Mar Biol (2014) 161:645–656
DOI 10.1007/s00227-013-2367-5

ORIGINAL PAPER

Movements, environmental associations, and presumed spawning locations of Atlantic halibut (*Hippoglossus hippoglossus*) in the northwest Atlantic determined using archival satellite pop-up tags

Shelley L. Armsworthy · M. Kurtis Trzcinski · Steven E. Campana

Received: 13 May 2013 / Accepted: 3 December 2013 / Published online: 25 January 2014

Abstract Large Atlantic halibut (*Hippoglossus hippoglossus*) off the eastern coast of Canada were tagged with pop-up satellite archival transmission tags ($N = 17$) to track movements, determine ambient depth and temperature, and infer spawning activity. Many halibut showed seasonal movements from deepwater slope areas in fall and winter to shallower feeding grounds on the Scotian Shelf and Grand Banks in summer. Halibut depths ranged between 0 and 1,640 m. Mean temperature of occupation was 4.7 °C. Multiple short-term vertical ascents from a consistent baseline depth, characterized as spawning rises, were identified in seven of the tagged halibut south of the Grand Banks. All presumed spawning rises occurred in multiples of 2–6 events at 2- to 9-day intervals between October and January, spanning an average vertical extent of 50–100 m at depths of about 800–1,000 m. Given the direction and velocity of the slope water currents and the duration of the pelagic stage, the calculated 300–500 km drift of the eggs and larvae would take them onto the Scotian Shelf, as well as into the Gulf of St. Lawrence. Therefore, the location of the presumed spawning grounds is consistent with expectations based on migration compensation theory, the northeasterly migratory patterns of the juveniles, the relatively static distribution of the adults off southern Newfoundland, and the prevailing currents at depth.

Communicated by D. Righton.

S. L. Armsworthy (✉) · M. K. Trzcinski · S. E. Campana
Bedford Institute of Oceanography, Fisheries and Oceans Canada, P.O. Box 1006, Dartmouth, NS B2Y4A2, Canada
e-mail: shelley.armsworthy@dfo-mpo.gc.ca

Introduction

Atlantic halibut (*Hippoglossus hippoglossus* L.) is the largest of the flatfish species in the Atlantic Ocean and ranges widely over the North Atlantic, supporting national and international fisheries off the coasts of Canada, Greenland, Iceland, Faroe Islands, and Norway. Despite having the highest commercial value per landed weight of all groundfish in the North Atlantic, many of the basic life history characteristics of Atlantic halibut remain unknown. Growth is sexually dimorphic, with females reaching a substantially larger maximum size (~230 cm) than males (~189 cm) (Devold 1938; McCracken 1958; Bowering 1986; Trumble et al. 1993; Sigourney et al. 2006). Females also mature at a larger size (103–125 cm) and age (7–13 years) than males (55–80 cm and 5–12 years, respectively), with a longevity of 38–50 years (Armsworthy and Campana 2010). The timing and location of spawning in the NW Atlantic population has never been reported. In Pacific halibut, however, the presumed spawning grounds have been located based on short-term vertical ascents ("spawning rises") recorded in archival tag data (Seitz et al. 2005; Loher and Seitz 2008).

Conventional tagging studies indicate that Atlantic halibut are capable of moving throughout the northwest Atlantic (McCracken 1958; Stobo et al. 1988; Kanwit 2007), often well outside Canada's 200-mile exclusive economic zone (McCracken 1958; Jensen and Wise 1961). A tendency for small halibut (<75 cm) to move farther than large halibut has been reported by Stobo et al. (1988), although Bowering (1986) reported that both small (<57 cm) and large (120 cm) halibut could travel long distances. In both the northeast and northwest Atlantic, conventional tagging studies of Atlantic halibut have suggested that very young halibut remain close to their nursery grounds, juveniles move widely and somewhat indiscriminantly, and that adults engage in seasonal onshore–offshore movements to and from the spawning grounds on the continental slope (McCracken 1958; Godø and Haug 1988a, b; Stobo et al. 1988). However, the seasonal nature of the directed halibut longline fishery, focused in a relatively small area, suggests that movements based on conventional tag returns are unlikely to be representative of their distribution, since tag recaptures can only reflect the distribution of the commercial fishery and cannot show movements to areas where there are no recaptures.

Pop-up Satellite Archival Transmission (PSAT) tags are externally mounted electronic tags that can provide unbiased information on fish movements (Loher and Seitz 2008; Block et al. 2001; Campana et al. 2011). The tags record ambient depth, light level, and temperature for periods of up to a year before physically releasing from the fish and transmitting the accumulated data to a satellite. Since the tag data transmission does not require the recapture of the fish, the tag pop-up location is not dependent upon recapture in any fisheries and thus provides an unbiased determination of net movement from the tagging location. In this study, we deployed PSAT tags on large Atlantic halibut in the northwest Atlantic in order to determine unbiased seasonal movement patterns as well as depth and temperature associations throughout the year. We were also interested in attempting to identify spawning rises, which would be indicative of the date and location of spawning.

