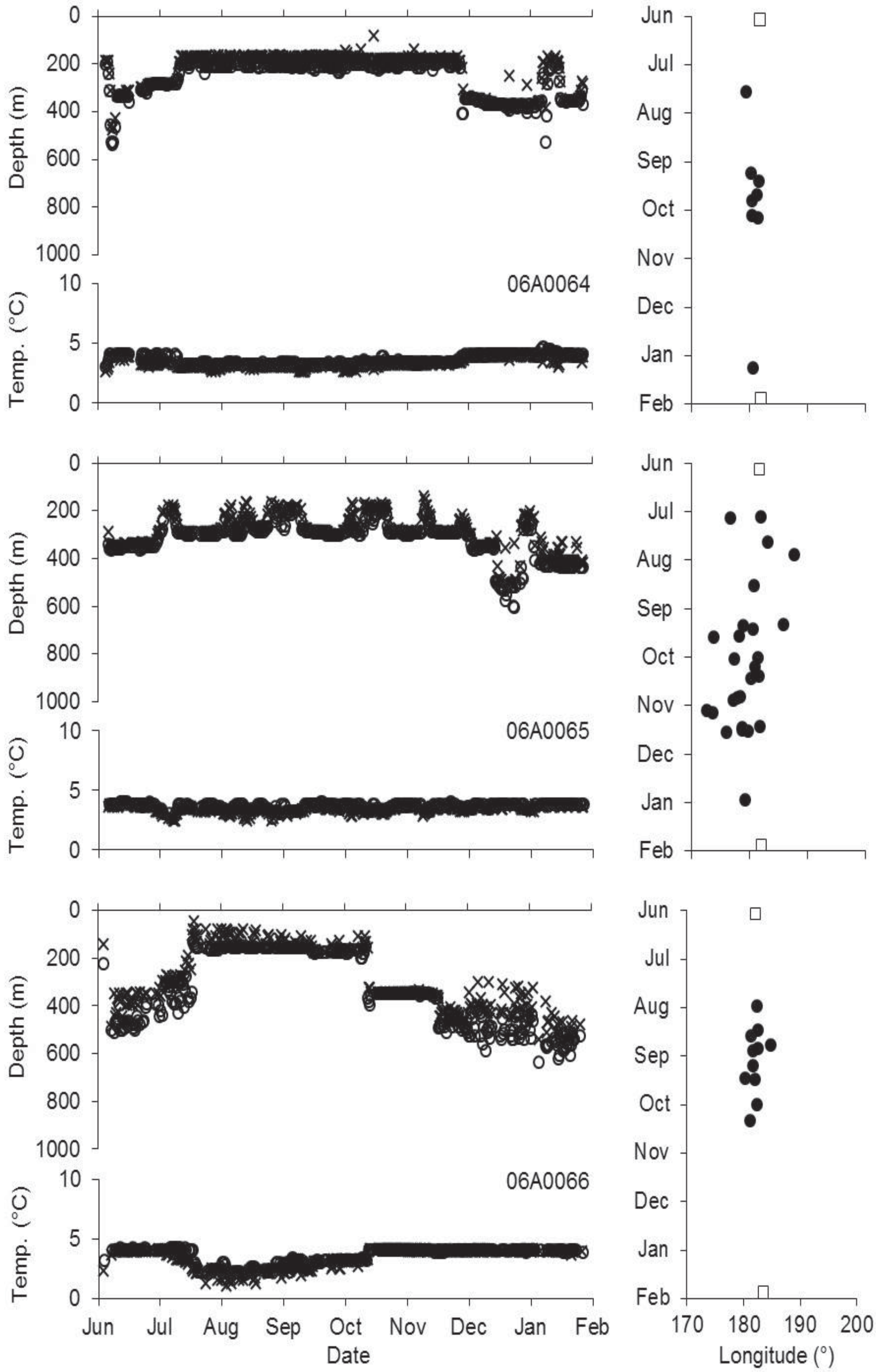


Figure 3. Continued.



