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Seasonal migration and environmental conditions experienced by Pacific halibut in the Gulf of Alaska, elucidated from Pop-up Archival Transmitting (PAT) tags

by

Timothy Loher[a] and Andrew C. Seitz[b]
[a] *International Pacific Halibut Commission*
[b] *U.S. Geological Survey/University of Alaska Fairbanks*

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P.O. BOX 95009
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www.iphc.washington.edu

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Contents

Abstract

Pop-up Archival Transmitting (PAT) tags were used to study seasonal migration in adult halibut in the Gulf of Alaska (GOA). PAT tags collect and store environmental data at regular intervals. They release from their host fish on a pre-programmed date, float to the surface and emit radio signals that are received by the Advanced Research and Global Observation Satellite (ARGOS) system. The satellite uses each tag's signal to calculate locations following pop-up and to download historical data, providing information on the environmental conditions experienced by the fish throughout their time at liberty. Twelve adult halibut were tagged with PAT tags during the 2002 IPHC summer setline survey. Six halibut were tagged in the eastern Gulf of Alaska (GOA) at six locations spanning a total of 995 km from northern Vancouver Island, B.C. to Chichagof Island, Alaska. Another six halibut were tagged in the western GOA at six locations spanning 1015 km from Sanak Island to south of Cape Cleare, Alaska. Three tags were deployed in each of IPHC Regulatory Areas 2B, 2C, 3A and 3B between June 13 and August 6, 2002. Tags were programmed to release from the halibut (i.e., "pop up") and transmit data on January 15, 2003. Ten tags successfully detached and transmitted; two tags deployed in Area 2C were lost. Six fish moved considerable distance between the tagging and date of tag pop-up; all of these fish moved northward to some extent. Two halibut tagged in Area 2B were located in Area 2C at the end of the tagging period. One fish moved from Area 3B to 3A. Four fish showed little evidence of geographic displacement over the tagging period. Light-based geopositions provided little evidence that halibut tagged in Area 2 moved into Area 3 during their time at liberty, or that fish tagged in Area 3 moved into Area 2 at any time.

Most halibut moved to relatively deep water and offshore by the end of the tagging period, but two fish moved inshore: one to deep water in Chatham Strait and one into shallow water in Cook Inlet. Timing of movement to deeper water varied among fish, beginning as early as August and as late as January. Vertical movement (short-period changes in depth) varied among fish and over time. Some fish displayed only very limited changes in depth within 12-hr observation periods throughout their time at liberty; others displayed considerable and repetitive vertical movement. A few fish displayed series of vertical active periods interspersed with relatively quiescent intervals. Tagged halibut experienced temperatures ranging from 2.6-11.6^{o} C, but spent the majority of time at 5-7^{o} C. Fish tagged in western GOA encountered a broader range of temperatures than those tagged in the eastern GOA, some spending considerable time in water 7-11^{o} C. Short-period temperature variability experienced by fish differed among individuals and over time. The maximum temperature difference recorded for a single fish over a 12-hr observation period was 5 ^{o} C.

The PAT tag results generally corroborate the results of conventional tagging, indicating northward movement of GOA halibut towards spawning grounds in Area 3A and movement of fish to deep water in the fall and early winter. However, no single stereotypic behavior was observed, whether seasonal migration, vertical movement patterns, or temperatures encountered. Even with a relatively small number of fish observed, a number of behaviors were observed: long distance migration versus remaining locally, migration to deep shelf edge waters versus potential winter residence in shallow water, considerable vertical activity versus relative vertical quiescent, and subjection to eurythermal versus isothermal conditions. This study represents a glimpse into *in situ* behaviors exhibited by adult halibut. The continued use of archival tags offers the possibility of closing information gaps with respect to halibut life history, information that is not easily elucidated by any other technique.

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Introduction

The bulk of the eastern Pacific halibut (*Hippoglossus stenolepis*) fishery occurs on the coastal shelf from the US Pacific Northwest through the eastern Bering Sea and Aleutian Islands. Halibut management is the responsibility of the International Pacific Halibut Commission (IPHC), a treaty body established by the United States and Canada that sets harvest quotas, seasons, and fishing regulations for the stock. The commercial fishery in Alaska and Canada is presently managed under an Individual Quota (IQ) system with a season that extends from March through mid-November. Annual harvest guidelines are established independently for Regulatory Areas that encompass the geographic range of the stock. Regulatory Area borders have been established at the US and Canadian national borders and at geographic features believed to define natural separation points, such as between the Gulf of Alaska (GOA) and the Bering Sea. The IPHC uses an annual assessment process to establish area-specific catch limits, wherein commercial catch per unit effort (CPUE), age and size structure of harvests, and data from annual setline stock assessment surveys represent the primary inputs to the assessment model (Sullivan et al. 1999).

Given the nature of the stock assessment process, area-specific catch limits largely reflect the summer distribution of the species. There is no targeted winter fishery and IPHC setline surveys are conducted from June through August. In recent years the fishing community has become concerned that without fresh fish available during winter, the halibut market could become susceptible to an influx of farmed product, potentially depressing wholesale prices. Thus, the IPHC has begun examining the possibility of allowing commercial harvest during winter months. To predict the potential impacts of winter fishing on the stock, seasonal migration patterns and differences between summer and winter distribution must be understood.

Whereas summer commercial fisheries concentrate primarily upon halibut located along the shelf on shallow-water feeding grounds, spawning has been documented during winter in deep slope waters (>200 m) from the Queen Charlotte Islands, British Columbia, to the southeast Bering Sea (St.-Pierre 1984). Rather than simply moving to the continental slope to spawn, conventional tagging data suggest that halibut may also move considerable distances along shore during their seasonal migration. Many appear to move northward during winter and congregate in the north-central GOA. Of particular management concern is that a considerable proportion of fish tagged off southeast Alaska during the winter have been recaptured in Canadian waters in summer (Leaman et al. 2002). This suggests that a considerable degree of seasonal mixing might occur across national boundaries and among IPHC Regulatory Areas. Winter fisheries in Alaska could have the potential of intercepting halibut that would spend the summer in Canadian waters. These interceptions would effectively transfer exploitable biomass among areas by making halibut that summer in Canada available to Alaskan fishers during a portion of the year.

If a winter fishery were to occur, catch limit adjustments or time-area management may be necessary to account for interception of halibut moving among areas. Additional information regarding seasonal migration would be of great value in determining the degree of movement among geographic regions, but conventional tagging has some drawbacks. To use mark-recapture methods to elucidate population structure, factors that influence tag recovery, including spatial distribution in fishing effort and tag reporting must be quantified (Hilborn et al. 1995, Heifetz and Maloney 2001). Patterns of tag recovery and migration estimates can be influenced by spatial variability in fishing effort, efficiency associated with different gear types, and differential reporting rates.

During 2003 the IPHC began a coastwide summer PIT tagging study that largely eliminates tag reporting problems (Kaimmer and Geernaert 2004). However, recovery patterns are still fishery-dependent and PIT tags are not recovered in winter because there is no targeted winter fishery. Alternatively, winter redistribution could be indirectly studied by deploying tags in winter and recovering them during the summer fishery. But for winter tag deployments to quantitatively address questions of fishery interception, the deployments would need to conform to the overall abundance of halibut on their winter grounds and the spatial distribution of winter fisheries that would occur. Neither an adequate understanding of the wintertime spatial distribution nor the ability to predict the structure of future fisheries presently exists.

In addition, little is known regarding the vertical distribution of halibut during winter months, the behavior of individuals *in situ*, or the environmental conditions to which they are subjected. Halibut have been reported from as deep as 1100 m (Mecklenburg et al. 2002) and the IPHC presently uses a depth of ~550 m to define the summertime limit of halibut habitat based on survey catch rates (Clark and Hare 2002). However, detailed reports of depth-specific distribution are lacking, especially during winter. St. Pierre (1984) is the most complete documentation of winter distribution, but provides very little regarding specific depth strata at which individuals are expected to reside, and no temperature data. There is strong evidence that abundance and distribution of juveniles are governed by temperature and the same may be true for adults. For example, the majority of juvenile captured by surveys in the southeast Bering Sea in the 1960s were found at temperatures of 4-5°C; very few individuals were encountered at or below 2°C (Best 1977). Soviet researchers reported similar results in the southeastern Bering Sea, finding highest juvenile catch rates at 3.5-5.5°C (Novikov 1964). Preferred temperatures may influence movement and distribution of adult halibut, but information regarding distribution of individuals in relation to oceanographic parameters is lacking.

In this study, Pop-up Archival Transmitting (PAT) tags were used to study seasonal migration and environmental conditions experienced by large halibut. PAT tags represent a novel technology that has proven effective for use on halibut in Alaska (Seitz et al. 2003). PAT tags allow us to study movements and behavior without the need to recapture fish. They collect temperature, depth, and light data at regular intervals, release from the fish on a pre-programmed date, and broadcast the stored data and endpoint position information to polar-orbiting satellites. The primary objective of this study was to tag fish on the summer feeding grounds of the eastern and western GOA and observe their movement to winter grounds without the need to recapture fish during the winter. The work was primarily observational, providing fishery-independent verification of conventional tagging studies. In addition, we hoped to collect behavioral data from the tagged individuals to examine the depth and temperatures encountered.

Methods

Tagging

Twelve adult halibut were tagged with PAT tags (manufactured by Wildlife Computers, Redmond, Washington) during the 2002 IPHC Standardized Stock Assessment survey (SSA) between June 14 and August 6, 2002. PAT tags (Fig. 1a) were attached to the halibut with a titanium dart tethered to the tag with 130 kg test monofilament fishing line covered in adhesive-lined shrink-wrap tubing. The dart was inserted on the eyed side of the fish and lodged beneath the dorsal pterigiophores (i.e., the bones extending from the tips of the ribs to the fin rays). The insertion was approximately 4 cm below the lower edge of the dorsal fin, just posterior to the widest point of the body (Fig. 1b). Halibut were tagged in the Gulf of Alaska from June 13 to August 6 along at sites spaced roughly 200 km apart (Fig 2; Table 1). In the eastern GOA fish were tagged at six locations spanning 955 km extended from Vancouver Island, BC to the north end of Chichagof Island, Alaska. Halibut were tagged in the western GOA at six locations spanning 1015 km, from just east of Sanak Island to south of Cape Cleare, Alaska.

Figure 1. Pop-up Archival Transmitting (PAT) tags. A) The tag attached to the tagging leader, prior to deployment. The tag's antenna is on the left, and the leader and dart extend to the right. B) A tagged halibut ready for release (*lower photo credit*: Lynn Mattes, ADF&G).

Table 1. Size of fish tagged, release date, tag release and pop-up locations, reception time of transmissions used for location determination, Argos Location Class (LC) associated with the pop-up transmissions, linear displacement of each tagged halibut between release and pop-up, and the depth associated with the release station, and fish's depth on the pop-up date. The notation "d.n.r." indicates that a tag did not report after pop-up. Errors associated with each pop-up location are estimated by Argos, based on Location Class; see methods section for details. Note S-133 popped up on January 17; all other tags popped up on January 15.

Tag no.	Halibut length (cm)	Release date	Release location		Pop-up location		Time (UTC)	LC	Linear displacement (km)	Depth (m)	
			N lat	W lon	N lat	W lon				Release	Pop-up
Eastern GOA											
S-101	141	7/14	50.324	128.183	55.970	135.399	0450	1	790	168	420
S-102	106	6/13	51.834	129.787	51.667	130.134	0334	1	30	266	304
S-103	130	7/18	53.336	133.100	55.051	134.354	0247	2	207	223	516
S-104	125	7/12	55.167	134.018	d.n.r	d.n.r	-	-	-	174	-
S-105	115	7/02	56.500	135.550	56.564	134.621	0630	1	57	151	484
S-108	119	6/28	57.834	136.564	d.n.r.	d.n.r.	-	-	-	100	-
Western GOA											
S-133	111	7/28	59.486	147.876	59.756	152.431	0906	1	258	111	84
S-135	122	8/06	58.500	150.773	59.631	143.107	0312	1	455	100	324
S-136	122	6/14	56.833	152.581	58.823	148.429	0209	2	330	146	296
S-137	150	6/29	56.165	156.301	55.703	156.434	0249	2	52	236	256
S-138	112	7/30	54.675	158.417	58.772	140.968	0248	1	1153	196	456
S-139	117	6/20	54.177	161.561	54.669	160.909	1220	1	69	142	100

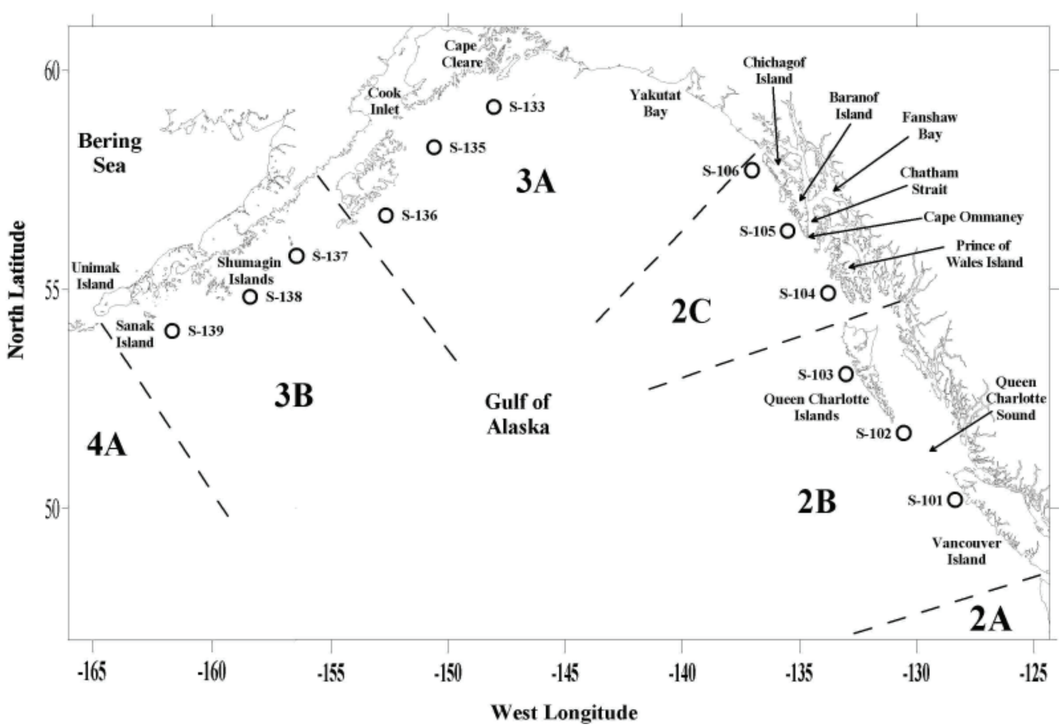


Figure 2. Geographic features referred to in this report, in relation to Regulatory Areas and PAT tag deployment locations. Dashed lines indicate Area boundaries, and small circles the PAT tags, which are labeled with the tag numbers referred to subsequently.