Materials and methods

Atlantic halibut used in this study were captured by Canadian commercial fishermen between 2007 and 2010 using longline gear. The measurements and tagging were made either by fishery observers or by commercial halibut fishermen with previous experience deploying satellite pop-up tags. The overall condition of the halibut was recorded, as was its fork length. Sex was unknown at the time of tagging, since it is not possible to determine the sex of Atlantic halibut using external examination.

A random sample of 17 large (>118 cm FL), healthy, and presumably sexually mature halibut were tagged with Wildlife Computers Mk-10 pop-up archival transmitting tags (PSATs) just prior to release (Table 1). Tagged halibut were on deck an average of about 3 min for tagging and measurement, and showed no obvious stress above and beyond that of capture. PSATs were attached to halibut by inserting a barbed plastic umbrella anchor about 4–5 cm into the dorsal side of the fish, a few cm ventral and posterior to the base of the widest part of the dorsal fin. Anchors were inserted at an angle so that the tag naturally towed behind the attachment point, and so that the dart was more likely to be anchored in the pterygiophores underneath the dorsal fin. The umbrella tip was attached to the PSAT with a monofilament leader of 400-pound test, sheathed in plastic to reduce trauma to the halibut near the point of insertion. Each PSAT was also fitted with an emergency cutoff device that physically released the tag if it went below 1,800 m (which is the maximum nominal safe depth for tag operation).

PSATs were programmed to record depth (± 0.5 m), temperature (± 0.1 °C), and light intensity at 10-s intervals for a period of 2–10 months after release (Table 1). Pop-off dates were mainly assigned across the period October–March, since a pop off around the time of spawning would have most accurately indicated spawning location. The tag data were internally binned at 6-h intervals and the summarized data transmitted to an Argos satellite after release of the PSAT from the halibut. Where the Argos transmission was incomplete and resulted in only a single depth bin being transmitted for a given time/date interval, the data were not used (<1 % of all records). More than 88 % of the tags transmitted successfully after release from the fish; two of the tags did not report (Table 1). None of the PSATs were programmed to release from the fish if a constant depth was maintained for an extended period, since a continued presence on the ocean floor would not necessarily be indicative of death in a bottom-dwelling fish such as a halibut.

Halibut location at the time of pop-up was determined with an accuracy of <1 km through Doppler-shift calculations provided by the Argos Data Collection and Location Service. The migration pathway between the time of tagging and pop-up would normally be reconstructed using sea surface temperature and ambient light at depth measurements recorded by the PSAT (i.e., Campana et al. 2011), but most of the halibut that were tagged spent too much of their time in darkness (>300 m) to allow any reconstructions of movement between the tagging and pop-up location.

Two of the PSAT tags were physically recovered after pop-up; the data from these tags could be downloaded directly and thus provided much greater detail (10-s interval) than the summarized data (6-h interval) that were transmitted to the satellite, allowing a closer inspection of halibut behavior.

Results

The halibut that were tagged ($N = 17$) off the eastern coast of Canada ranged between 118 and 188 cm FL (mean of 139 cm), with many of the larger fish likely being mature females based on size (Armsworthy and Campana 2010). Water depth at the tagging locations generally exceeded 250 m (165–819 m), but depths were recorded at only 65 % of the tagging sites.

Table 1 Pop-off satellite tag data for Atlantic halibut tagged in the northwest Atlantic, including tag identification number, deployment and pop-off dates, halibut fork length (cm), deployment and pop-off positions, days at liberty, and minimum distance travelled (km)

Tag ID #	Deployed date	Fork length (cm)	Lat release ddmm N	Long release ddmm W	Pop-off date	Lat popoff ddmm N	Long popoff ddmm W	Days at liberty	Minimum km travelled
67739	June 21, 07	175	4247	5021	December 31, 07	4419	5323	193	350
87666	January 7, 09	173	4432	5707	May 31, 09	4619	5837	144	228
87665	January 17, 09	188	4245	6351	July 31, 09	4430	6301	195	206
87667	January 30, 09	136	4330	5948	May 31, 09	4225	6545	121	500
87663[a]	February 20, 09	130	4242	6401	October 22, 09	4316	6516	244	119
93201	March 17, 09	118	4354	5846	February 3, 10	4347	5924	323	52
93195[b]	May 23, 09	123	4718	6013	Dart released from fish shortly after tagging				
93196	June 10, 09	158	4458	5518	February 1, 10	4456	5519	236	2
93197	June 10, 09	147	4509	5510	January 12, 10	4341[?]	5431[?]	264	91
93200	June 12, 09	125	4337	5205	February 22, 10	4352	5231	255	24
93202	June 12, 09	143	4340	5209	March 25, 10	4342	5209	286	1
93198	June 22, 09	154	4439	5019	March 2, 10	4353	4902	253	71
93199	June 23, 09	130	4407	5045	Did not report				
87663A	August 11, 10	150	4332	4911	November 15, 10	4244	5008	96	118
93195A	August 13, 10	177	4257	4945	Did not report				
87665A	August 23, 10	165	4255	4944	January 4, 11	4248	4939	134	14
87666A	November 8, 10	148	4454	5501	January 17, 11	4438	5630	70	122