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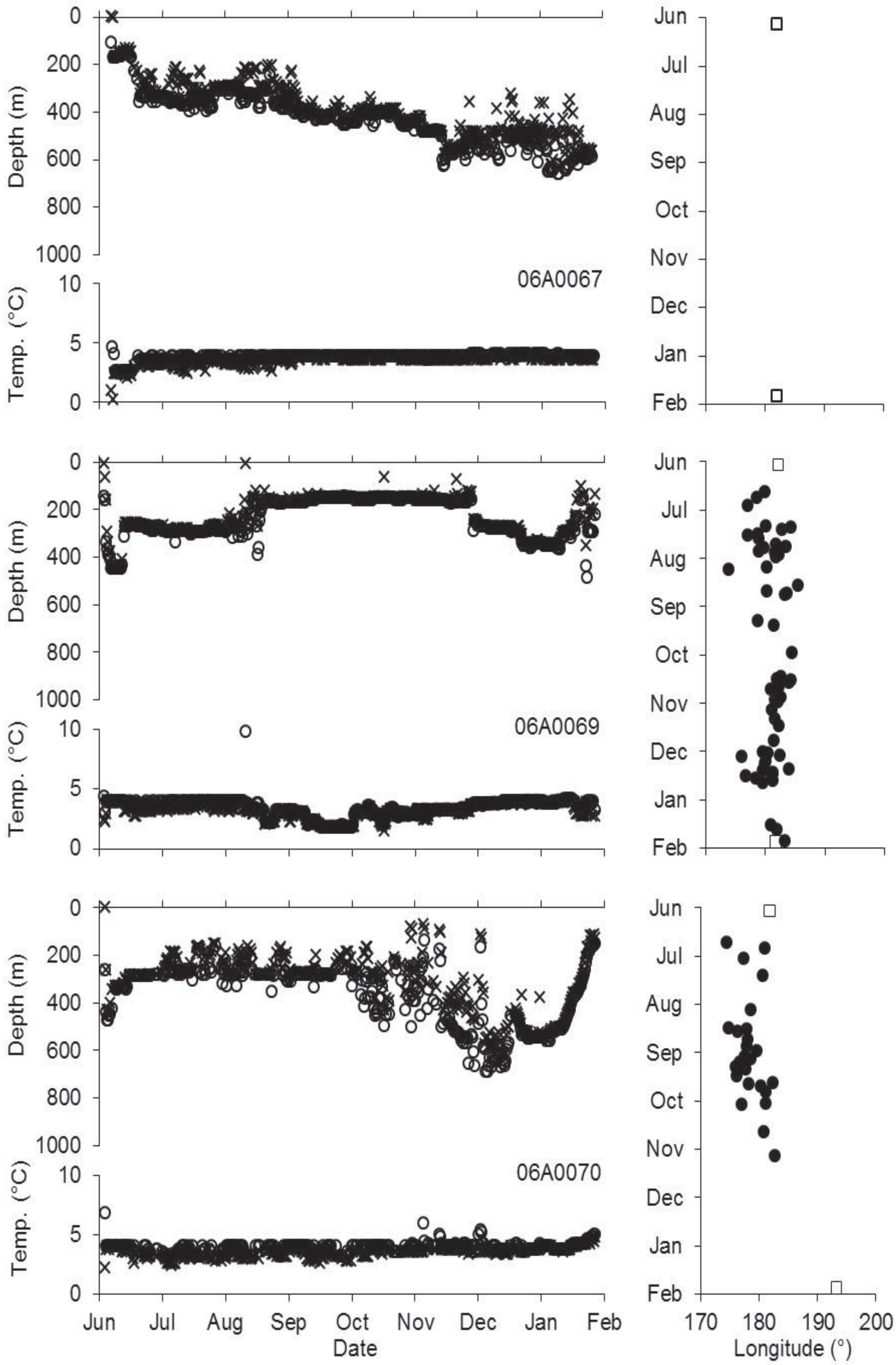


Figured 3. Concluded.

Table 1. Deployment summary for PAT tags on Pacific halibut released in Middle Canyon. The fish were tagged and released between 4 June and 7 June 2006, and the tags popped up on 1 February 2007, unless indicated otherwise. The first five days of tag deployment were excluded from minimum and maximum depths and temperatures. # denotes the tag that was recaptured while on the fish; on 3 October 2006. ^ denotes the tag that prematurely released from the fish sometime during the first two weeks of July 2006, and drifted on the surface of the ocean until it reported to Argos satellites as scheduled. The horizontal displacement is reported from the location of the tag when it started transmitting to Argos because the location of the tag on the day it released from the fish is unknown, while the depth, temperature and geolocation data are reported for only the period in which the tag remained attached to the fish.

Tag #	04P1018^	04P1019	04P1022	06A0061#	06A0062	06A0063	06A0064	06A0065	06A0066	06A0067	06A0069	06A0070
Fish length (cm)	139	124	122	113	115	114	112	113	116	122	110	115
Release date (m/d/yr)	6/6/06	6/4/06	6/4/06	6/6/06	6/7/06	6/7/06	6/4/06	6/6/06	6/4/06	6/7/06	6/4/06	6/4/06
Release latitude (°N)	59.50	59.00	59.00	59.50	59.50	59.50	59.00	59.50	59.00	59.50	59.00	59.00
Release longitude (°W)	178.31	177.90	178.18	178.31	177.95	177.95	178.18	178.31	177.90	177.95	177.90	178.18
Recovery date (m/d/yr)	2/1/07	2/1/07	2/1/07	10/3/06	2/1/07	2/1/07	2/1/07	2/1/07	2/1/07	2/1/07	2/1/07	2/1/07
Recovery latitude (°N)	52.299	58.885	52.891	59.442	59.322	59.416	58.928	59.507	58.566	59.320	59.269	55.108
Recovery longitude (°)	160.55E	177.69W	171.20W	178.28W	178.34W	178.09W	178.03W	177.95W	176.49W	177.95W	178.30W	166.74W
Horizontal displacement (km)	*1533*	18	805	7	30	12	12	21	95	20	38	815
Minimum depth (m)	168	112	20	144	88	160	88	144	48	136	8	72
Maximum depth (m)	216	484	752	472	752	688	544	608	640	664	488	688
Minimum temp. (°C)	2.4	2.0	2.0	2.2	1.4	2.2	2.6	2.4	1.0	2.0	1.4	2.4
Maximum temp. (°C)	2.8	4.4	8.0	4.0	3.8	4.0	4.6	4.0	4.2	4.0	9.8	6.0
Days with longitude	0	6	4	7	6	2	8	26	11	0	56	25
% of days with long.	0	2.5	1.7	5.9	2.5	0.8	3.3	10.8	4.5	0.0	23.1	10.3
# of comparison days	0	0	0	1	0	0	0	0	0	0	2	0
Long. error magnitude (º)	na	na	na	4.87	na	na	na	na	na	na	0.9	na
Long. bias (º)	na	na	na	4.87	na	na	na	na	na	na	-0.9	na

Ambient temperatures experienced by Pacific halibut tagged in Middle Canyon were generally between approximately 2° and 5°C (Fig. 3). The coolest and warmest ambient temperatures experienced by all fish, excluding the five days after release, were 1.0° and 9.8°C (Table 1) and all fish experienced temperatures between 2.6° and 3.8°C. There did not appear to be any seasonal warming or cooling trends of ambient temperatures experienced by any of the fish. Five fish experienced small shifts in ambient temperatures (~2°C) that corresponded to dispersal from the continental slope to the continental shelf, or *vice versa*. Two fish (04P1022 and 06A0069) experienced larger changes in temperature (~4.0° to 6.0°C) within 12 hour summary periods that corresponded to rapid changes in depth during the same time periods.