Location data

Tags were programmed to detach (pop up) from their host fish at 0100 hr Coordinated Universal Time (UTC) on January 15, 2003. Mid-January was chosen for pop-up because this is likely to represent the height of spawning season (St.-Pierre 1984). Tag locations after pop-up were estimated by Service Argos (the satellite data processing company; Largo, Maryland) using the Doppler shift of each tag signal as received by polar orbiting satellites on successive passes (Keating et al. 1991, Hays et al. 2001). For each tag, Service Argos produced a series of location estimates beginning with the first reception of the tag signal and continuing throughout the tag's battery life (7-10 days). If completely accurate, each tag's first Service Argos location estimate would represent the host halibut's location on the date of tag pop-up, recognizing that each tag would drift an unknown distance between detachment and initial signal reception. However, Service Argos location estimates are not error-free. Accuracy of individual estimates largely depends upon the length of time that the transmitter is in contact with the satellite and, therefore, the number of uplinks received during a satellite overpass (Hays et al. 2001). Service Argos provides an estimate of location accuracy in the form of a "location class" (LC). Each position estimate is assigned an LC ranging either from 0-3, or listed as the letters A, B, or Z, where latitudinal and longitudinal accuracy are as follows: LC3 <150 m, LC2 =150-350 m, LC1 = 350-1000 m, LC0 > 1000 m; A and B have no precision estimate, and Z is rejected as implausible. Pop-up locations reported here represent the first location for which an LC of 0-3 was provided. However, there could be considerable variability among tags with respect to lag time between programmed pop-up and the first acceptable location transmission. During such time, the tags were expected to drift away from the fish's final location by an unknown distance. To assess the impact of variable transmission-timing and tag drift on biasing presumed fish location, a series of mean tag locations was calculated for the first 72 hours of received transmissions. To smooth short-period error among individual Service Argos location estimates throughout the drift period, consecutive 10-location running averages were used to create drift tracks and determine overall drift speeds. Drift speed was multiplied by lag time to determine maximum expected drift distance between programmed pop-up and location transmission. Lag times were calculated assuming that each tag released from its host fish at 0100 UTC on the programmed date; if tags detached later than programmed, back-calculation of drift should overestimate the displacement between the fish and the tag location at first signal reception.

In addition to endpoint location estimates derived from Argos satellites, daily geoposition estimates during time at liberty were determined using the archived light data. Light levels can theoretically be used to determine tag location where time of solar noon is used an indicator of longitude and total day-length is an indicator of latitude (Welch and Eveson 1999). Light-based geolocation estimates were produced by Wildlife Computers' proprietary software, Global Position Estimator (GPE), using the ambient light data (for details, see Seitz et al., in press). GPE is a suite of three programs that post-processes light-level readings that are archived in PAT tags and then produces daily geolocation estimates. The first phase of estimating daily geolocation was extracting daily sunrise and sunset times from the light intensity data. Argos Message Processor (AMP) software was used to identify and format light level data in an intermediate file that contained encoded light level curves for location calculations, and to extract sunrise and sunset from these data. The second phase of estimating geolocation was the calculation of the tags' daily longitude using GPE. First, days were rejected if light level curves did not exhibit smoothly sloping light levels from high to low or low to high. 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. Estimated longitude values that were outside the published range of the Pacific halibut (west of Hokkaido, Japan (140º) or to the east of northern Baja California, Mexico (117º); Mecklenburg et al. 2002), were considered outliers and were rejected. Latitude was not calculated in the present study because light-based latitudes can have high error magnitudes for tags located at depth (Seitz et al., in press).

Environmental data

Tags were programmed to record temperature (0.05° C resolution), and depth (0.5 m resolution) every minute, and light level every 4 minutes. The depth and temperature time series data were then summarized into 12-hour summary periods by onboard software to reduce the amount of data sent through the Argos satellites. The transmitted data were received as "processed files" which contained the percent of time spent in specified depth and temperature intervals (i.e., bins). Depth data were received with 4 m resolution in the following user-programmed bins: surface, 0-10.0 m, 10.5-50.0 m, 50.5-100.0 m, 100.5-150.0 m, 150.5-200.0 m, 200.5-250.0 m, 250.5-300.0 m, 300.5-400.0 m, 400.5-500.0 m, 500.5-750.0 m, and 750.5-1000.0 m. Temperature data were received with 0.2° C resolution in the following user-programmed bins: <1° C, 1.1-3.0° C, 3.1-5.0° C, 5.1-7.0° C, 7.1-9.0° C, 9.1-11.0° C, 11.1-13.0° C, 13.1-15.0° C, 15.1-17.0° C, 17.1-20.0° C, 20.1-30.0° C, and 30.1-60.0° C.

Additionally, to provide insight into water column structure, ambient water temperatures were reported for a suite of eight specific depths (referred to by Wildlife Computers as "PDT data") during each 12-hr summary period. These provided the minimum depth experienced, maximum depth experienced, and six additional depths spaced equidistantly between the maximum and minimum, as well as the corresponding temperature at each of the eight depths. For example, if the minimum depth experienced by the fish was 100 m and the maximum depth 450 m, the PDT file would contain the maximum and minimum temperatures experienced by the fish at each of the designated interval depths: 100 m, 150 m, 200 m, 250 m, 300 m, 350 m, 400 m, and 450 m. For the purposes of this report, maximum and minimum observed temperatures represent the absolute maximum and minimum temperature reported among all reported interval depths. This temperature information should provide a reasonable indicator of the range of temperatures experienced by fish during each summary period. However, it should be noted that the actual range of temperatures experienced by a fish could have been greater than reported if the true temperature extremes occurred at depths not included in the processed file.

The daily maximum and minimum depths provide an indication of the range of depths experienced by fish during their time at liberty. However, they provide little information regarding the depths most commonly visited during each day. Thus, daily mean depth was also determined for each fish, calculated as a time-weighted average using the median depth of each bin visited during each day. For example, if a fish spent 20% of the day in the 50-100 m bin, 75% at 100-150 m, and 5% at 150-200 m, the time-weighted mean depth for that day would be:

$$(0.20 * 75 \text{ m}) + (0.75 * 125 \text{ m}) + (0.05 * 175 \text{ m}) = 117.5 \text{ m}.$$

The resulting value aids interpretation of long-term depth profiles, as it condenses large amounts of daily information into a single value. Brief vertical forays into shallow or deep water are largely eliminated, and the resulting profiles display the approximate depth at which the majority of the day was spent.

Fish movement terminology

The primary aim of this study was to examine seasonal changes in the distribution of halibut by comparing summer release locations to winter tag pop-up locations. Halibut are expected to move from shallow summer feeding grounds to deeper offshore winter spawning grounds, and then return to shallow water by the following summer. For the purposes of this report, we define this annual cycle of directed movement from one geographic location to another as "seasonal migration". Admittedly, a full assessment of a fish's migration requires knowledge of its location at numerous points throughout the year, information which it may not be possible to obtain from tagging data. Thus, when reporting tag pop-ups in relation to tagging locations, we will refer to the distance between these endpoints simply as "displacement" distances. Displacement indicates that the fish was located at different locations on the two dates without implying directed migration or the total amount of travel undertaken to move between those two points. Changes in depth will be referred to as "vertical movement". The concept of migration will be reserved for the discussion, where it can be assessed in the context of the accumulated data, including endpoint locations, geoposition estimates, and depths visited during time at liberty.

Results

Tagging

Tagged halibut ranged in fork length from 106-150 cm (Table 1). Based on the size-specific sex ratio observed in the Gulf of Alaska during the 2002 IPHC SSA, the smallest fish tagged possessed approximately 80% likelihood of being female, and the largest nearly 100% (Fig. 3).

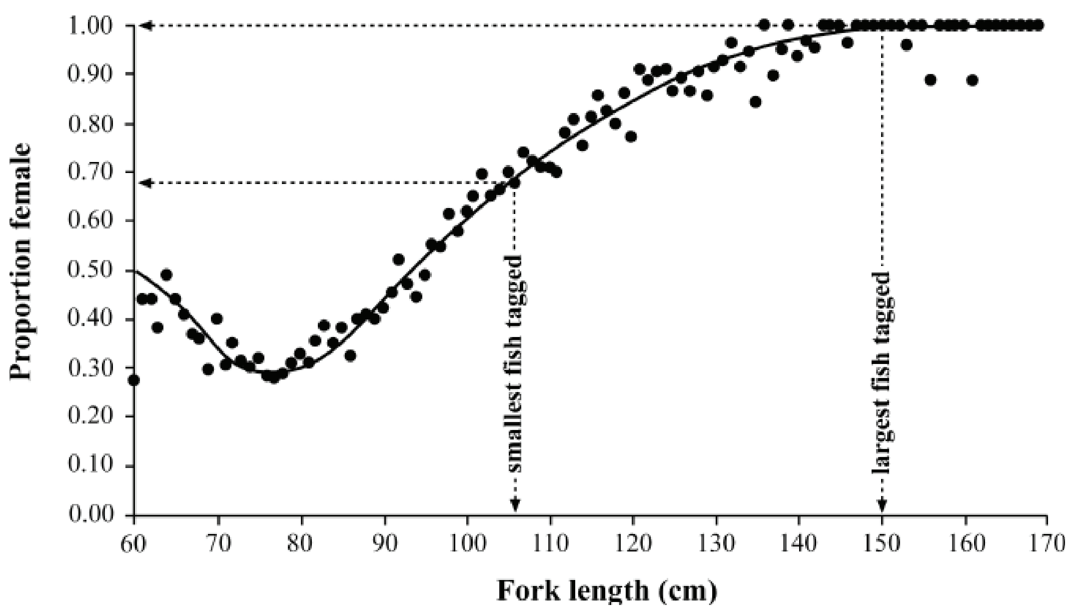


Figure 3. Size-specific sex ratio of all halibut captured in the Gulf of Alaska during the IPHC's 2002 stock assessment setline survey. Noted are the sizes of the largest and smallest halibut tagged in the present study, and the corresponding proportion of halibut of those sizes that were female in survey catches. Refer to Table 1 for the sizes of all fish tagged.

Location data

Pop-up locations

Of the 12 tags deployed, 10 successfully detached from their host fish and reported to the Argos system (Table 1). Two tags were lost, both of which were deployed in IPHC Regulatory Area 2C: tag S-104, deployed off southern Prince of Wales Island, and tag S-108, deployed off northern Chichagof Island (Table 2). Transmissions from nine of the successful tags were received on the expected date of tag pop-up (January 15). Reception time of the first acceptable location for these nine tags varied, ranging from 0209-1220 UTC. One tag (S-133) did not begin reporting until two days later, with its pop-up location determined at 0906 UTC on January 17.

Pop-up locations (Table 1; Fig. 4) demonstrated two types of displacement for adult halibut. Four tags popped-up within 70 km of initial release, providing little evidence of substantial overall displacement between summer and mid-January. The remaining six fish moved considerable distances between release and tag pop-up, with linear displacements ranging between 207 and 1154 km. The six halibut with displacement >200 km all moved northward to some extent between tagging and pop-up. Three fish crossed IPHC Regulatory Area boundaries: two halibut tagged in Area 2B moved into Area 2C, and one fish tagged in Area 3B moved into Area 3A. Most halibut moved offshore between tagging and pop-up, but two moved to inshore waters: S-105 was tagged ~35 km west of Baranof Island and moved into Chatham Strait, while S-133 was tagged ~30 km south of Cape Cleare and moved into Cook Inlet (Fig. 4).

Table 2. Estimated tag pop-up locations, position of each tag after roughly 12 hours of surface drift following initial transmission, and the speed and distance that each tag is expected to have drifted from the time it detached from its host fish until its first satellite transmission. The final calculation of tag drift conservatively assumes that all tags detached from their host fish at 0100 UTC on January 15, at the precise moment when their electro-mechanical releases were programmed to activate. Note that the large displacement reported for tag S-133 between the initial pop-up and inferrred detachment locations is due to a large delay prior to its first received transmission.