[a] Recaptured with tag

[b] Tag recovered

[?] Pop-off location is approximate

Data were transmitted or recovered from 15 of the 17 PSATs, although one of the tags detached from the fish only 1 day after tagging and was later physically recovered; based on the depth profile recorded by the tag, and on the fact that the tag was returned with the dart intact, the premature release is thought to have been due to a poorly embedded dart and not a mortality. Another tag was recovered before the scheduled pop-up when the halibut was caught 244 days after tagging, thus allowing the downloading of a complete data set from the recovered tag (as opposed to the summarized data transmitted to the satellite). A third tag (PTT 93197) reported on the pop-up date, but only after drifting for a month at the surface before reporting; thus the exact pop-up location of this tag is unknown, although the drift rate of the Argos locations suggests that it popped off over the continental slope. All of the remaining tags popped off on the programmed date. The time at liberty for the analyzed tags ranged between 70 and 323 days, with a mean of 201 days (Table 1).

The tagged halibut travelled a minimum (straight line or displacement) distance of 1–500 km (mean ± SE of 135 ± 38 km) from the tagging site by the time of tag pop-up, although actual travelling distance could have been much greater (Fig. 1). Most of the tags were applied, and subsequently popped off, near the edge of the continental shelf. However, there was a pronounced seasonal pattern, with summer pop-ups occurring farther inshore than those popping off in the winter. For example, Tags 87663, 87665, and 87667 all popped off on the Scotian Shelf between May and October after being tagged on the edge of the continental shelf in January and February (Table 1; Fig. 1). A similar pattern was observed on the Grand Banks, where Tag 93198 left the top of the Bank after tagging in June to pop off near the edge of the shelf in March. None of the tags popped off substantially offshore of the continental shelf. Aside from the seasonal pattern, there was no significant relationship between days at liberty and distance travelled (regression, $P > 0.1$), although the greatest distances tended to be associated with halibut at liberty <200 days. Nor was there a significant relationship between the size of the halibut and distance travelled ($P > 0.1$), despite the fact that three of the four largest distances were associated with the largest halibut. Mean net displacement rate from the tagging site was 0.9 km day^{-1} (range of 0.0–4.1 km day^{-1}). There was no significant relationship between direction or rate of movement with the length of the fish ($P > 0.1$). However, there was a significant negative relationship between net displacement rate and days at liberty ($P = 0.015$), suggesting that there might be a return to the area around the tagging location every year at around the same time, thus minimizing the net displacement rate. Since none of the halibut were definitively sexed, migration differences between the sexes could not be determined.