For the tags that remained attached to the fish, the percentage of days with longitude estimates ranged from 0% to just over 23% (median = 3.3%; Table 1). Every light-based longitude estimate was west of Unimak Pass (-165° longitude; Fig. 3). Longitude estimates were produced for the six day period after release and the six day period before recovery for only two of the tags (Table 1). Longitude error magnitudes for these tags were 0.9° (50 km) and 4.9° (280 km) while longitude biases ranged from -0.9° to 4.9° (Table 1).

There appeared to be an obvious trend in longitude estimates indicating mesoscale (>150 km) movement of the fish out of the tagging area (Fig. 3) for only one of the tags that remained attached for the duration of the experiment. For all other fish, 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, but the true positions of the fish were probably a function of an average of a series of adjacent longitude estimates (Seitz et al. 2006).

In contrast to the other fish, the longitude estimates of fish 04P1022 showed a trend of movement, albeit based on only three estimates, away from the tagging area towards the east, beginning in late summer. This trend in longitude estimates approximately corresponds with large variations in maximum depths from 200 to 750 m, possibly indicating the fish traveled at varying depths along the continental slope on its way to Yunaska Island. Tag 04P1018 also produced longitude estimates with an obvious trend of movement, in this case westward. This occurred after the tag prematurely detached from the fish and was advected in the prevailing surface currents.

Bering Canyon tagging site

Data were recovered from 11 tags (92%) that were attached to fish 111 to 125 cm FL (Table 2; Figs. 2 and 4). Two tags, 06A0055 and 06A0057, prematurely released on 10 September 2006 (time at-liberty = 17days) and 24 December 2006 (time at-liberty = 124 days), respectively, floated on the surface for eight days and then reported to Argos satellites. One tag, 04P0646, prematurely released during the last week of August 2006, drifted on the surface of the ocean for approximately 160 days and transmitted to Argos satellites as scheduled. One tag did not report. The rest of the tags remained attached to fish for the duration of the experiment (~165 days) and reported to Argos as scheduled.

The maximum horizontal displacement of the tags that remained attached to the fish for the duration of the experiment and reported on 1 Feb 2007 was 190 km while the minimum was 4 km (median = 25.5 km; Table 2; Figs. 2 and 4). Of these tags, seven were located in Bering Canyon: six tags less than 40 km from their release locations and one tag (04P1010) 63 km offshore of its release location. One tag (04P1037) was located just north of Umnak Island, 190 km from its release location. For the tags that prematurely released and then drifted for eight days, one (06A0057) was located in Bering Canyon, 13 km from its release location and the other (06A0055) was located in Unimak Pass, 126 km from its release location. The remaining tag (04P0646) that prematurely released was located in the central Gulf of Alaska, more than 1200 km from its release site.

The fish released in Bering Canyon displayed a wide range of depths during their time at-liberty (Fig. 4). The shallowest and deepest depths of all fish, excluding the five days after release, were 0 and 776 m (Table 2) and all experienced depths between 400 m and 440 m. Two fish showed frequent diel depth changes: the minimum depths and maximum depths did not correspond closely to one another for fish 04P1037 during December 2006 and January 2007 and for fish 06A0056 during early September and late November 2006. The remaining fish 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. These occurrences of large depth deviations within 12 hour periods occurred as early as 21 December 2006 (06A0056) and as late as 27 January 2007 (06A0060). Individual fish exhibited between two and six depth deviations each, with nearly regular time intervals between them of three to six days. The exact time intervals between depth deviations were specific to individual fish.

All but one fish were tagged on the continental slope where they generally remained for the duration of the experiment (Fig. 4). By the end of the experiment these fish were typically located in deeper water than their release locations. Four of the fish released on the continental slope visited the continental shelf. Fishes 04P1037, 06A0054 and 06A0057 were on the continental shelf for less than ten days, while fish 06A0056 remained there from September through November 2006 before returning to the continental slope. Fish 06A0060 was released on the continental shelf but moved to the continental slope soon after tagging where it remained for the duration of the experiment. None of the fish were located on the continental shelf on the pop-up date.

Ambient temperatures experienced by Pacific halibut tagged in Bering Canyon were generally between approximately 3° and 5°C, with the exception of fish 06A0056 which occupied slightly warmer water (5–6°C) while on the continental shelf during the summer (Fig. 4). The coolest and warmest ambient temperatures experienced by all fish, excluding the five days after release, were 3.0° and 9.2°C (Table 2). There did not appear to be any seasonal warming or cooling trends of ambient temperatures experienced by any of the fish, probably because they were located at a depth that isolated them from seasonal temperature fluctuations.