Tag no.	Tag pop-up location (t_0)		Tag location at t_0+ ~12 hr		Linear tag drift speed (m sec^{-1})	Estimated tag drift from detachment to pop-up (km)
	N lat	W lon	N lat	W lon		
Eastern GOA						
S-101	55.970	135.399	56.108	135.553	0.51	7.04
S-102	51.667	130.134	51.920	130.361	0.66	6.10
S-103	55.051	134.354	55.333	134.538	0.74	4.75
S-105	56.564	134.621	56.537	134.671	0.07	1.39
Western GOA						
S-133	59.756	152.431	59.702	152.602	0.19	38.40
S-135	59.631	143.107	59.602	143.291	0.27	2.14
S-136	58.823	148.429	58.992	148.864	0.64	2.65
S-137	55.703	156.434	55.531	156.646	0.41	2.68
S-138	58.772	140.968	58.834	141.194	0.30	1.94
S-139	54.669	160.909	54.609	160.483	1.27	51.82

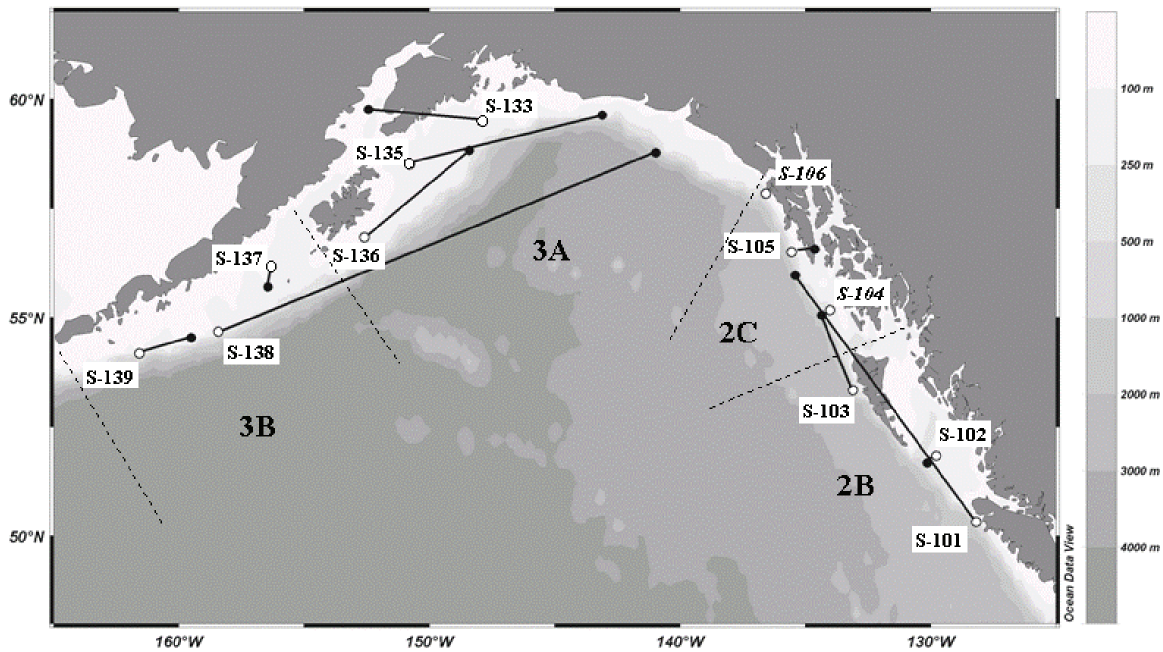


Figure 4. Release locations (open circles) and pop-ups (closed circles) for PAT tags deployed on adult Pacific halibut in the Gulf of Alaska. Lines connect each tag's release and pop-up location, but the reader should note that these lines are not meant to imply the path taken by the fish to reach the pop-up location. Tags labeled in italics (S-104 and S-106, in the eastern Gulf) did not successfully

Drift tracks

Sequential location estimates indicated that all tags underwent surface drift, and that pop-ups were likely displaced from where the host fish were when the tags actually detached. Average linear drift speeds over 72 hours of signal reception ranging from 0.07-1.27 m sec-1, with most tags drifting at 0.30-0.74 m sec-1 (Table 2). However, tag drift tracks (Figs. 5-9) suggested that the pop-up locations were unlikely to have been markedly different from actual fish locations: with the exception of S-133 and S-139, the back-calculated position of each host fish at programmed detachment was rather small, ranging from ~1-7 km (Table 2). Drift of S-139 was the greatest estimated (~50 km) due to a delay in receiving a good position estimate and the fastest observed drift rate. If the tag's drift trajectory is extrapolated backwards by 50 km, the fish is expected to have been located closer to the Shumagin Islands than the reported pop-up location, and somewhat farther from its initial tagging location. Potential drift of S-133 was also considerable, estimated at ~40 km towards the southwest, assuming that the tag detached from the fish at 0100 on Jan 15. Although it was subjected to drift speeds that were relatively low compared to the other tags (Table 2), it experienced an exceptionally long delay between programmed detachment and first signal reception (Table 1). If the reporting delay was due to late release of the tag from its host fish, then the pre-reporting drift distance was presumably <40 km.

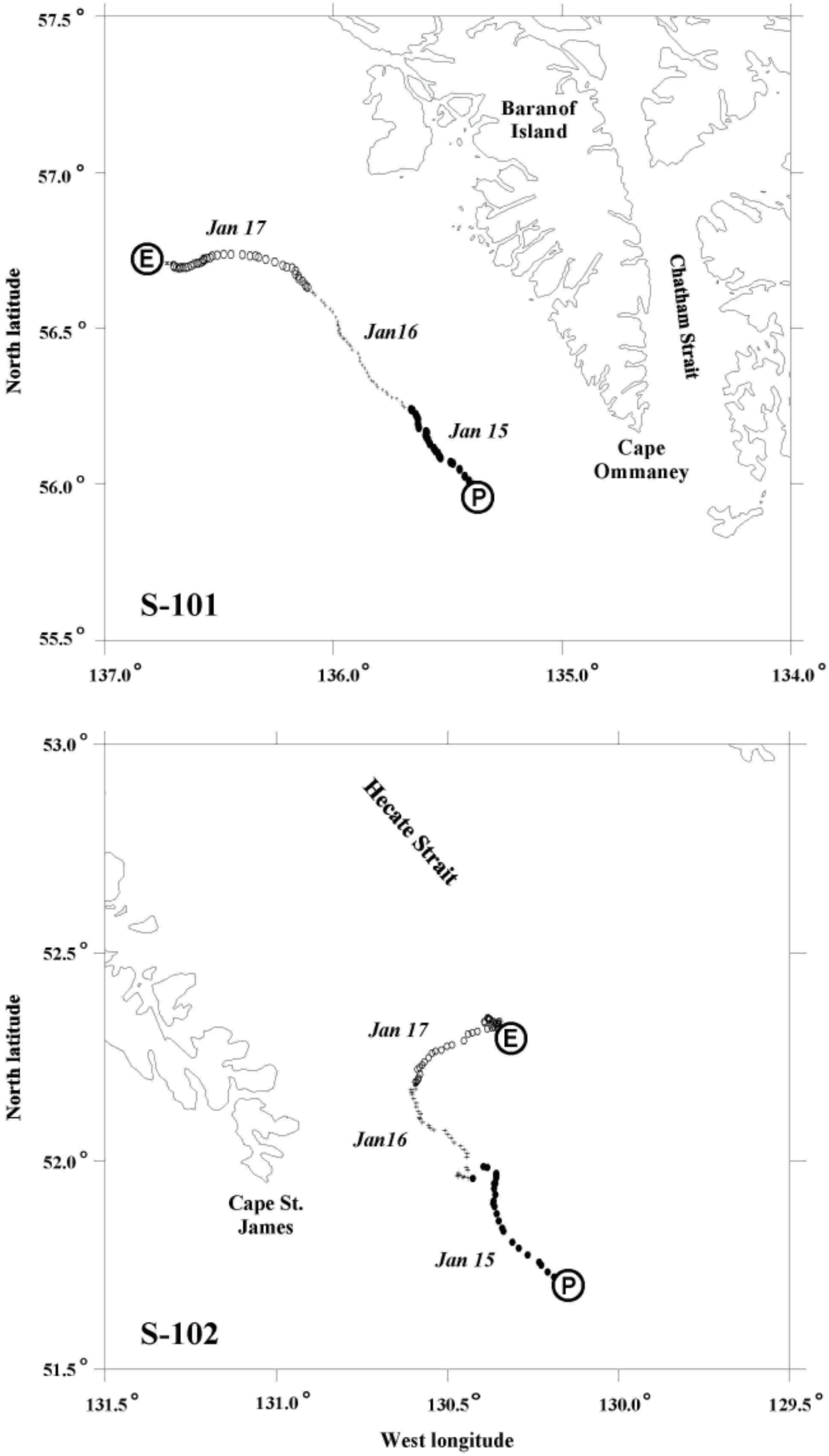
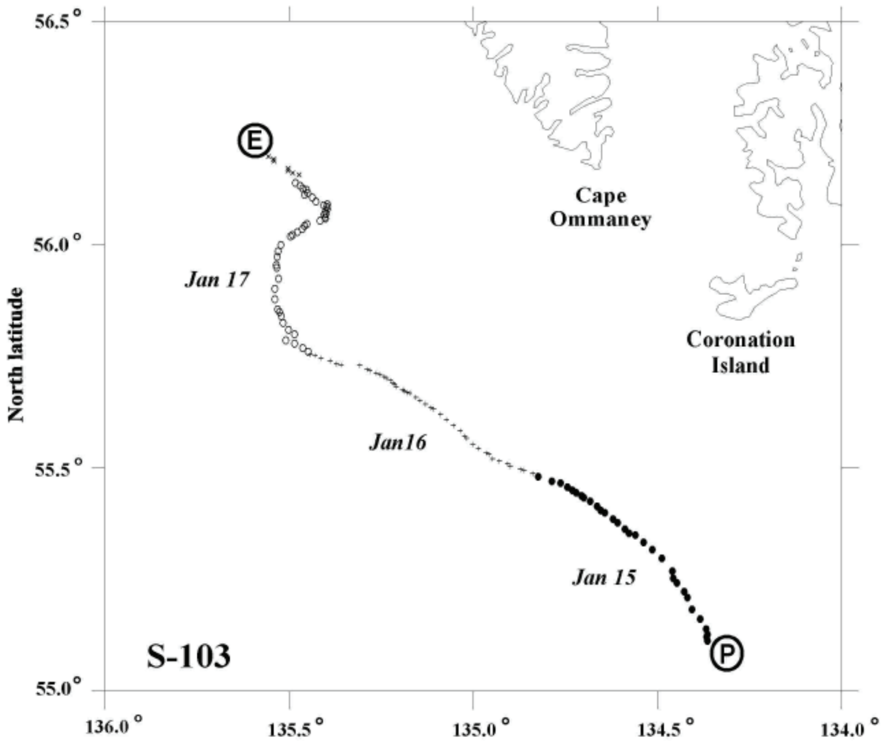


Figure 5. Three day surface drift trajectories for tags S-101 and S-102. Points represent consecutive location estimates calculated as running means over periods averaging roughly five hours (see text). The circled "P" indicates pop-up location, and running means for each calendar day are depicted with a different symbol, as labeled. The circled "E" indicates the tag's location after roughly 72 hours drift.



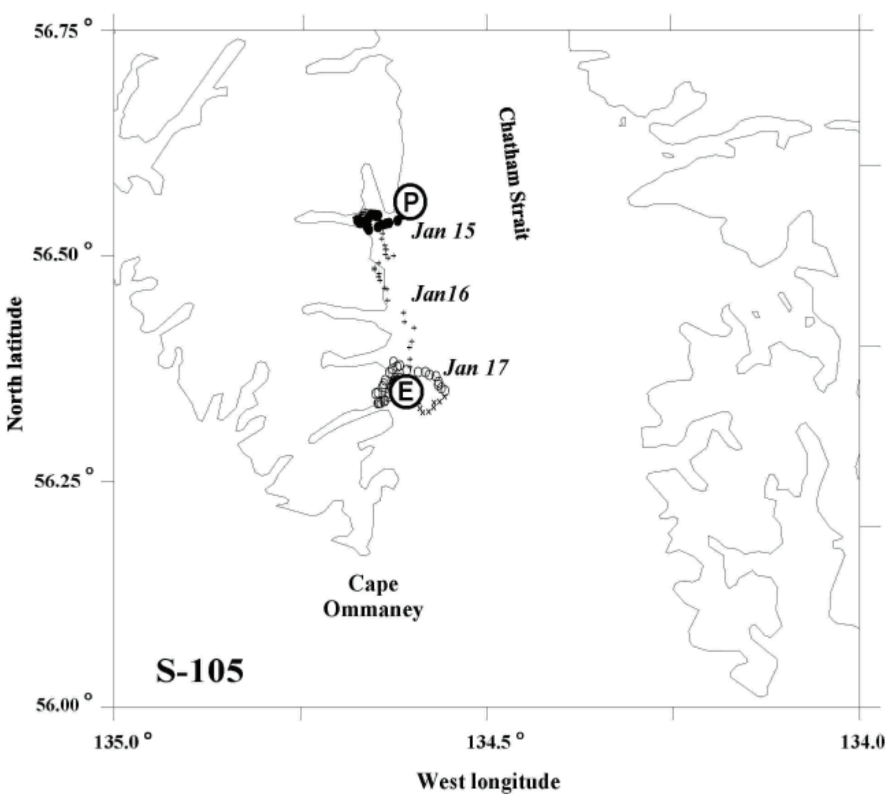


Figure 6. Three day surface drift trajectories for tags S-103 and S-105. Points represent consecutive location estimates calculated as running means over periods averaging roughly five hours (see text). The circled "P" indicates pop-up location, and running means for each calendar day are depicted with a different symbol, as labeled. The circled "E" indicates the tag's location after roughly 72 hours drift.