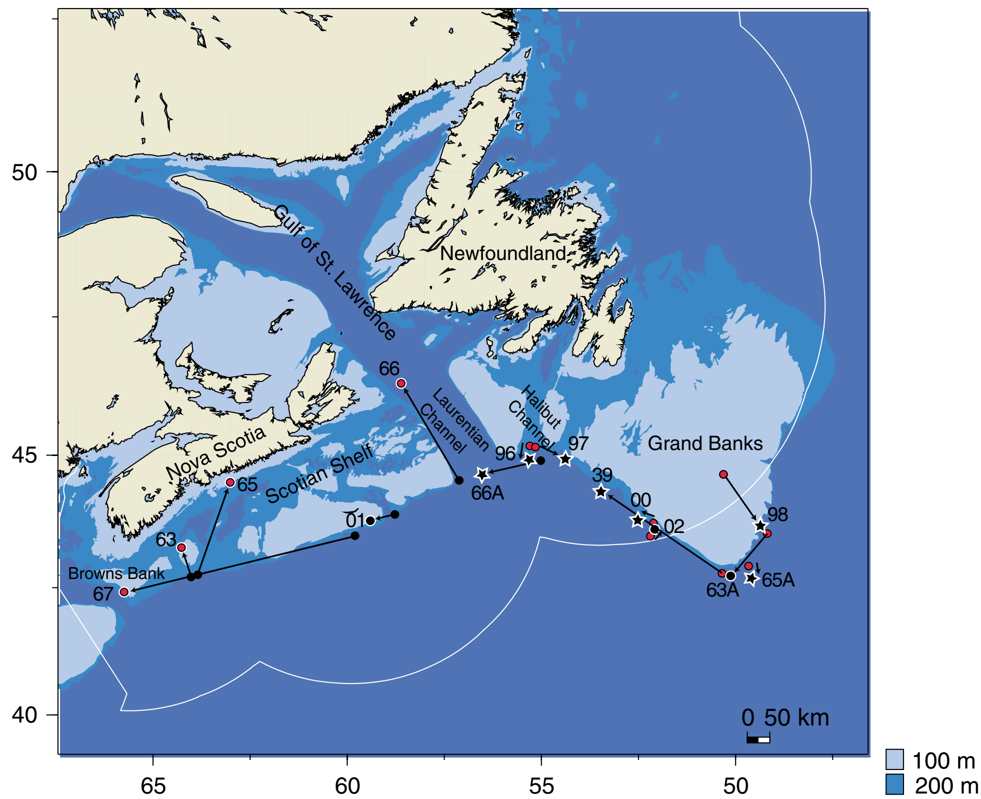


Fig. 1 Atlantic halibut PSAT tag and pop-up locations for 14 Atlantic halibut tagged off the eastern coast of Canada. *Solid circles* show deployment locations while *symbols* with *white borders* show pop-up locations. *Black* represents deployment/pop-up in winter (November–March) and *red* represents summer (April–October). Pop-up locations shown as *stars* refer to halibut that displayed possible spawning rises. *Numbers* represent the last two digits of the tag's Argos PTT identification number (see Table 1). The pop-up location of Tag 97 is only approximate

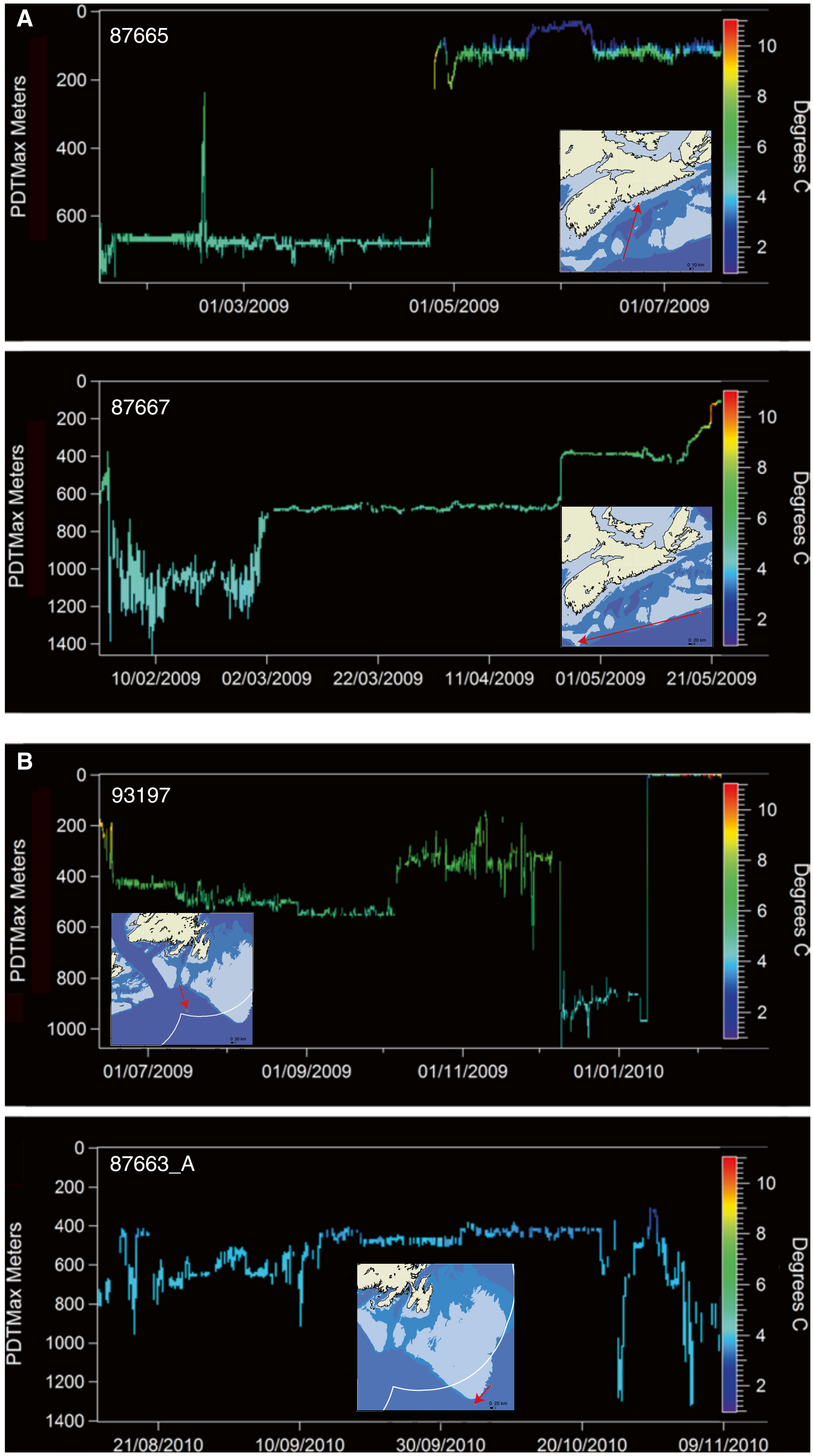
The depth–temperature profiles for individual halibut generally showed extended periods of time (i.e., several months) at a narrow depth range, with relatively abrupt transitions to an extended period at a very different depth (Fig. 2). Transition periods of <2 days for a change in depth exceeding 500 m were not uncommon. Many halibut seemed to spend the winter months at depths exceeding 600 m before moving to much shallower waters for the remainder of the year. The recovered tag showed much greater detail in the time course of the vertical excursions, but the overall pattern was similar to that observed in the satellite-transmitted summarized data.