For the tags that remained attached to the fish, the percentage of days with longitude estimates ranged from 0% to just over 1.2% (median = 0.6%; Table 2). Longitude estimates were produced for the six day period after release and the six day period before recovery for only four of the tags (Table 2). Longitude error magnitudes for these tags were generally small, averaging 0.7° (45 km), while longitude biases averaged 0.6° (39 km) (Table 2). Although there were very few light-based longitude estimates, none were east of Unimak Pass (-165° longitude; Fig. 4) and none indicated any obvious trends in movement, except tag 04P0646. However, these longitude estimates were from after the tag prematurely detached from the fish and the tag was advected in the prevailing surface currents.

Table 2. Deployment summary for PAT tags on Pacific halibut released in Bering Canyon. The fish were tagged and released between 22 August and 25 August 2006, and the tags popped up on 1 February 2007, unless indicated otherwise. The first five days of tag deployment were excluded from minimum and maximum depths and temperatures. * denotes tags that prematurely released from the fish (06A0055 on 2 September 2006; 06A0057 on 16 December 2006) and then reported to Argos satellites after drifting on the surface of the ocean for eight days. ^ denotes the tag that prematurely released from the fish during the first week after it was released and drifted on the surface of the ocean until it reported to Argos satellites as scheduled. The horizontal displacement is reported from the location of the tag when it started transmitting to Argos because the location of the tag on the day it released from the fish is unknown.

Tag #	04P0646^	04P1010	04P1037	06A0047	06A0054	06A0055*	06A0056	06A0057*	06A0058	06A0059	06A0060
Fish length (cm)	118	114	113	120	125	123	117	119	111	111	120
Release date (m/d/yr)	8/24/06	8/24/06	8/24/06	8/25/06	8/24/06	8/24/06	8/24/06	8/22/06	8/25/06	8/25/06	8/25/06
Release latitude (°N)	54.83	54.83	55.00	54.50	54.50	54.50	54.50	54.65	54.67	54.50	54.50
Release longitude (°W)	166.84	166.89	166.89	166.60	166.86	166.89	166.89	166.17	166.58	166.58	166.58
Recovery date (m/d/yr)	2/1/07	2/1/07	2/1/07	2/1/07	2/1/07	2/1/07	2/1/07	2/1/07	2/1/07	2/1/07	2/1/07
Recovery latitude (°N)	51.03	54.46	53.54	54.43	54.37	54.22	54.51	54.73	54.35	54.53	54.41
Recovery longitude (°W)	149.97	167.62	168.40	166.52	166.39	165.01	166.63	166.01	166.73	166.61	166.80
Horizontal displacement (km)	*1208*	63	190	10	34	126	17	13	37	4	17
Minimum depth (m)	na	228	0	0	288	344	8	400	320	224	328
Maximum depth (m)	na	644	728	744	760	440	672	592	744	608	776
Minimum temp. (°C)	na	3.0	3.4	3.4	3.2	3.8	3.4	3.4	3.2	3.4	3.0
Maximum temp. (°C)	na	4.6	6.8	4.8	4.2	4.0	9.2	3.8	4.4	4.4	4.2
Days with longitude	na	0	1	0	1	1	2	1	0	0	1
% of days with long.	na	0.0	0.6	0.0	0.6	5.9	1.2	0.8	0.0	0.0	0.6
# of comparison days	na	0	0	0	1	1	0	1	0	0	1
Long. error magnitude (º)	na	na	na	na	1.91	0.39	na	0.07	na	na	0.31
Long. bias (º)	na	na	na	na	-1.91	0.39	na	-0.07	na	na	-0.31