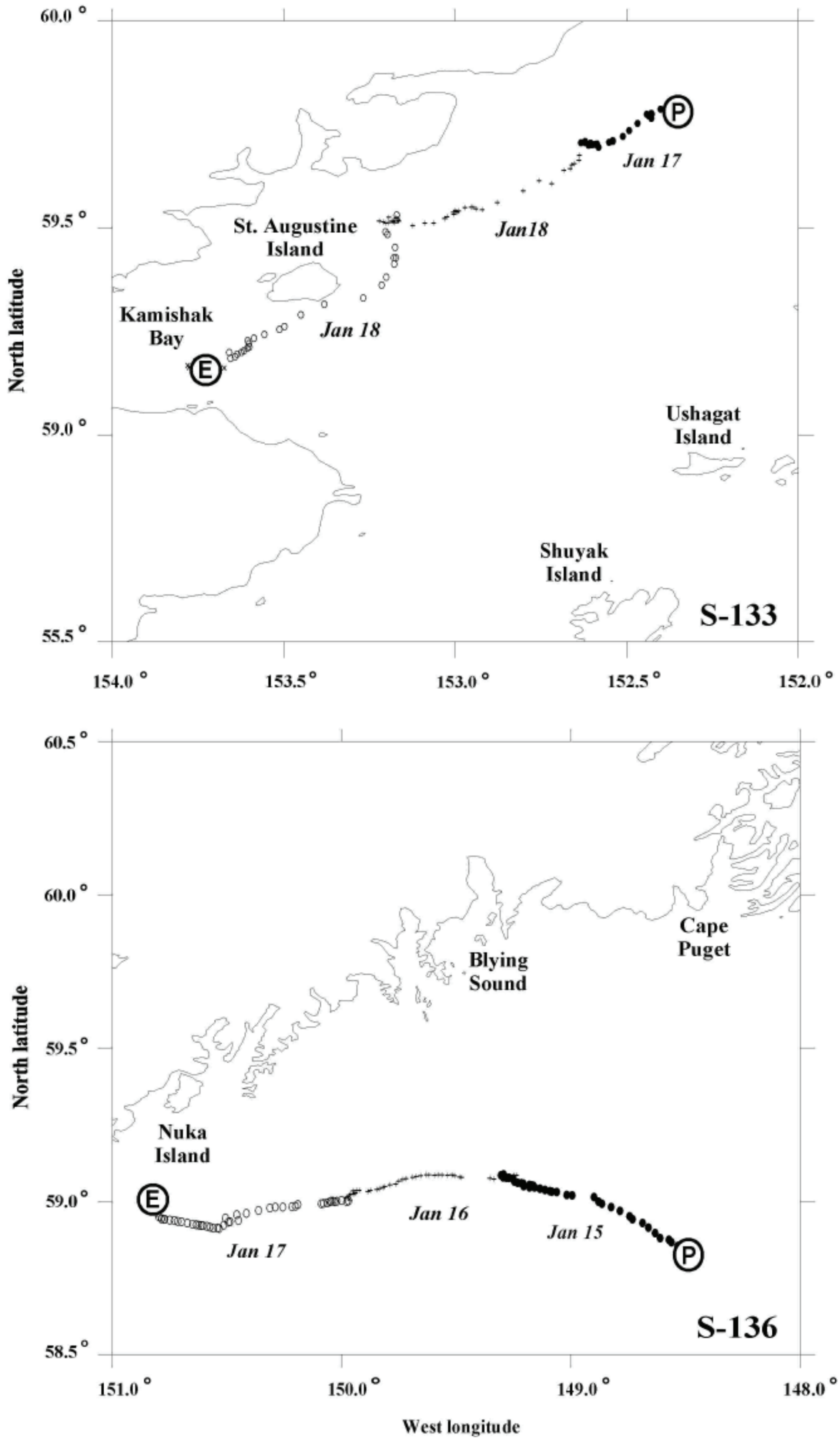


Figure 7. Three day surface drift trajectories for tags S-133 and S-136. Points represent consecutive location estimates calculated as running means over periods averaging roughly five hours (see text). The circled "P" indicates pop-up location, and running means for each calendar day are depicted with a different symbol, as labeled. The circled "E" indicates the tag's location after roughly 72 hours drift. Note that tag S-133 did not first report until January 17, two days after the programmed date of tag pop-up.

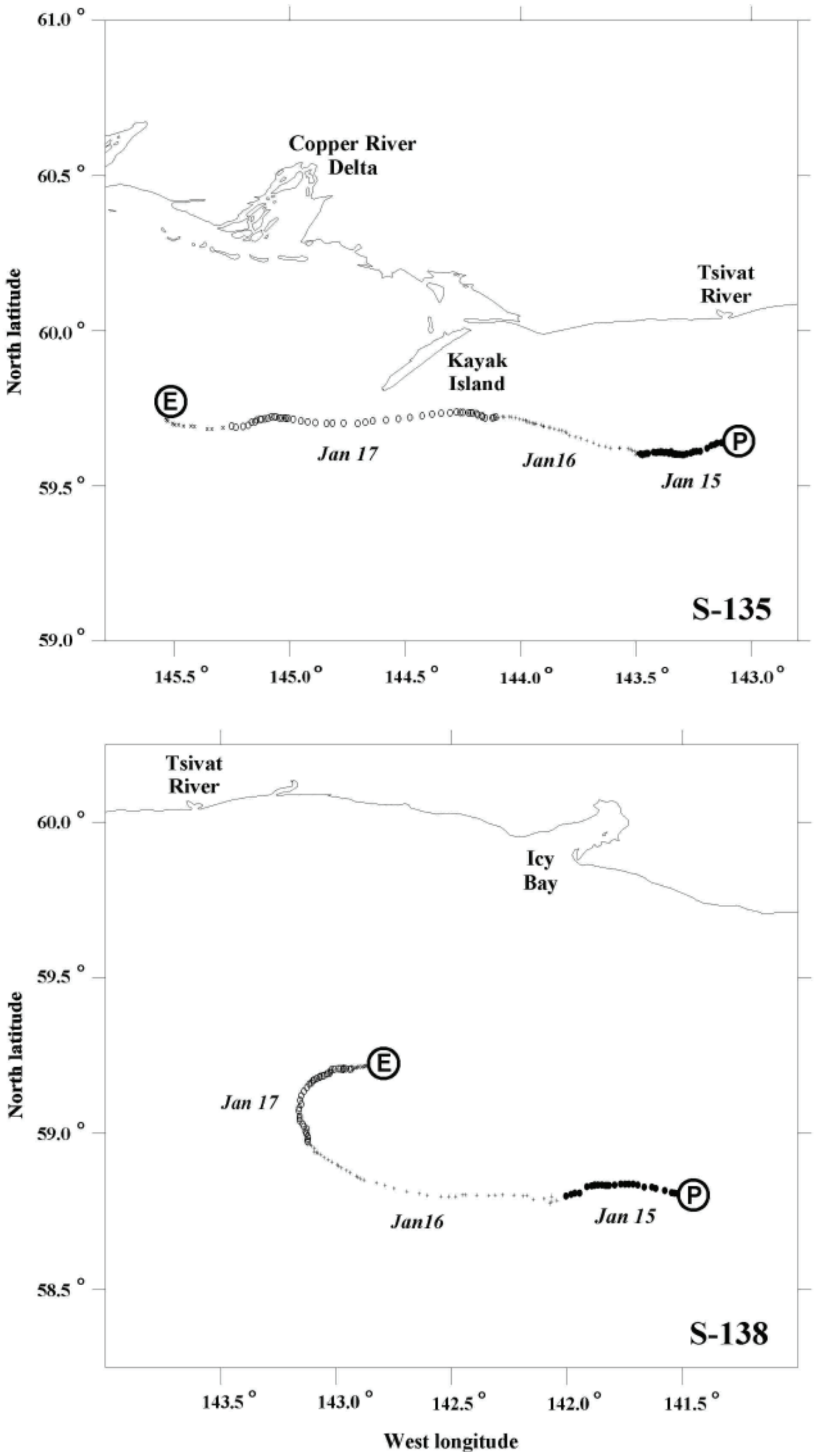


Figure 8. Three day surface drift trajectories for tags S-135 and S-138. Points represent consecutive location estimates calculated as running means over periods averaging roughly five hours (see text). The circled "P" indicates pop-up location, and running means for each calendar day are depicted with a different symbol, as labeled. The circled "E" indicates the tag's location after roughly 72 hours drift.

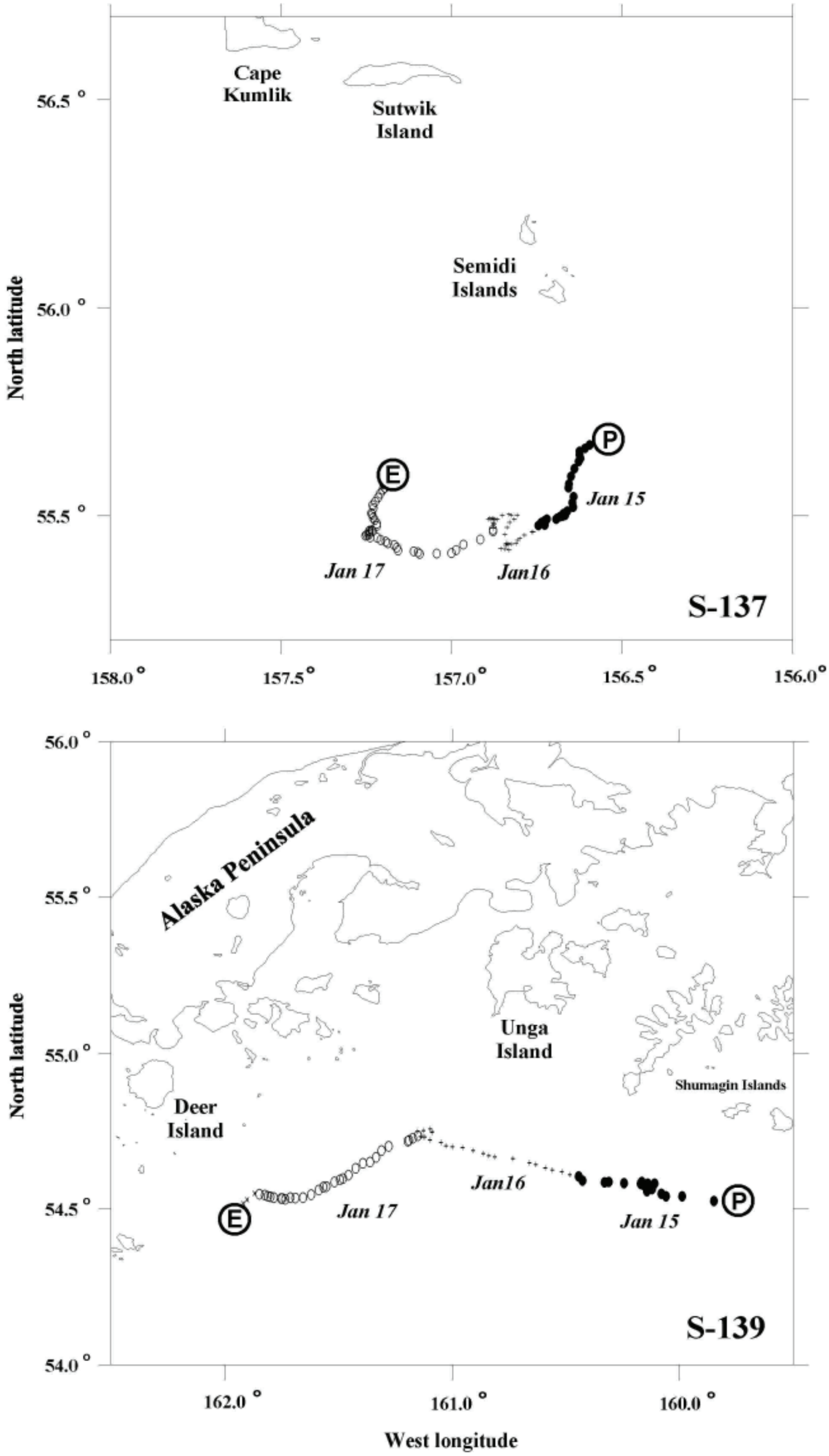


Figure 9. Three day drift trajectories for tags S-137 and S-139. Points represent consecutive location estimates calculated as running means over periods averaging roughly 5 hours (see text). The circled "P" indicates pop-up location, and running means for each calendar day are depicted with a different symbol, as labeled. The circled "E" indicates the tag's location after roughly 72 hours drift.

Light-based geoposition estimates

For most fish, light-based geolocation estimates did not provide strong evidence of movement between Areas 2 and 3, or from Area 3 into Area 4, during time at liberty. Halibut tagged in Area 2B (Canada) generated no geolocation estimates that would have placed them anywhere in Area 3 (Fig. 10, right panels). For S-105, tagged in Area 2C, the geoposition estimates are a bit more ambiguous. Tagging and pop-up were both within Area 2C, but light data produced July and August geopositions ranging from roughly 118-149^{o} W lon. The westerly locations would place the fish in Area 3A, offshore of Cape Cleare, and the eastern position at least as far south as the southern California Bight (SCB), near the most southerly recorded occurrence of the species (Mecklenburg et al. 2002). If accurate, the fish would have migrated from its tagging location off Sitka to the shelf-edge south of Seward during its first week at liberty, to the SCB in the next five weeks, then back to the northern Gulf of Alaska in another two weeks. This would entail at least 8,000 km of travel in two months, after which the fish eventually returned to within 60 km of the tagging location. While this may be possible, we are hesitant to suggest such. Alternatively, variable light conditions caused by excessive light at high latitudes during summer, local weather patterns, or fish behavior may have generated errors in the geolocation estimates.