Four of the tagged halibut appeared to move <25 km between the tagging and pop-off locations, despite being at liberty an average of more than 7 months. In the absence of a light-based track reconstruction, it was not possible to reconstruct the movements (if any) between the time of tagging and pop off. However, all four of the "non-migratory" halibut moved across a substantial depth gradient (a minimum range of 400–1,200 m) during their time at liberty, indicating either substantial movement up and down the continental slope, or on/off/along-shelf movement, or both. None of the four "non-migrants" travelled to the depths of <200 m, which would clearly characterize on-shelf habitat (Fig. 3). However, movement onto the shelf was not necessarily characteristic of migrating fish either; of the seven halibut that travelled a minimum distance of 100 km after tagging, three (43 %) never rose to depths shallower than 300 m. And of the remainder, most spent less than 10 % of their time at depths less than 200 m (e.g., Tag ID 87667 in Fig. 2, which travelled 500 km). Therefore, the "non-migrants" may or may not have travelled laterally as well as up and down the continental slope.

Depth varied much more within and across halibut than did temperature. The mean ± SE time-weighted depth (within a 6-h interval) of halibut was 580 ± 4 m (Fig. 4). Minimum and maximum depths were 0 and 1,640 m, respectively. Time-weighted temperature distributions tended to be much more uniform (Fig. 4), with an overall mean of 4.7 ± 0.01 °C, and a temperature range of 1.2–11.8 °C. Although there was some month-to-month variation in the number of fish and depth/temperature observations (range of 321–602 observations per month), frequency histograms that were inversely weighted by the number of monthly observations did not differ appreciably from those shown in Fig. 4.

Diel vertical migrations were not apparent in any of the halibut, either on an individual level or when aggregated across all fish. The mean within-day, noon versus midnight difference in maximum depth did not differ significantly from zero ($P > 0.05$). Nor was there any significant difference from zero in the mean within-day, 6 a.m. versus 6 p.m. difference in maximum depth. Therefore, if diel vertical

Fig. 2 Depth–temperature profiles (**a**) of individual halibut (Tag IDs 87665 and 87667; see Table 1 for details). *Inset* shows tagging and pop-off location. Depth–temperature profiles (**b**) of individual halibut (Tag IDs 93197 and 87663_A; see Table 1 for details). *Inset* shows tagging and pop-off location