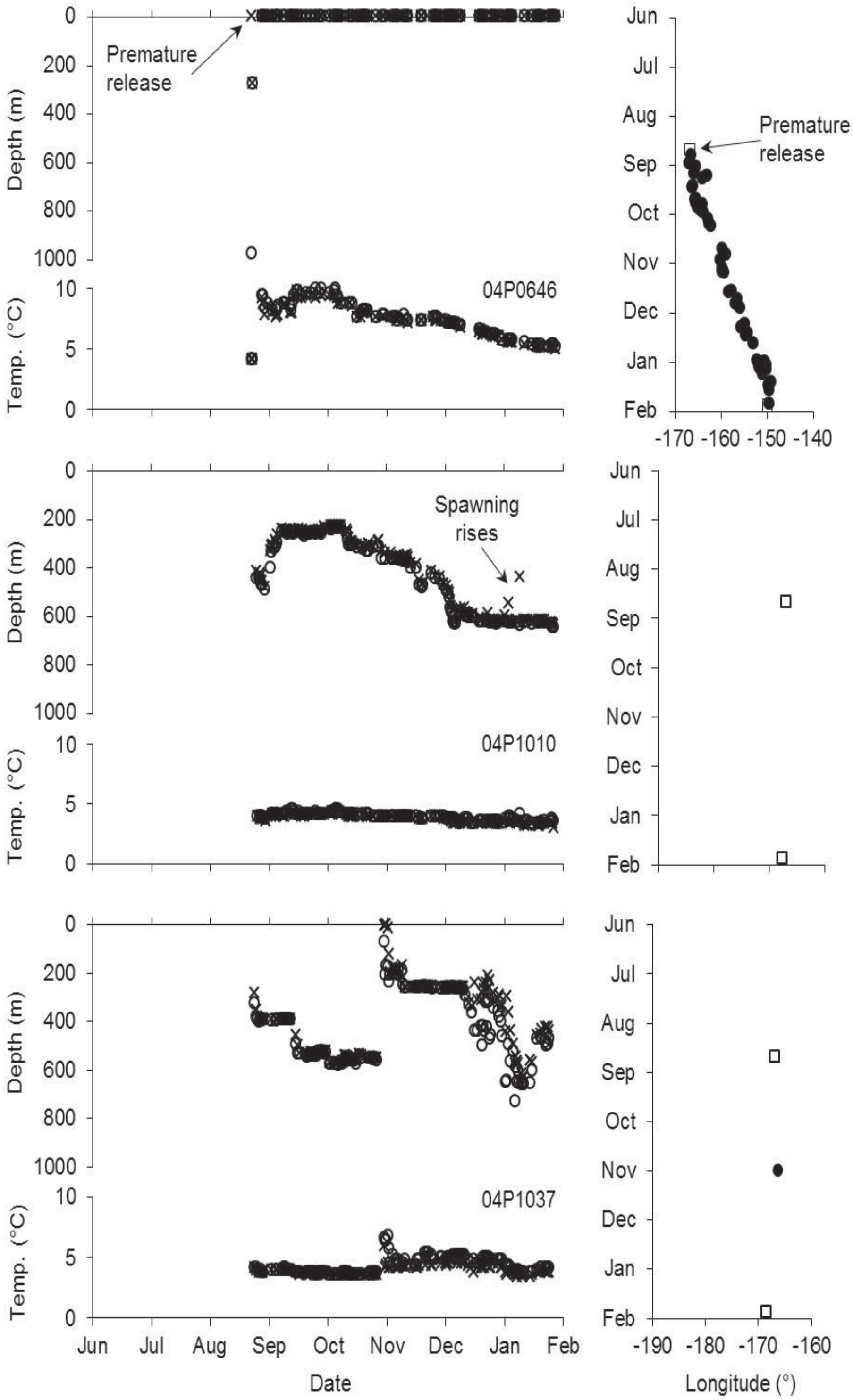


Figure 4. Maximum (o) and minimum (x) depths and temperatures for each 12-hour summary period, and daily longitude estimates after outliers were rejected for Pacific halibut tagged in Bering Canyon. For longitude plots, □ = release position and location at which the tag reported to Argos and ● = estimated position. 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-liberty. Note the different longitude scale for tag 04P0646 that was used because the tag prematurely released from the fish and drifted into the Gulf of Alaska.