For five of the six fish tagged in Area 3, geopositions were confined to Area 3: from 140-165^{o} W lon, between Yakutat Bay and the western tip of Unimak Island (Fig. 11, right panels). For S-137, tagged at the Semidi Islands, two geoposition estimates generated in August and September would have placed the fish in the Unimak Pass area between 165^{o} and 166^{o} W lon. This suggests the possibility that it may have moved briefly into Area 4A but all other estimates were well east of Unimak Pass, suggesting residence primarily within Area 3B.

Environmental data

Depth

S-133, tagged in the northern GOA and located in Cook Inlet on the date of tag pop-up, recorded the shallowest overall depth profile spending considerable time within the 0-10 m depth bin during October (Appendix 1E) and recording minimum depths of 0 m on several days (Appendix 1E). Deepest depths were recorded by S-103 and S-105, tagged in the eastern GOA, both of which made forays to depths of over 600 m in December and January (Appendices 1C and 1D). S-103 visited the deepest absolute depth, recording 736 m on December 31 (Appendix 1C).

Halibut demonstrated a broad range of vertical movement behaviors over time, ranging from extended periods at relatively constant depth to periods of frequent or abrupt change in depth, both seasonally and over short periods of time. Average release depths ranged between 100-200 m whereas average depths at the end of the tagging period ranged from ~300-350 m. Shallowest daily mean depths varied among individuals, ranging from ~5-125 m (Table 3; Figs. 10 and 11). Some individual halibut occupied relatively shallow water to some degree from early summer into early January. Deepest daily mean depths ranged from ~175-515 m. Eight halibut demonstrated a descent into deep water (>200 m) near the end of the tagging period, occupying their deepest mean depth during either December or January. S-133 and S-139, tagged in the western GOA, occupied their deepest mean depths in September and July, respectively; neither demonstrated prolonged residence below 200 m during their time at liberty.

For the eight fish that descended to deep water in early winter, the time to make that descent varied considerably, where descent time was defined as the number of days that elapsed between their latest residence at their shallowest mean depth and the day upon which they reached their deepest mean depth. For western GOA fish, descent time ranged from 4-78 days, and three fish

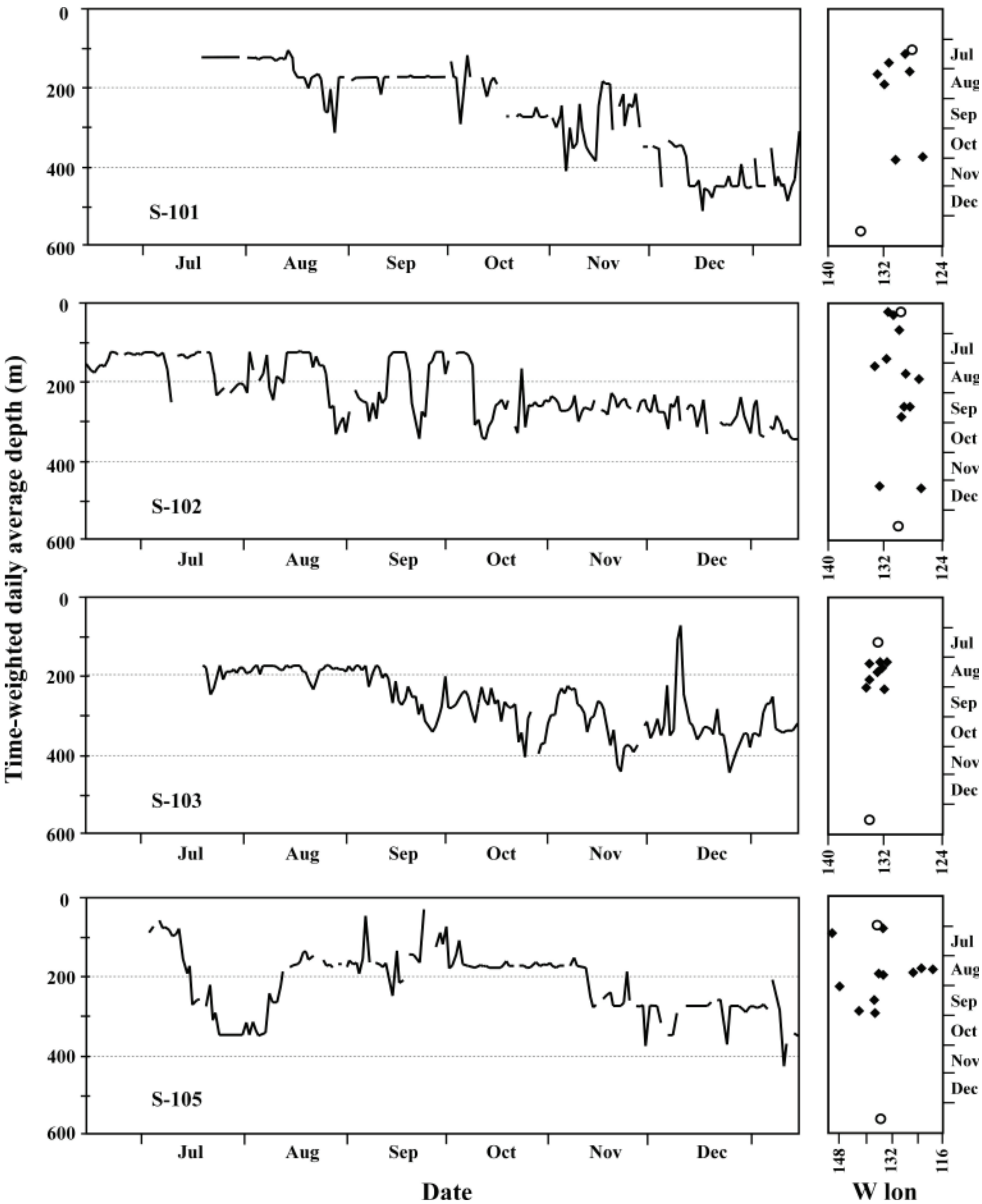


Figure 10. *Left panels*: **Time-weighted daily mean depths experienced by halibut tagged in the eastern Gulf of Alaska from tagging through mid-January.** *Right panels*: **Tag locations for each fish throughout the tagging period. Open circles in early summer and mid-January represent tagging and pop-up locations, respectively. Solid diamonds represent geolocation estimates determined from daily light data during time-at-liberty. Note that 124° W longitude is the equivalent of the Oregon coast, while Yakutat Bay is located at 140° W, and western Prince William Sound at 148° W.**

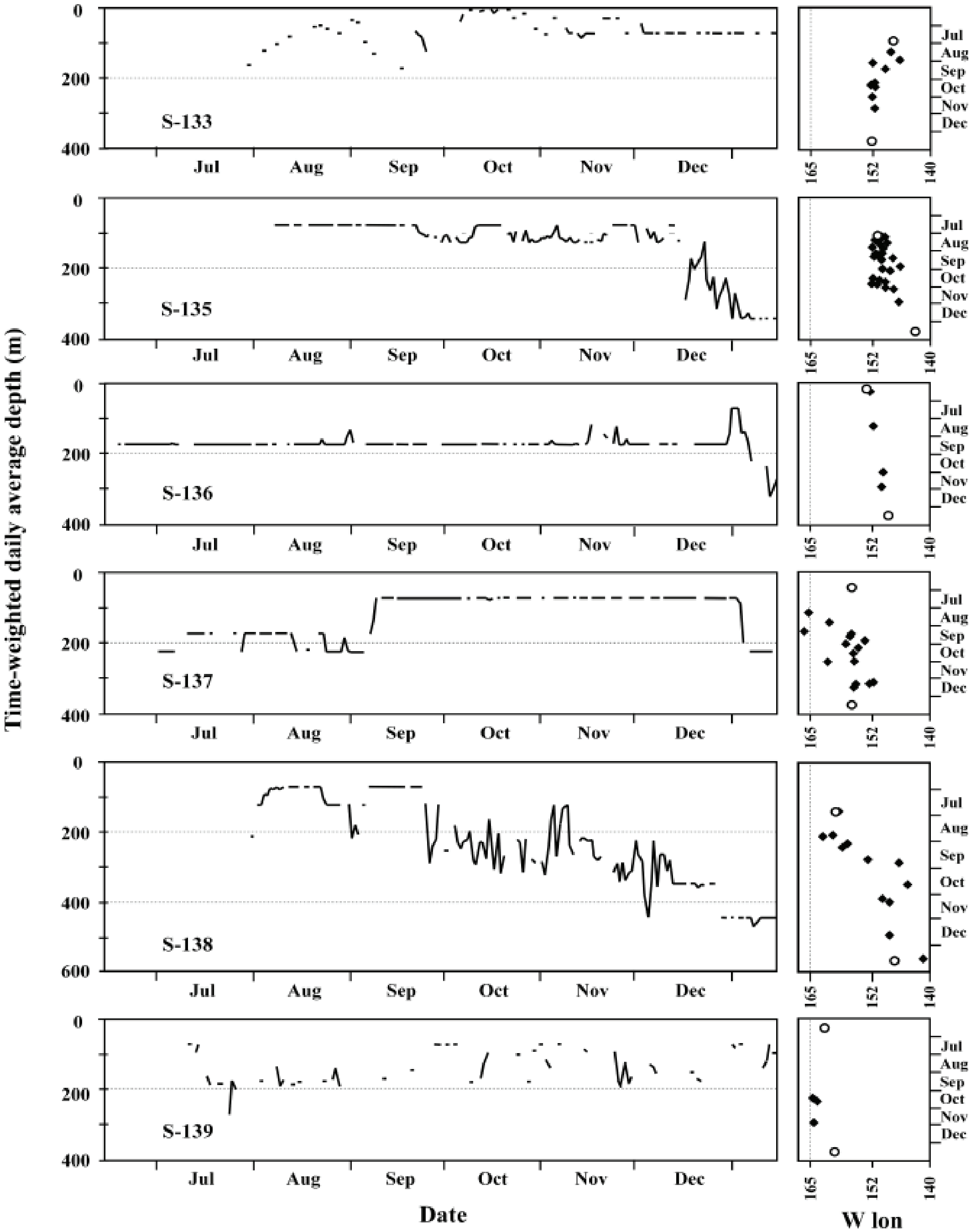


Figure 11. *Left panels*: **Time-weighted daily mean depths experienced by halibut tagged in the western Gulf of Alaska from tagging through mid-January.** *Right panels*: **Tag locations for each fish throughout the tagging period. Open circles in early summer and mid-January represent tagging and pop-up locations, respectively. Solid diamonds represent geolocation estimates determined from daily light data during time-at-liberty. Note that 140° W longitude is the equivalent of Yakutat Bay, while the easternmost edge of Unimak Pass is located at roughly 165° W.**

completed their descents in less than three weeks (Table 3). S-135 descended from 75 m to 350 m in 19 days; S-136 moved from 73 m to 325 m in 11 days. S-137 exhibited a shallower overall average depth profile, but much the same pattern: it remained at an average depth of 75 m for over three months, then in early January it descended to 225 m in four days. S-138 displayed the most gradual movement to deep water of all of the western GOA fish, as well as the most marked overall change in average depth. This fish moved from average depths of 75 m to a final depth of 475 m, but its vertical movement began in September and was not completed until late December, representing 107 days of gradual change in depth. Descent times for eastern GOA halibut were generally longer than western fish, ranging from 15-117 days; only one eastern fish completed its descent in less than three weeks (Table 3).

Table 3. Shallowest and deepest time-average daily depths and dates upon which they occured. In the case of shallowest depth, fish often spent more than one day at the same average depth. In such cases, the latest occurance of that depth is listed. Descent duration is the number of days that elapsed between the listed shallowest depth and the deepest depth, provided that the shallowest depth preceded the deepest. Where the deepest depth occured prior to the shallowest depth, no descent duration is listed.

Tag number	Shallowest daily ave depth (m)	Date	Deepest daily ave depth (m)	Date	Descent duration (days)
Eastern GOA					
S-101	105	Aug13	515	Dec16	64
S-102	125	Sep18	350	Jan13	117
S-103	75	Dec10	450	Dec25	15
S-105	30	Sep23	431	Jan9	108
Western GOA					
S-133	5	Oct20	176	Sep16	-
S-135	75	Dec12	350	Dec31	19
S-136	73	Jan1	325	Jan12	11
S-137	75	Jan2	225	Jan6	4
S-138	75	Sep22	475	Jan7	107
S-139	75	Jan3	279	Jul24	-

Two halibut failed to demonstrate any directed late-season movement to deep water: S-133 and S-139. Although relatively few data were successfully transmitted from tag S-139, this fish appears to have spent the summer at depths typical of the other fish (100-200 m), but did not relocate to deep water by the date of tag pop-up. It regularly displayed daily maximum depths >200 m throughout the majority of the tagging period (Appendix 1J), but its daily mean depth was >200 m on only one day (Fig. 11). S-133 was more anomalous. It moved into very shallow water in October, remained at relatively shallow depths throughout the remainder of the tagging period, and was located inside Cook Inlet in mid January.