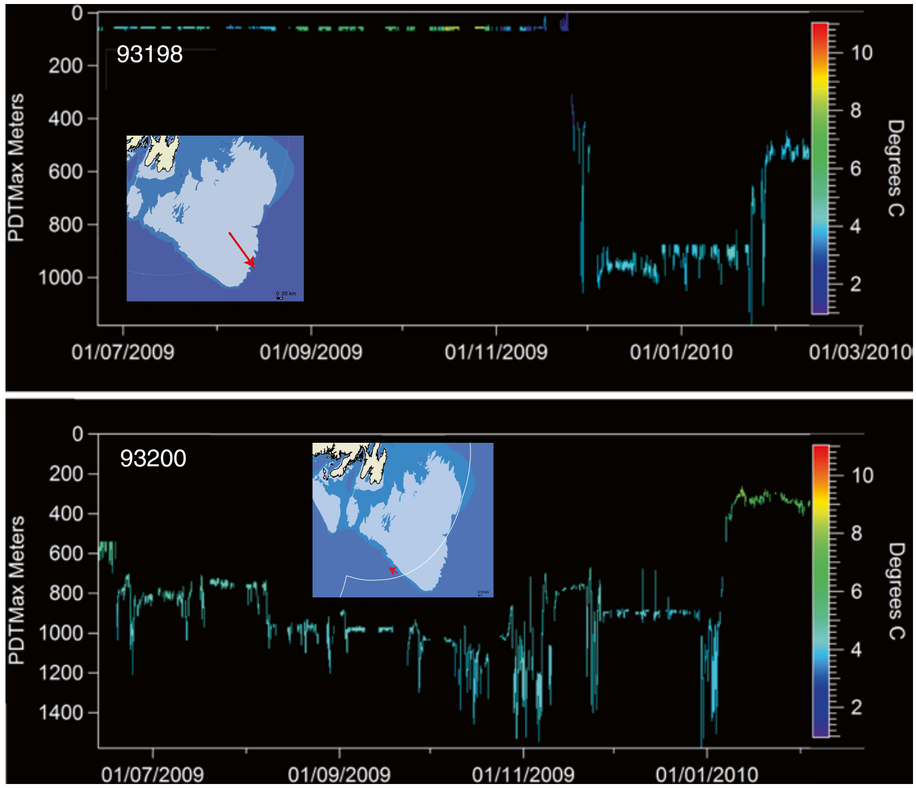


Fig. 3 Depth–temperature profile of two halibut tagged on the Grand Banks, one of which moved at least 71 km between tagging and pop off (Tag ID 93198), and the second of which was caught relatively close to the tagging location (Tag ID 93200). Based on possible spawning rises, both halibut appear to have spawned while in water depths >800 m during December

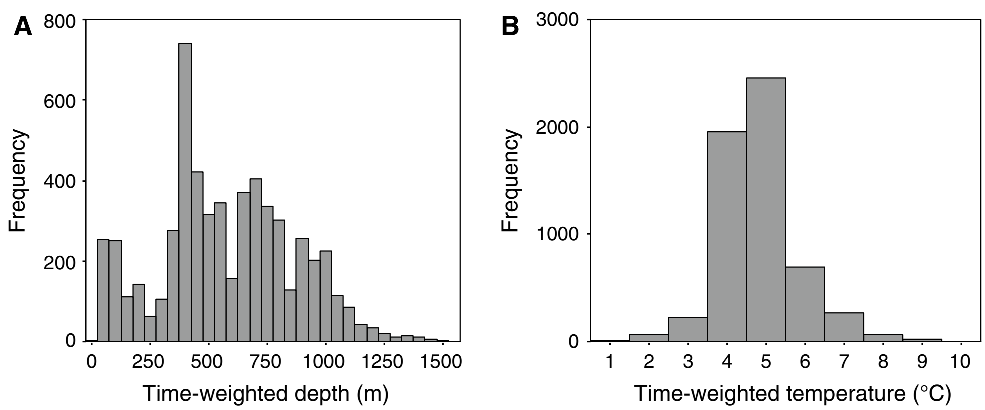


Fig. 4 Frequency histograms at 6-h intervals of time-weighted depths (**a**) and temperatures (**b**) occupied by tagged Atlantic halibut

migrations were taking place, either in the water column or along a sloped bottom, we could not detect them.

A seasonal pattern in depths and temperatures was clearly evident (Fig. 5), and both variables differed significantly across months (ANOVA, $P < 0.001$). Since not all tags reported data for all months, monthly means (of individual readings) were based on variable numbers of tagged halibut (range of 4–11 fish), with April and May being represented by the fewest tags. Mean monthly time-weighted depths varied by up to 500 m across the year, with April to June being the only months where mean depth was shallower than 500 m. Mean time-weighted depths were greatest in December. Mean monthly time-weighted temperatures ranged between 4.8 and 5.1 °C in the first half of the year, dropping to 4.4–4.7 °C in the latter half of the year, with temperature maxima occurring in February and March (Fig. 5).

Since there was no definitive test for spawning rises in Atlantic halibut and since the PSAT tags do not differentiate between vertical movement through the water column and vertical ascent along a bathymetric slope, we developed a working assumption that spawning rises would be evident as vertical ascents (defined as the difference between maximum and minimum depths) of at least 25 m from an otherwise consistent baseline depth within a single 6-h interval. We also felt it important to attempt to identify

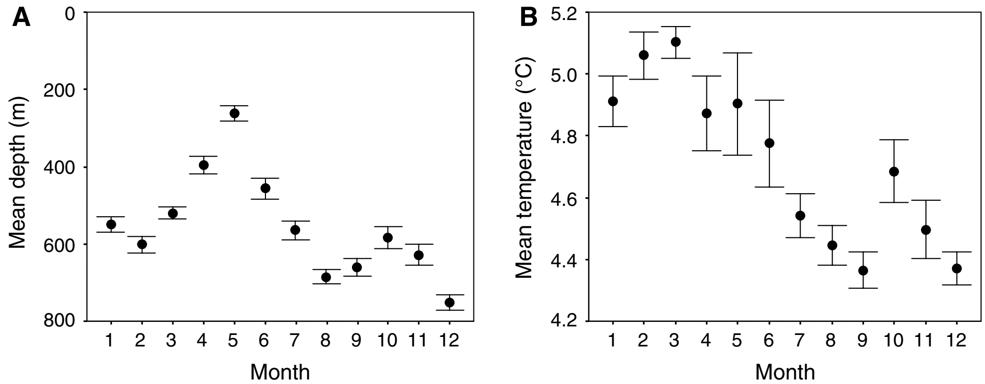


Fig. 5 Monthly patterns (mean of individual readings ± 95 % CI) in depth (m) and temperature (°C) occupied by tagged Atlantic halibut. Each month was represented by data from 4 to 11 halibut