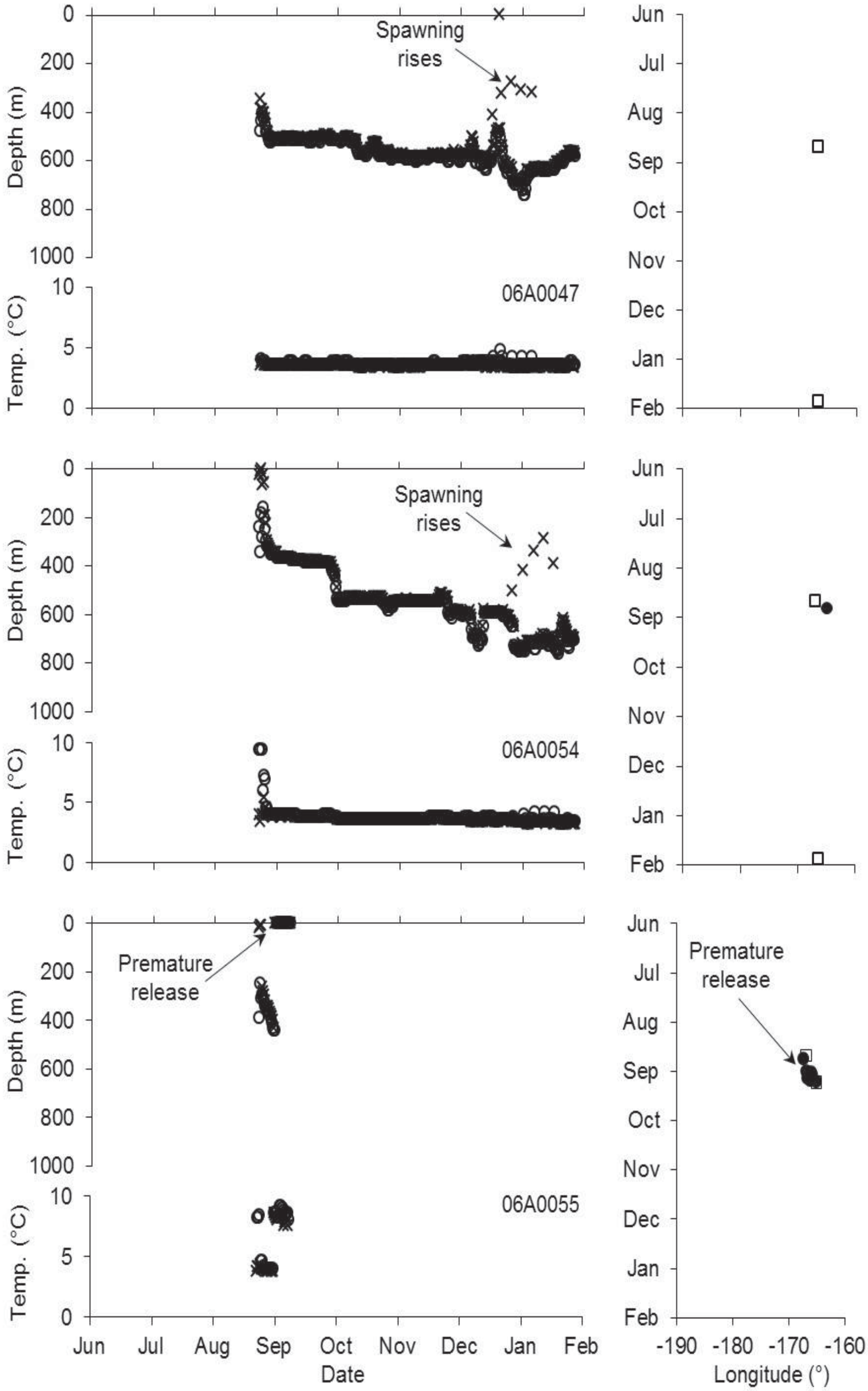
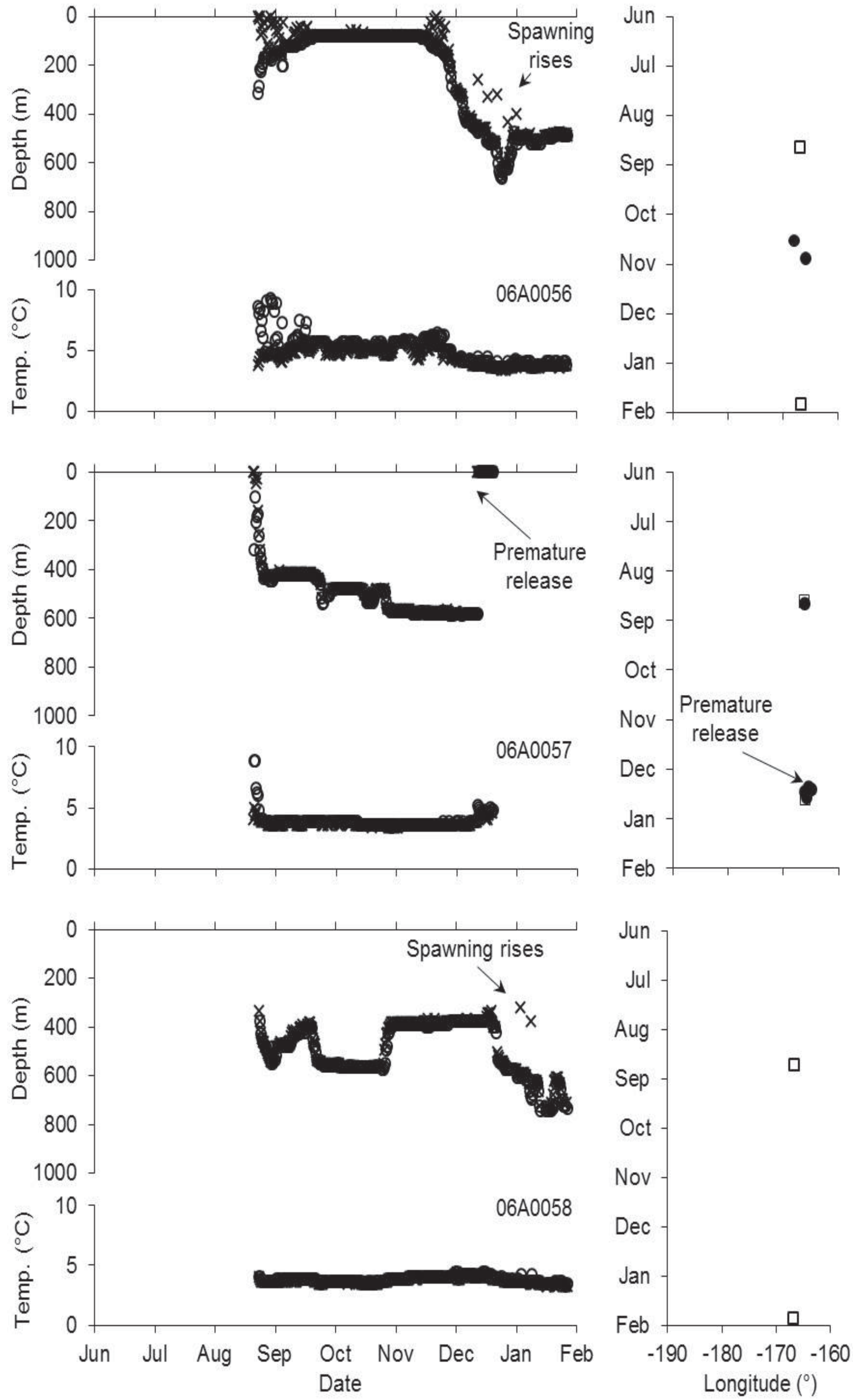
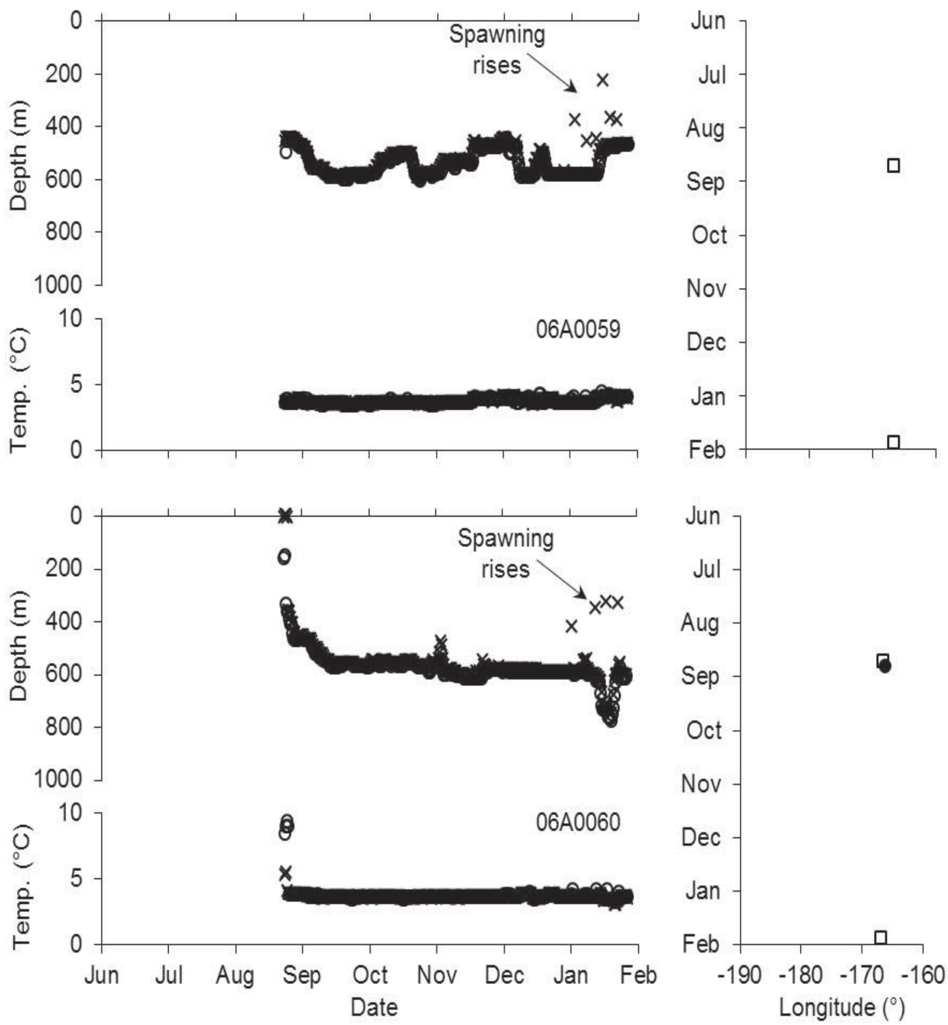