Over the shortest time scale available for analysis (12 hr summary periods), some fish engaged in considerable vertical movement whereas others tended to remain at relatively constant depth, as demonstrated by 12 hr maxima and minima. S-102 and S-103 commonly engaged in short-period depth changes of 100-300 m or more, and in the case of S-103, as much as 700 m (Fig. 12; Appendices 1B and 1C). S-139 appears to have been vertically active over short time-scales throughout its time at liberty, with 12 hr depth variability of 100-200 m. In contrast,

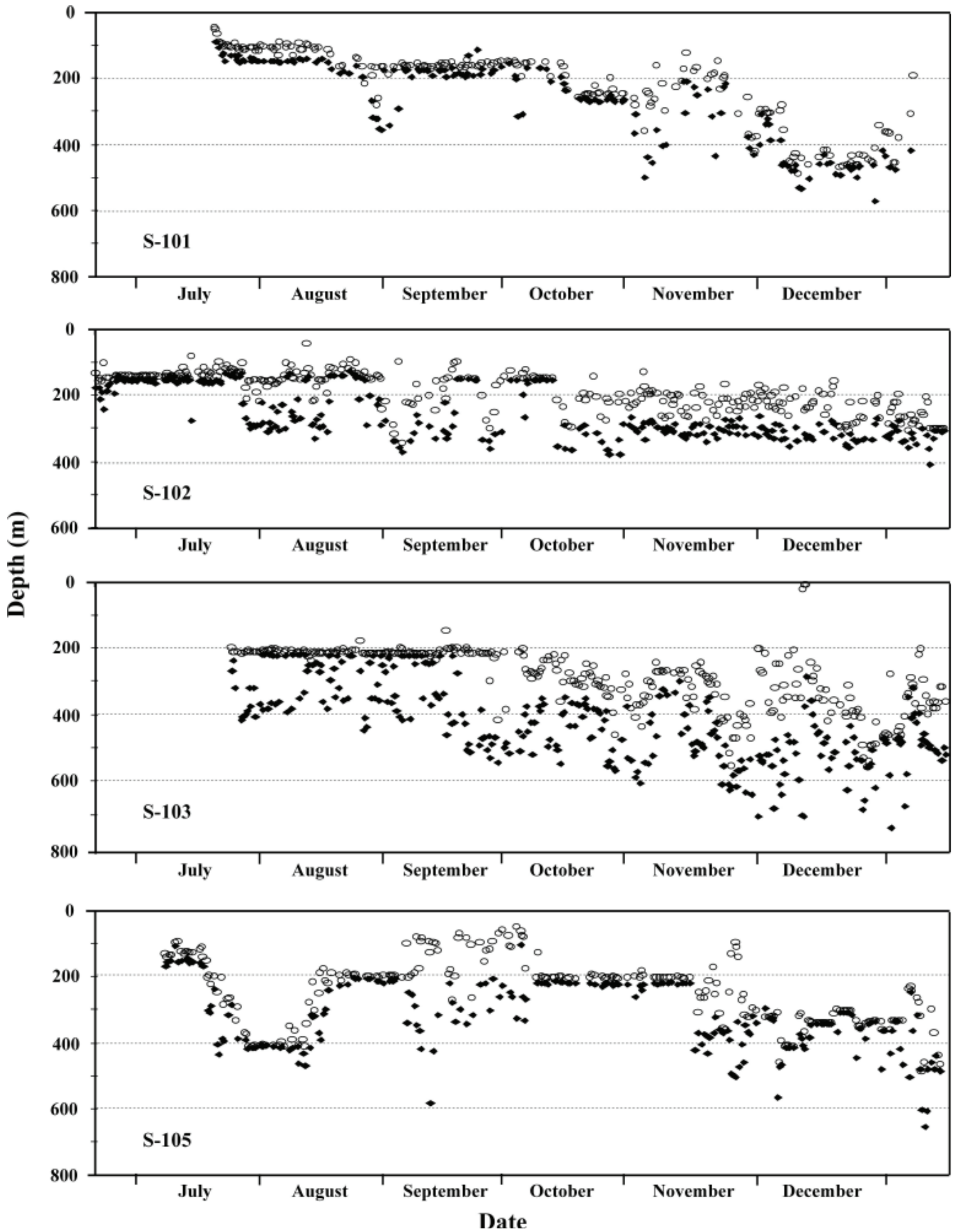


Figure 12. Maximum (solid diamonds) and minimum (open circles) depths experienced by halibut tagged in the eastern Gulf of Alaska, during 12-hr periods from tagging through mid-January.

short-period depth variation displayed by S-135, S-136, and S-137 (Fig 13; Appendices 1F, 1G, and 1H) was typically about an order of magnitude lower, rarely more than 20-30 m throughout the summer and fall. Other fish exhibited a combination of behaviors, with periods of vertical quiescence interspersed with periods of considerable vertical activity. For example, S-105 (Fig. 12) generally confined its short-period vertical movements to about 50 m throughout July and August. This fish became quite vertically active in September experiencing variations of 100-300 m. It then returned to a pattern of restricted vertical movement from early October through mid-November, and again reverted to considerable depth variability through early winter. Although somewhat less pronounced, similar shifts in behavior were also observed from S-101, S-138, and from S-135 and S-136 late in their tagging periods.

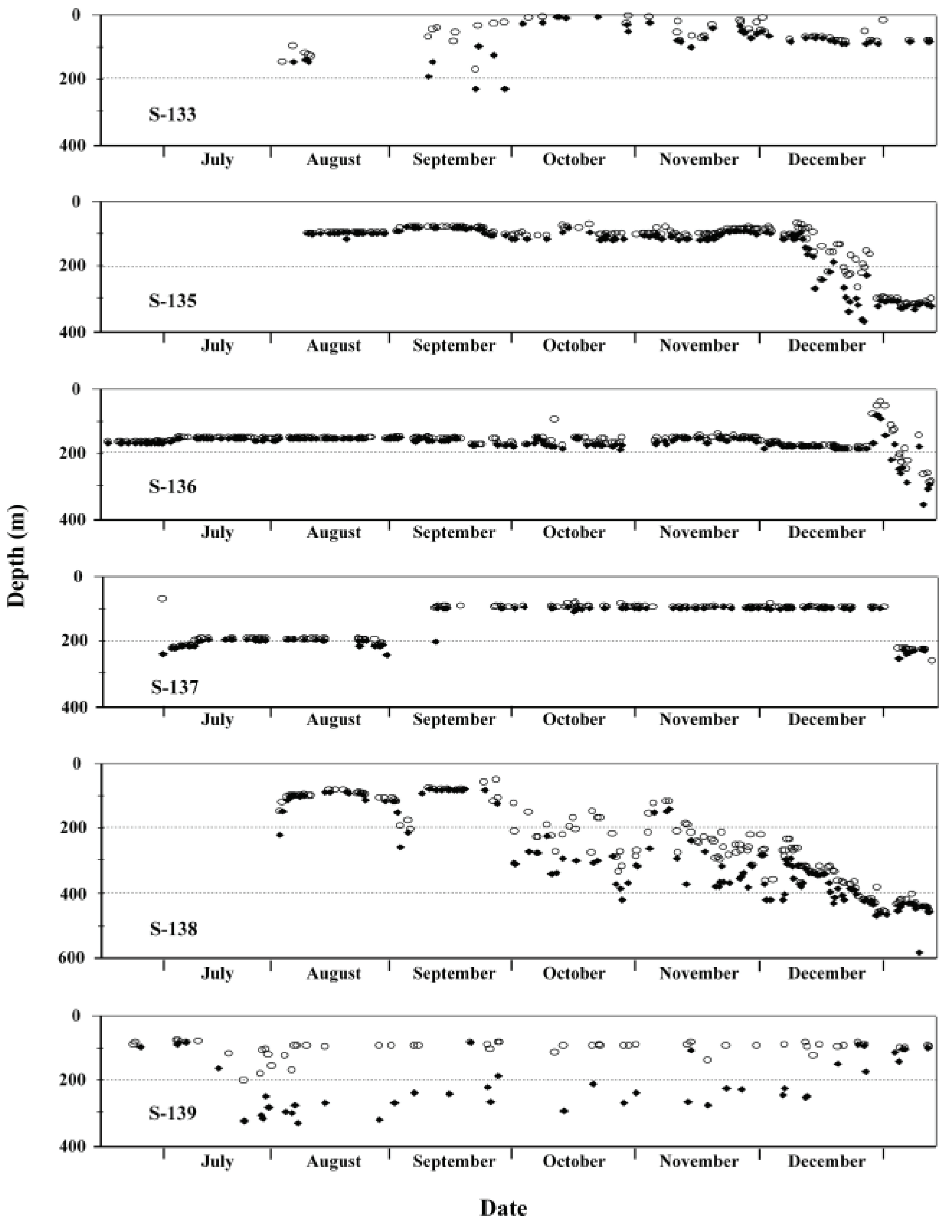


Figure 13. Maximum (solid diamonds) and minimum (open circles) depths experienced by halibut tagged in the western Gulf of Alaska, during 12-hr periods from tagging through mid-January.

Temperature

Tagged halibut experienced temperatures (Figs. 14, 15, and 16) ranging from 2.6° C (S-103, November 12; Appendix 2C) to 11.6° C (S-133, September 20; Appendix 2E). However, the typical range was narrower, with most fish spending the majority of time at 5-9° C (Table 4). All halibut tagged in the eastern GOA spent the majority of time at 5-7° C during all seasons, although it is noteworthy that S-102 was in relatively warmer water (7-9° C) during a substantial proportion of December and January (Table 4; Appendix 2B). Halibut tagged in the western GOA tended to experience more variable conditions than eastern GOA fish. S-133 encountered both the broadest temperature range and the overall warmest conditions, spending considerable time in waters 7-11° C throughout the year. Note that this was the fish located in Cook Inlet in mid-January and exhibited the shallowest overall depth profile. S-135 spent considerable periods of time in 7-9° C during summer and autumn, S-137 spent the majority of its time at >7° C during the autumn, and S-139 experienced similar conditions in autumn and winter. Only S-105 and S-137 experienced temperatures that were < 5° C for extended periods (Table 4). This occurred during July and August for both fish (Figs. 14 and 15). However, these cool temperatures were only slightly below 5° C: in the case of S-105 the minimum experienced temperature was 4.8° C (Appendix 2D), and 4.6° C for S-137 (Appendix 2H).

Short-period (within 12 hr summary periods) temperature variability differed among individuals and over time. Some fish were subjected to only very limited changes in temperature (e.g., S-136; Fig 15; Appendix 2G), while others experienced considerable short-period fluctuations, the greatest of which approached 5° C (S-133; Fig 15; Appendix 2E). Short-period temperature variability encountered by individual fish was not necessarily consistent throughout time at liberty. In many cases halibut exhibited weeks to months during which they experienced considerable temperature variability, interspersed with weeks characterized by relative thermal stability (e.g., S-105, September versus October; Fig. 14; Appendix 2D).

Table 4. Proportion of time that each fish spent within each tag-programmed temperature range (bin), pooled within three seasons defined as follows: summer = June 1 through September 15; autumn = September 16 through November 30; winter = December 1 through January 15. Note that data tranmissions were intermittant for some tags, resulting in relatively few observations relative to other tags; see Appendix 2 for detailed daily time-at-temperature data for each tag.

Temp.bin (degrees C)	Eastern GOA				Western GOA					
	S-101	S-102	S-103	S-105	S-133	S-135	S-136	S-137	S-138	S-139
Summer:										
3-5	-	-	1.2	24.4	-	-	-	55.5	-	3.4
5-7	98.3	99.9	98.8	75.1	63.6	31.9	100.0	37.0	100.0	96.6
7-9	1.7	0.1	-	0.5	20.8	64.4	-	7.5	-	-
9-11	-	-	-	-	8.6	3.7	-	-	-	-
11-13	-	-	-	-	6.9	-	-	-	-	-
Autumn:										
3-5	-	0.3	7.9	-	-	-	-	-	6.8	-
5-7	99.3	99.4	92.1	99.5	12.8	79.5	100.0	19.0	93.2	59.6
7-9	0.7	0.3	-	0.5	47.7	20.4	-	78.3	-	40.4
9-11	-	-	-	-	38.8	0.1	-	2.7	-	-
11-13	-	-	-	-	0.8	-	-	-	-	-
Winter:										
3-5	0.9	-	4.5	-	4.1	-	0.8	-	5.1	-
5-7	96.2	56.4	92.2	100.0	46.2	94.2	99.2	93.6	94.9	70.4
7-9	2.9	43.5	1.4	-	49.7	5.8	-	6.4	-	29.6
9-11	-	0.1	1.9	-	-	-	-	-	-	-
11-13	-	-	-	-	-	-	-	-	-	-