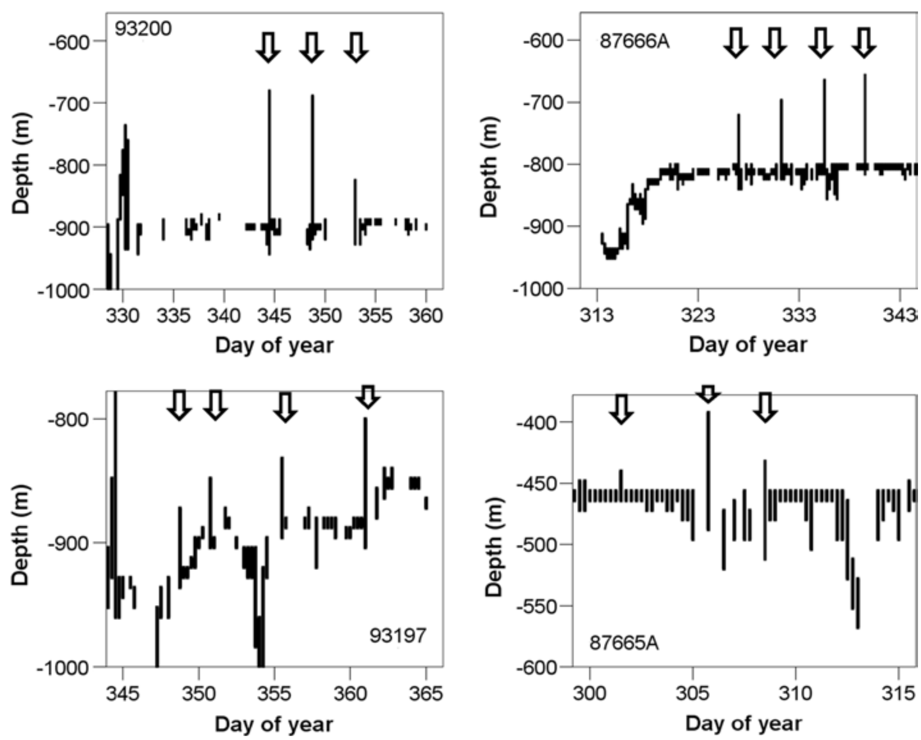


Fig. 6 Range plots from halibut PSAT tags showing possible spawning rises. *Bars* represent minimum and maximum depths occupied within each 6-h time interval. Possible spawning rises (*arrowed*) are visible as individual vertical excursions >25 m at 3- to 6-day intervals. PSAT tag numbers are indicated

spawning rises in our data without reference to the specific characteristics of spawning rises reported for Pacific halibut to prevent predetermining our expectations. Small-scale depth changes were commonplace; on average, halibut changed their depth by 42 m within each 6-h time interval. The magnitude of these vertical ascents/descents increased significantly with depth ($P < 0.05$), reaching mean within-interval ascent/descent values >200 m at depths exceeding 1,000 m. Several halibut displayed multiple short-term vertical ascents that appeared to be spawning rises, in that they occurred from a depth which had changed very little over several consecutive 6-h intervals. The most obvious example was visible in Tag 87666A, where four vertical excursions exceeding 100 m were visible in November and December (Fig. 6). The putative spawning rises occurred at 4- to 5-day intervals from a baseline depth of around 800 m. No other comparable vertical ascents were evident in the 3-month record from this fish, which was tagged and popped off near the mouth of the Laurentian Channel.

Other examples of possible spawning rises were less clear-cut than that of Tag 87666A, but all appeared to show consistent patterns in timing, vertical extent, and location (Table 2; Fig. 6). All of the presumed spawning rises occurred in multiples of 2–6 events at 2- to 9-day intervals between October and January. Each potential spawning rise spanned an average vertical extent of 50–100 m,

Table 2 Possible spawning rises detected in depth records from PSAT-tagged Atlantic halibut

Argos PTT	Location	Number of rises	Vertical extent (m)	Baseline depth (m)	Month of rises	Inter-rise interval (days)
67739	edge GB	2	70–80	770	December	5
93196	HC	3	100–130	1,050	November–December	4–9
93197	HC-offshore	5	50–70	900	December	2–5
93200	edge GB	3	80–180	900	December	4–5
93198	GB and edge	1	60	900	January	
		5	50	550	January–February	2–6
87665A	edge GB	2	40–50	360	October	3
		3	25–80	450	November	3–5
87666A	LC	4	100	800	November–December	4–5

Locations: *GB* Grand Banks, *HC* Halibut Channel, *LC* Laurentian Channel

and two-thirds of the events occurred at depths exceeding 770 m. All appeared to occur at the edge of the southern Grand Banks (starred symbols of Fig. 1).