Figure 4. Continued.



Figured 4. Continued.



Figured 4. Concluded.

Discussion

This study did not provide evidence that adult Pacific halibut that feed in the BSAI leave the region in the winter to spawn in the GOA. This is consistent with prior PAT-tagging results, although previous to this study, the sample size of Pacific halibut tagged in the BSAI that yielded putative winter spawning locations was small (n = 24), and only seven were tagged on the southeastern Bering Sea continental shelf. This study yielded winter locations of an additional 18 fish, all from the Bering Sea continental shelf and slope, thus increasing the total sample size of the study by 75%. None of these fish were located in the GOA on the pop-up date, nor were there any at-liberty longitude estimates produced from outside of the BSAI region. Therefore, there was no supporting evidence that these halibut may have spent time in the Gulf of Alaska and then returned to the Bering Sea between the release and pop-up dates. These dispersal observations, in conjunction with our previous investigations (Seitz et al. 2007; Seitz et al. 2008), are consistent with the possibility of a separate sub-population of Pacific halibut existing within the BSAI region, with specific respect to spawning structure. Prior observations of inter-basin dispersal of early life-history stages (Best 1971, St-Pierre 1989, Hilborn et al. 1995) and of individuals of harvestable size whose maturity status was unconfirmed (Webster et al. 2013) may indicate considerable population-level mixing, predominantly prior to joining spawning groups. Our current results do not, and cannot, evaluate the probability that any of the tagged individuals were the progeny of Bering Sea spawners, or were recruited from Bering Sea nursery grounds. However, these results suggest that upon reaching maturity, individuals of the tagged sizes and likely sex (i.e., females) that reside in the Bering Sea during the summer are most likely to represent Bering Sea spawning stock, and should not be expected to contribute to any considerable degree to GOA reproductive output.

The fish tagged in this investigation combine with prior results to provide a more representative view of Pacific halibut seasonal dispersal patterns across the southeastern Bering Sea than did our prior PAT-tagging studies alone, by filling two geographic gaps in the distribution of PAT tag release sites; thus, completing our five-site circum-Bering tagging experiment. The fish in this study showed similar dispersal patterns to Pacific halibut previously tagged on the Bering Sea continental shelf near St. Paul Island, despite having been tagged in somewhat deeper water closer to the continental slope. The percentage of fish undertaking small-scale (<200 km) vs. large-scale (>200 km) dispersals in this study (87.5% vs. 12.5%) was nearly identical to the dispersal patterns of fish tagged near St. Paul Island (86% vs. 14%; Seitz et al. 2007). Another interesting similarity is that one Pacific halibut from this study that was tagged in Middle Canyon and one fish tagged near St. Paul (Seitz et al. 2007) both undertook long-distance dispersals to the continental slope west of Yunaska Island. While this observation may be merely coincidental, it calls attention to the possibility of that area as an important Pacific halibut wintering area.

Although one tag reported to Argos from Unimak Pass, the prevailing evidence suggests that the fish was not located in the pass when the tag detached from it, nor east of Unimak Pass in the GOA. From the drift patterns of the tag, as well as the depth and temperate of the water in which tag 06A0055 was located, it is inferred that the tag prematurely released in the Bering Sea, probably in Bering Canyon, and then drifted south into Unimak Pass. The tag prematurely released from the fish and floated for eight days before reporting. During the eight days of floating, its exact location was unknown, but after it reported to Argos, the tag drifted on a southwesterly course before heading directly south. Therefore, it is reasonable to assume that the tag drifted the same direction before reporting, which probably transported the tag from Bering Canyon to its reporting location in Unimak Pass. Additionally, it is unlikely that the Pacific halibut swam into Unimak Pass or the GOA given the fact that the tag was not in water depths as shallow as Unimak Pass nor did it experience any abrupt changes in temperature while attached to the fish; these features would have occurred had the fish swam into the shallow saddle of Unimak Pass and then into warmer GOA water (Ladd et al. 2005).