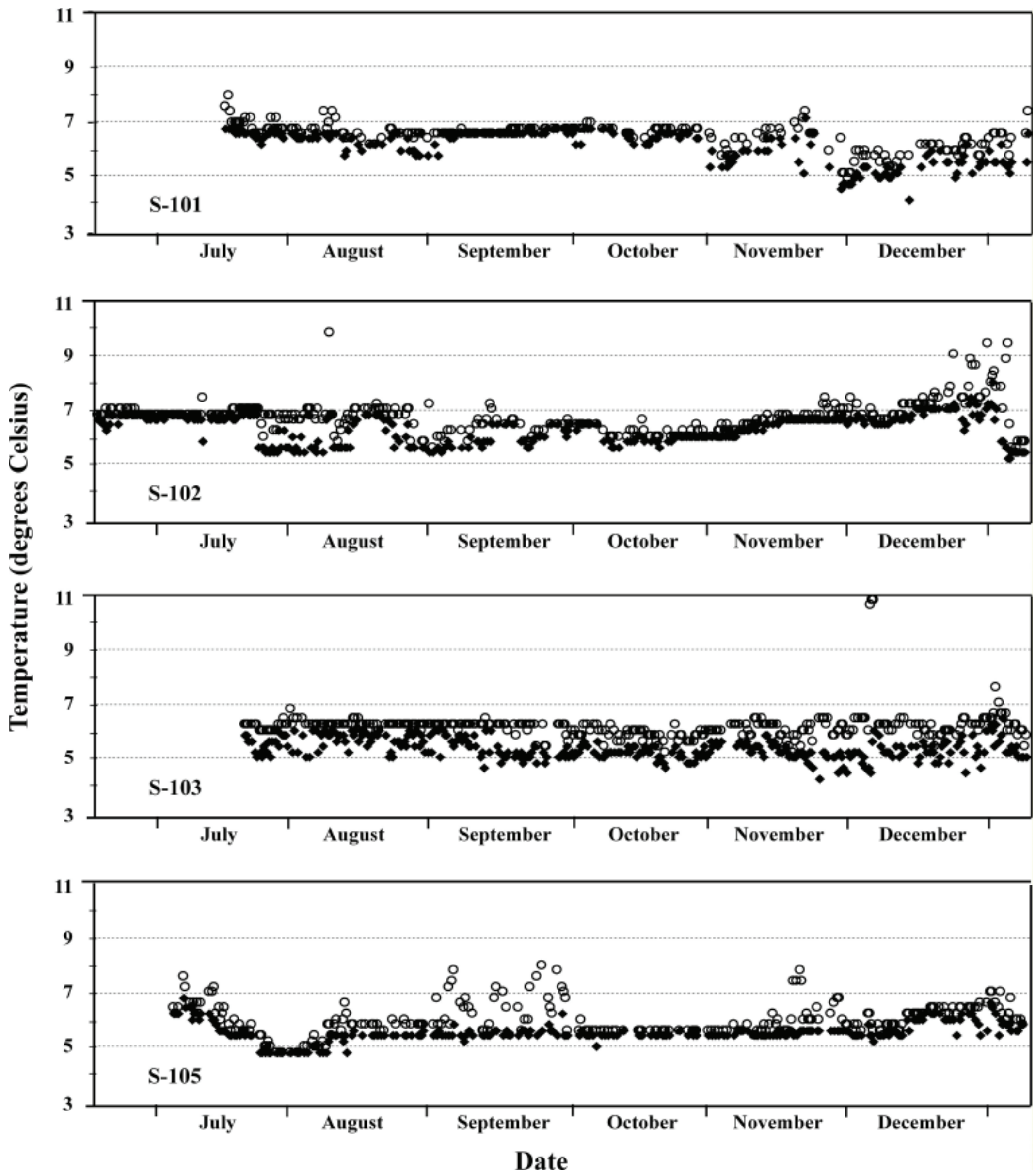


Figure 14. Maximum (solid diamonds) and minimum (open circles) temperatures experienced by halibut tagged in the eastern Gulf of Alaska, during 12-hr periods from tagging through mid-January.

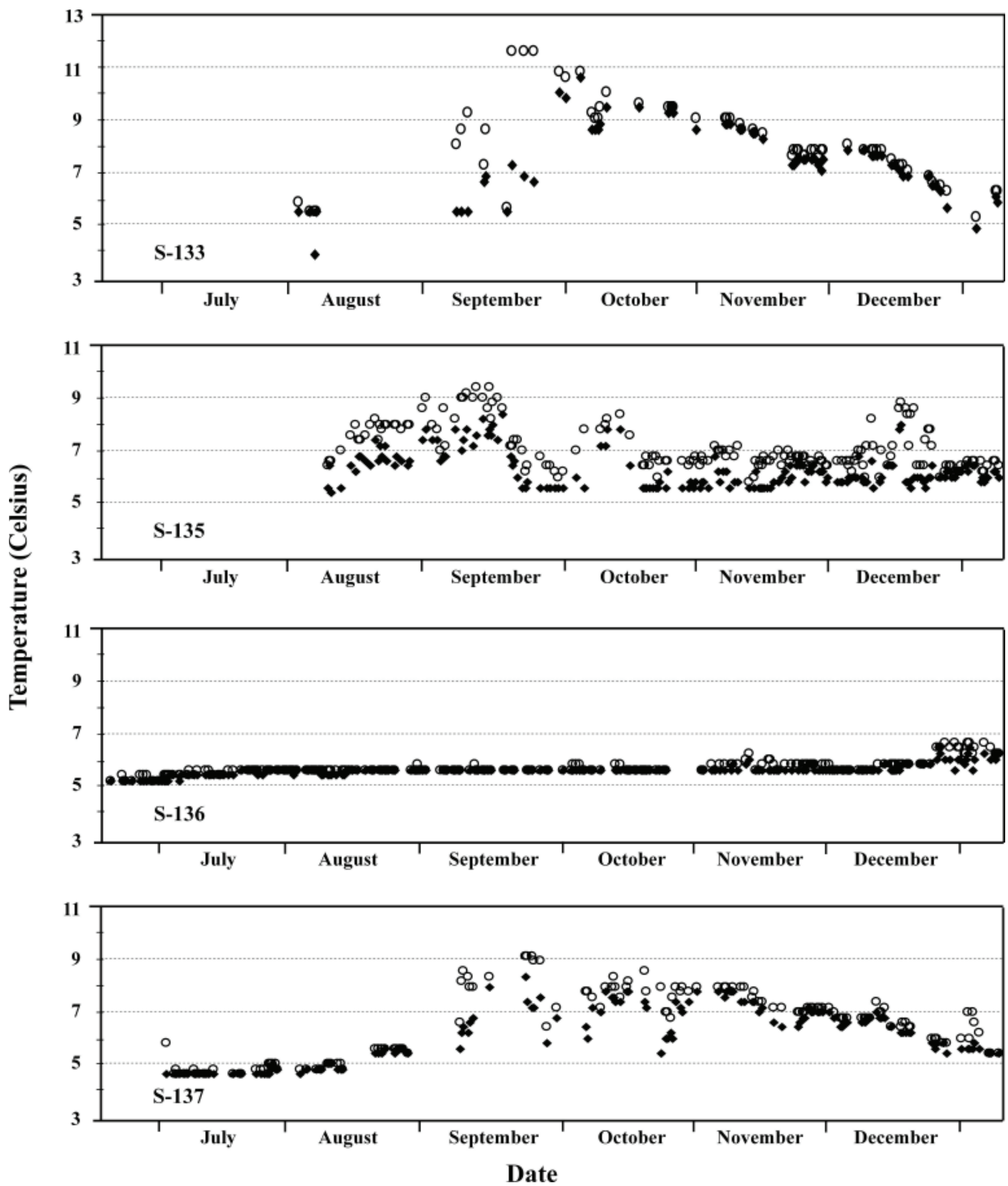


Figure 15. Maximum (solid diamonds) and minimum (open circles) temperatures experienced by halibut tagged in the western Gulf of Alaska, during 12-hr periods from tagging through mid-January.

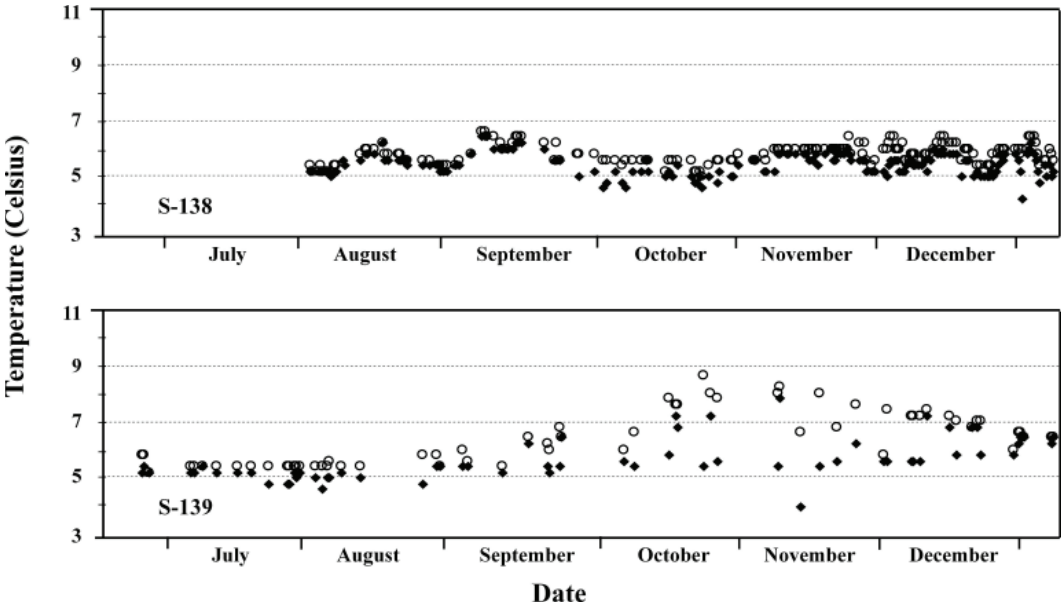


Figure 16. Maximum (solid diamonds) and minimum (open circles) temperatures experienced by halibut tagged in the western Gulf of Alaska, during 12-hr periods from tagging through mid-January.

Discussion

Location data

The study of spatial population structure requires identifying proportions of a population that display long-distance seasonal migrations versus local residency. Movement patterns, the extent of overlap between adjacent population components, and fidelity to seasonal grounds define the nature of interdependence among groups throughout a species' geographic range. Marine populations may be comprised of individuals that disperse little and take advantage of physical processes that serve to retain their reproductive output within a localized area. In contrast, individuals may undergo extensive migrations as adults or juveniles, or experience large-scale larval advection, affording considerable potential for mixing. Variance among individuals and nuances of site fidelity (philopatry) can combine to result in either segregation into coherent metapopulations, or considerable overlap in space or time that results in separation-by-distance or true panmixis. Examples of flatfish representative of various degrees of segregation can be found in the scientific literature. Western Atlantic winter flounder (*Pleuronectes americanus*) spawn demersal eggs in estuaries that favor larval retention (Howe et al. 1976, Crawford and Carey 1985, Manderson et al. 2003), leading to local population structure (Phelan 1992, Sogard *et al*. 2001). Northeast Atlantic Dover sole (*Solea solea*) undergo modest seasonal dispersion combined with overlap of source populations while on spawning grounds (Horwood 1993, Koutsikopoulos et al. 1995). This species seems to conform to a model of separation-by-distance, with a possible restriction created by the English Channel (Exadactylos et al. 1998, 2003). Western Atlantic summer flounder (*Paralichthys dentatus*) are offshore spawners with extensive cross-shelf larval advection to estuarine nurseries (Morse 1981, Able et al. 1990). This process results in a population that appears to be reasonably homogeneous at least with respect to subpopulations north versus south of Cape Hatteras, North Carolina (Jones and Quattro 1999, Burke et al. 2000, Kraus and Musick 2001).

From tag returns in the present study, Pacific halibut exhibited four general seasonal migration behaviors: A) northward displacement coupled with movement to the slope at the end of the tagging period (S-101, S-103, S-135, S-136, and S-138), B) little displacement, coupled with movement to the slope (S-102, S-137), C) movement to deep inshore waters (S-105), and, D) movement to shallow waters (S-133). It is impossible to know whether any of the fish were actually engaged in spawning at any time or whether they were on their ultimate winter ground by the date of tag pop-up. Furthermore, sample sizes from this study are too small to conduct quantitative analyses of the spatial patterns. However, the first two behaviors (A and B) are consistent with the accepted paradigm of a seasonal spawning migration to deep slope waters (St.-Pierre 1984) and northward redistribution during winter (Leaman et al. 2002). The current results corroborate the notion of seasonally altered biomass distributions among Regulatory Areas that might require unique management actions if commercial harvests occur during either migratory or spawning periods.

From an ecological perspective, the observed long-distance migration to offshore putative spawning grounds (e.g., S-101 and S-138), coupled with potentially large larval advection distances (St.-Pierre 1989, Bailey and Picquelle 2002), suggests potential for considerable population mixing. However, local spawners (eg., S-102 and S-137) could complicate that conclusion if they exhibit philopatry. The data suggest that distant and local seasonal migration patterns may coexist among individuals on the same summer feeding grounds. As such, mixing could occur in the central GOA area where halibut congregate from distant areas to spawn while local sub-populations are maintained at range edges where some individuals remain to spawn locally. Multiple life history strategies add complexity to spatial population analysis and the determination of metapopulation structure because local feeding grounds might be viewed as stock complexes with respect to spawning strategy. Maintenance of all components of a stock complex can be important to preserve within-species biodiversity, adaptive potential, and the composite stock's compensatory characteristics under exploitation (Frank and Brickman 2000, 2001, Stephenson et al. 2001). In particular, low abundance spawning groups might be more vulnerable to exploitation and need to be surveyed and monitored closely if a winter fishery were allowed. Monitoring of catch rates should occur with the understanding that spatial concentration on the winter grounds could yield high CPUE even at relatively low abundance.

For hypotheses regarding seasonal migration patterns to be fully addressed, further research must include greater sample sizes, assessment of philopatry, and spatially-explicit examination of juvenile dispersal. Even if alternative migration scenarios exist, small sample sizes do not allow for adequate identification of strategies or the proportion of the population employing them. It is easy to hypothesize the existence of discrete migration scenarios involving distant versus local spawning, but the population may be composed of a continuum of dispersal behaviors that appear to be discrete strategies because individuals migrating intermediate distances were not sufficiently observed. Movement of individual fish must also be tracked for two or more seasons to determine whether they are faithful to their spawning grounds because philopatry is critical in establishing long-term metapopulation structure. Research on North Sea plaice (*Pleuronectes platessa*) using data storage tags indicates that flatfish are capable of migration route and spawning site fidelity over considerable annual home ranges (Hunter et al. 2003). Mark-recapture studies of early (age-0) juvenile plaice indicates philopatric behavior beginning at a very young age (Burrows et al. 2004). Conventional tagging studies support the hypothesis that halibut may exhibit summer feeding site fidelity (Skud 1977), but migration pathways and spawning site fidelity have not been studied. Finally, dispersal of larvae and pre-reproductive stages requires formal investigation. If the progeny of philopatric spawners display behaviors different than their parents, mixing may be re-established on intergenerational scales.

The shelf-edge migrations discussed above describe the behavior of seven of the tagged halibut, but two fish displayed unexpected behaviors: movement to deep inshore water and shallow water residence throughout time at liberty. The observation that S-133 did not move to deep water may simply indicate that its offshore migration did not coincide with the programmed date of tag pop-up. Spawning is expected to occur until at least March in the Gulf of Alaska (St. Pierre 1984) and the IPHC received many anecdotal reports from fishers that ripe and running fish were captured in early March during the 2004 commercial fishing season (T. Geernaert, IPHC, P.O. Box 95009, Seattle, WA 98145, pers. comm.). A mid-January pop-up may be too early to identify seasonal migration for fish that spawn in late winter or early spring. Alternatively, some spawning may occur in shallow shelf waters, or the behavior may have been characteristic of a proportion of the mature population that foregoes spawning each year.

Although an annual spawning cycle is the accepted paradigm for halibut across their geographic range (Leaman et al. 2002), Novikov (1964) reported capture of a substantial proportion of non-spawned mature individuals in the Bering Sea during late winter. He concluded that halibut "does not spawn every year but possible once in two years or even more seldom". The tendency to spawn biennially or at irregular intervals based on environmental factors or somatic condition has been clearly established in taxa as disparate as crustacea (Jensen and Armstrong 1989, Eiriksson 1993, Comeau and Savoie 2002) and marine birds (Reville 1983, Olsson and Brodin 1997, Jouventin and Dobson 2002). In fish, skipped spawning and/or pre-spawn mass atresia have been documented in populations of Atlantic cod (*Gadus morhua*; Rideout, Rideout et al. 2000), orange roughy (*Hoplostethus atlanticus*; Bell *et al*. 1992), Greenland halibut (*Reinhardtius hippoglossoides*; Fedorov 1971), and winter flounder (Burton and Idler 1984, 1987), and experimentally demonstrated in captive North Sea plaice (Rijnsdorp 1990). Research examining variable fecundity and gonad development should be conducted as it might indicate whether skip-spawning occurs in halibut, and identify conditions that could lead to this reproductive strategy.

In the case of S-105, movement to the deep inshore waters of southeast Alaska may have represented its spawning migration. It may be an oversight that the inside waters have not been recognized as important spawning grounds. St. Pierre (1984) states that inside waters "are very deep and reports indicate the possibility of some spawning". But he dismissed this, hypothesizing that post-spawn fish captured there during spring might not have "spawned in the inside waters but rather on the continental edge from which they had recently returned". While he then concluded that "data to confirm this … could be obtained by fishing in December and January", the hypothesis has not been actively investigated. Evidence exists to support the hypothesis that adult halibut reside within deep inside waters during winter and may spawn there. Large halibut occur as bycatch in the winter fishery for demersal shelf rockfish (*Sebastes* spp.) (V. O'Connell, Alaska Department of Fish and Game (ADF&G), 304 Lake St., Sitka, AK 99835, pers. comm.) and nearly 400 halibut of legal size (>82 cm fl) were captured in Chatham Strait in January-February, 2005, during ADF&G sablefish assessment charters (V. O'Connell, ADF&G, unpub. data). Furthermore, IPHC studies have confirmed the presence of early juvenile (young-of-year to age-2) nursery grounds in Frederick Sound, including in Fanshaw Bay at the Sound's easternmost extent (Loher 2005). While it is possible that far eastern inside waters nurseries could be supplied with larvae from offshore spawning sites, a more reasonable hypothesis may be that larvae are produced locally.

Finally, it is important to note that the 3-day tag drift tracks demonstrate that tag locations reported for pop-up were robust to tag drift between the time of tag release and initial satellite reception. For most tags, there was only a small time lag and estimated drift was small. The signal for tag S-133 was not received until more than 2 days following programmed release, but if the tag was adrift for the entire time the resultant estimated drift does not alter the conclusion that its host fish was well inside Cook Inlet in mid-January. Why the tag's signal was not received on the date of tag pop-up is a matter of speculation. It is possible that the tag did not physically detach for two days or that it released properly but experienced satellite reception problems, perhaps surfacing underneath a layer of sea ice or in rough seas. Ice cover analyses indicated that the pop-up was considerably south of the Cook Inlet ice edge at the time (P. Olsson, Alaska State Climate Center, 707 A Street #205, Anchorage, AK 99501, pers. comm.), but reception problems due to sea state are plausible. Gale force winds were reported at nearby St. Augustine Island from January 15-17 (R. Page, US National Weather Service, 222 W. 7th Ave #23, Anchorage, AK 99513, pers. comm.), the period during which the tag was not in contact with the Argos network. Rough conditions can interrupt signal transmission and result in intermittent uplinks or no contact at all.

Environmental data

The observations of summertime activity concentrated at <400 m depth and movement to deep water by mid-winter is in agreement with observations made by Seitz *et al*. (2003) for similar-sized halibut in the northern GOA. In that study, summertime activity was concentrated at 50-350 m. Two fish were observed through winter and the deepest portion of their profiles indicated residence at 300-500 m from December through early February. Halibut tagged in the southeastern Bering Sea undertook similar movements (Seitz and Loher, in review), but with shallower summer distributions (primarily <200 m) and deeper winter depths (400-800 m).

Vertical migratory behavior observed in the present study was quite variable among individuals over a variety of time scales. Unfortunately, from data averaged over 12 hr periods it is nearly impossible to determine whether the fish moved into the water column or remained near the benthos and followed local bathymetry. If tags are physically recovered and detailed data accessed it may be possible to infer movement into the water column based on rate of change in depth. For example, Seitz et al. (2005) report depth changes as great as 168 m in 4 minutes for adult halibut. While vertical movement of that magnitude may represent benthic travel along a steep slope or pinnacle, movement into the water column may be a more parsimonious explanation. Halibut actively forage in the water column, as evidenced by pelagic and epibenthic prey in their diet (Best and St.-Pierre 1986, Orlov 1997, Yang 1997) and the incidental capture of halibut in the salmon troll fishery (Gilroy et al. 2004). Movement into the water column has also been observed during spawning in numerous other flatfish species (Moyer et al. 1985, Manabe et al. 2000, Manabe and Shinomiya 2001, Carvalho et al. 2003), and may also be exhibited in halibut (Seitz et al. 2005).

To a certain degree, daily depth variability may be related to local bathymetry. Over long time scales (weeks to months) vertical profiles of halibut tagged in the northwestern GOA were generally less variable than those tagged in the eastern GOA and Alaska Peninsula. The northern GOA is characterized by broad, sloping bathymetry, whereas the shelf is considerably less broad off the Alaska Peninsula and in the eastern Gulf. Northwestern GOA halibut were likely to encounter little change in bottom depth even if they moved considerably offshore. Halibut tagged in regions where small onshore-offshore travel would subject them to considerable change bottom depth displayed the most variable short-period depth profiles.

Eventual descent into deep water was observed in most individuals, but timing and rapidity of movement was not consistent among fish. Some fish moved quickly from their summer depth range while others exhibited protracted periods of gradual descent. We hypothesize that the observed period of consistent descent into deep water may represent onset timing of seasonal migration. Furthermore, we hypothesize that halibut that reside on summer feeding grounds at the southern edges of the GOA (Areas 2B and 3B) and spawn in the northern GOA will begin their migrations earlier than fish that spend the summer in Area 3A. Earlier departure from feeding grounds would be required if long-distance travelers are to arrive on spawning grounds at the same time as those migrating short distances. This is supported by the observation that fish displaying little displacement completed their descents within a 2-3 week period, whereas extensive migration was associated with more protracted descent (>2 months). Similar results were found in a concurrent study in the southeast Bering Sea (Seitz and Loher, in review).

The hypothesis that descent to depth represents onset of migration, and therefore the timing of biomass redistribution, follows from the interpretation that movement to deep water coincides with longshore movement. However, fish might migrate cross Regulatory Area boundaries while still in shallow water, in which case movement to deep water would lag behind longshore migration. Alternatively, fish could move to deep water near feeding grounds prior to crossing Area boundaries. For most of the tagged fish it is difficult to assess the relative likelihood of these scenarios, but the light-based longitude estimates for S-138 support the notion that descent coincides with longshore migration. One must keep in mind that light-based longitude estimates contain error and latitudinal estimates lack suitable accuracy to be useful (for more detail on geopositional error, refer to Seitz et al., in press). Individual longitude estimates should be considered carefully, but overall trends can be informative. Geopositions for S-138 (see Fig 11) followed a linear trend beginning in August with westerly coordinates near the tagging location followed by progressively easterly values that eventually approximated the pop-up longitude by mid-October. The trend suggests steady eastward travel over the course of 4-8 weeks. Correspondingly, the fish moved from a relatively constant average depth of 75 m in mid-September to over 300 m by mid-October. The notion that halibut may migrate along the slope and not in shallow water is further corroborated by the observation of similar behavior from a long-distant migrant tagged in the southeast Bering Sea (Seitz and Loher, in review).

Temperature data demonstrate a strong tendency for GOA halibut to occupy waters within a range of 5-7^{o} C. These results are similar to those reported by Seitz et al. (2003) in the northwestern GOA; those fish experienced primarily temperatures of 6^{o} C during summer and 4-8^{o} C in winter. Whether these temperatures represent active preference or are simply the ambient temperatures encountered throughout their preferred habitat cannot be determined from the data. However, the GOA observations depart from southeast Bering Sea data, where halibut have been shown to experience winter temperatures persistently as low as 2-3^{o} C (Seitz and Loher, in review). In addition, the GOA observations presented here demonstrate that halibut can be subject to considerable thermal variability over relatively short periods. Such temperature changes might be caused by passage of tidally-generated internal waves over stationary fish (*sensu* Witman et al. 1993) or active movement of fish among different water masses. Temperature and depth data from archival tags have been used to track the movement of pelagic fish relative to thermoclines (*sensu* Brill et al. 1999), and PDT data provided by PAT tags are designed for this purpose. Seitz et al. (2003) demonstrated the use of these data with halibut. However, we were reluctant to conduct such analyses here due to the coarse nature of the data and ambiguities associated with interpreting the nature of short-period depth changes.

Finally, the reader should bear in mind that the results presented here may represent only a specific segment of the halibut population due to the size of the fish that were tagged (>100 cm). Halibut this large are primarily reproductive females (see Fig. 3). Thus, the data presented here may exclude males and pre-reproductive individuals whose behavior may differ. In particular, large females may have unique energetic needs and employ specific life-history strategies to optimize energy allocation to egg production. Sex-specific variability in seasonal distribution and migration strategies has been demonstrated in other flatfish species (Arnold and Metcalfe 1995, Sabrowski and Bucholz 1997), as have temperature-specific differences in habitat choice (Swain 1997, Swain and Morgan 2001). Regardless of sex, total body size may also determine home range size, (Minns 1995) migration rate (Rijnsdorp and Pastoors 1995), and migration timing (Eltink 1987, Poole and Reynolds 1996). Future research should seek to investigate the behavior of mature males and immature halibut of both sexes; smaller instruments will be required in order to do so. Although fish bearing data storage tags (DSTs) must be recaptured to recover the data, archival DSTs have proven effective in the study of small flatfish (Hunter et al. 2003, Walsh and Morgan 2004), and the use of similar instruments on small Pacific halibut might add considerably to our understanding of the species.

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List of Appendices

The following appendices are included on the attached cd.

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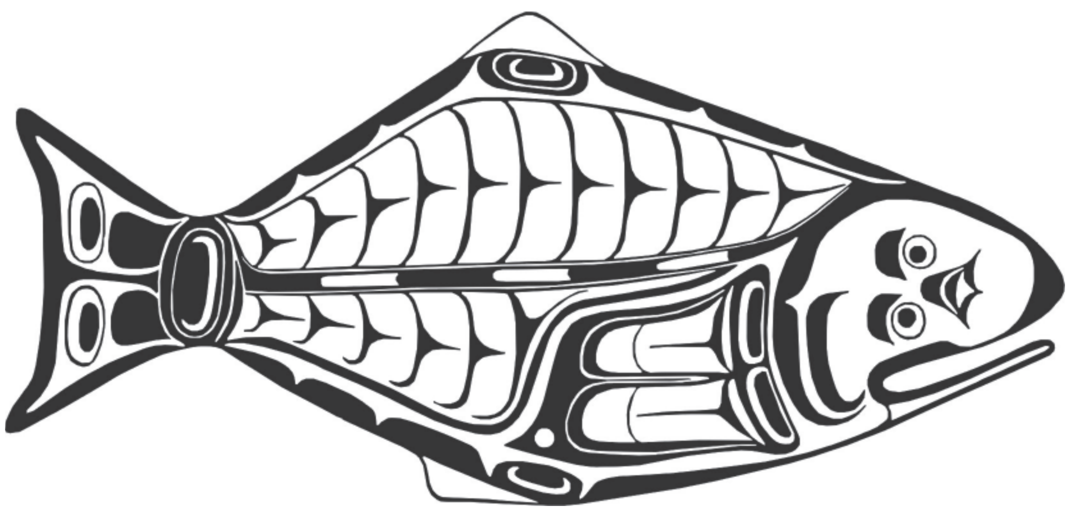

Halibut Crest - adapted from designs used by Tlingit, Tsimshian and Haida Indians