The mid-winter aggregation patterns of fish in Middle and Bering Canyons suggest that these are locally-important Pacific halibut spawning grounds. These PAT tag results corroborate findings from previous research surveys that identified Bering Canyon as a major spawning area (St-Pierre 1984). However, the latter research surveys did not extend as far north as Middle Canyon, therefore this location's potential importance as a spawning area has been unknown. Unfortunately, it is impossible to know whether the fish actively spawn in this area unless future research is conducted to assess spawning condition and/or egg and larval presence in the overlying water column. However, it is reasonable to believe that these fish spawn in Middle Canyon because almost all Pacific halibut >110 cm are mature females (Clark et al. 1999), their inhabitation of the continental slope in mid-winter is consistent with spawning activity in other locations in their range (St-Pierre 1984), and given the currently-accepted paradigm of annual spawning frequency for the species (Leaman et al. 2002). If Middle Canyon is indeed an important spawning ground for Pacific halibut, it represents an extension of the known winter spawning range as it is approximately 600 km northwest of the nearest documented spawning area: Pribilof Canyon south of St. Paul Island.

Furthermore, the existence of spawning at Middle Canyon indicates a possible link between the eastern and western Bering Sea halibut populations. Prevailing currents would be expected to carry larvae out of US waters and towards the east coast of Kamchatka (Stabeno et al. 1999). It is unknown whether those larvae would be advected far enough to reach coastal nursery sites, or would instead become stranded in unsuitable deepwater habitat farther from the coast. However, estimated westward drift speeds (Stabeno and Reed 1994) suggest that such larvae would be able to reach the Russian coast, a notion that is further supported by the fact that a PAT tag which prematurely released from a halibut tagged in the Pribilof Islands reached the central eastern shore of Kamchatka in roughly six months (Seitz et al. 2007), a period roughly equivalent to the larval period of Pacific halibut (Thompson and VanCleve 1936, IPHC 1998) over a distance that considerably exceeds that from Middle Canyon to Cape Navarin.

For the first time, the summarized depth data transmitted via satellites may be useful for identifying spawning behavior. Putative spawning in Pacific halibut has been previously described using minute-by-minute archival records from physically recovered PAT tags (Seitz et al. 2005). This putative spawning behavior consisted of a conspicuous routine in which a Pacific halibut conducted a series of seven abrupt ascents, or "spawning rises", spaced regularly over 20 days during mid-winter. These abrupt ascents closely parallel the actions of other spawning flatfish observed *in situ* (Carvalho et al. 2003), although being approximately two orders of magnitude greater in vertical extent. The regular temporal spacing of these abrupt rises is consistent with ovulatory intervals observed in Atlantic halibut (*Hippoglossus hippoglossus*) during which each new batch of eggs is hydrated (Finn et al. 2002). These purported spawning rises have never been identified in summarized depth data transmitted via satellites because typically Pacific halibut undertake diel depth changes throughout the year, therefore the minimum and maximum depths are often quite different, which masks potential spawning rises. However, there were several fish in this study that undertook large diel migrations that resulted in considerable depth deviations within 12 hour summary periods 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.

If the short-period depth deviations observed in the current study are indeed discrete acts of spawning, they may be used to refine some assumptions of spawning characteristics of Pacific halibut. First, it is assumed that the spawning season of Pacific halibut lasts from November through March (St-Pierre 1984). The fish in this study did not commence putative spawning until mid-December. Unfortunately, it is not possible to infer how late in the season spawning may occur because the tags popped up in early February. Second, in previous investigations, it was assumed that mere occupation of the continental slope may be indicative of active spawning (Seitz et al. 2003; Seitz et al. 2007). However, from this study, it appears that inhabitation of the continental slope may not be a valid indicator of active spawning because several fish spent much of their time at-liberty on the continental slope and migration times to and from this area varied widely, but putative spawning was observed only in December and January. Therefore, Pacific halibut may use the continental slope as habitat for activities other than spawning, such as feeding; which would be entirely consistent with recent observations of increasingly greater proportions of Bering Sea commercial harvest coming from continental slope depths (Hare et al. 2011).

This study, in conjunction with two previous studies in the BSAI region, provides evidence of possible spawning sub-structure within the eastern Pacific halibut stock, created by reproductive separation of mature BSAI halibut from those in the GOA. If continued for many generations in the absence of substantial mixing of early life-history stages, this observed reproductive separation may lead to some level of genetically-detectable population structure throughout the range of Pacific halibut. Even in the absence of genetically-detectable segregation, structure can exist at shorter time-scales relevant to prosecution and management of a fishery, and populations comprised of discrete spawning units are often more accurately described using metapopulation models (Hanski and Gilpin 1997) than as homogenous single-unit stocks (Stephenson 1999). Identifying and preserving population substructure has been identified as an important goal of modern fishery science (Stephenson 1999, Frank and Brickman 2001). If there is indeed a separate sub-population of Pacific halibut in the BSAI, its dynamics may vary from those of the GOA and determining its population dynamics will be necessary for correct modeling to predict how different population components will respond to future fishing pressure and changes in environmental conditions.

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