In all cases for which the appropriate months were monitored, the period following the presumed spawning was followed by a rapid rise to shallower depths (400–500 m) in January–February, both among halibut that had moved long distances after tagging and those that showed little net displacement (Fig. 3).

Recovered tag 87663 provided high-resolution depth data that were analyzed in more detail for the evidence of spawning rises, despite the fact that the period covered (February–October) did not include the spawning period identified in the other halibut (Table 2). Using a linear filter of the time series, there were seven instances where the apparent speed of ascent was greater than 2.5 m s^{-1} in a 50-s window, all occurring at depths ranging from 640 to 860 m. However, none of the ascents were followed by rapid descents, suggesting that these movements were along the sea floor and probably not spawning rises.

Discussion

Atlantic halibut are known to be capable of long-distance migrations, but most tagging studies using conventional tags have reported either local movements, or a suggestion of strong seasonal homing behavior (Haug 1990; Trumble et al. 1993). A large-scale conventional tagging study of both juvenile and adult halibut off the eastern coast of Canada reported net movements of up to 3,100 km, but the median net movement across 368 recaptures was only 27 km (den Heyer et al. 2013). Earlier studies in the same area also reported movements usually limited to <200 km (McCracken 1958; Kohler 1964; Godø and Haug 1988b; Stobo et al. 1988), albeit with some suggestion of a net movement from the Scotian Shelf to the Grand Banks and other locations in the northeast. Closer to the southern extent of its range, in US waters, many tagged juvenile halibut moved somewhat greater distances to the northeast. Kanwit (2007) reported that 28 % moved distances of up to 1,800 km into Canadian waters, including onto the eastern Scotian Shelf, Gulf of St. Lawrence, and Grand Banks. Similarly, juvenile halibut tagged on Browns Bank travelled up to 1,100 km to the eastern Scotian Shelf and Grand Banks (Jensen and Wise 1961), although many of those tagged earlier in similar locations were recaptured within 50 km of the tagging location (Wise and Jensen 1959). The possibility that all of these conventional tagging results were biased by the spatial and seasonal distribution of the fishery, and hence the likelihood of tag recovery, cannot be ignored. Since PSAT tags transmit their pop-off location to a satellite, and do not require the recapture of the fish, their net movement transmissions are unbiased by the presence or absence of fishermen. Nevertheless, our results using PSAT tags were consistent with the earlier reports, indicating that most of the tagged adult halibut did not stray more than 120 km from their tagging location, at least in terms of net displacement. Similar results in terms of net movement have been reported for Pacific halibut, albeit with evidence of seasonality and differences between juveniles and adults (Loher 2008). Since PSAT tags were not applied to juvenile halibut in our study, our results pertain only to adults. However, a large-scale conventional tagging study of the same population reported no obvious difference between juvenile and adult movements (den Heyer et al. 2012).

There were strong indications of seasonal movements onto and off the continental shelf, whereby many of the presumably mature halibut tagged in this study spent the May–October period in shallower waters of the continental shelf, and the November–April period around or on the continental slope. In many cases, PSAT tags that were programmed to release about 1 year after tagging popped off relatively close to the tagging site; if these results had been based on conventional tags, it would have suggested either residency in the tagging area or some form of homing behavior, as has been reported both in the northwest Atlantic (Godø and Haug 1988b; Stobo et al. 1988) and the northeast Atlantic (Devold 1938; Godø and Haug 1988a). However, the depth records recorded in the PSAT allow for better discrimination of the two alternatives and clearly show that the halibut must have moved between the time of tagging and pop-up, even if only over a substantial depth gradient on the continental slope. Indeed, there were no instances where a halibut remained resident at a particular location and depth throughout the tagging record. In the absence of a light-based track reconstruction, it was not possible to determine whether a shift to shallower depths by a tagged fish that showed little net movement between tagging and pop off also corresponded with a movement onto the shelf. However, the most likely explanation for all of the results is that the summer period on the shelf represents a foraging period, while the fall/winter period is associated with a return migration to the spawning grounds (Haug 1990). Based on the studies off Norway, Godø and Haug (1988a) suggested that very young halibut remained close to their nursery grounds, juveniles (age 6 +) tended to move widely and somewhat indiscriminantly, and adults engaged in seasonal onshore–offshore movements to and from the spawning grounds on the continental slope. Atlantic halibut appear to undertake a similar pattern in the northwest Atlantic (McCracken 1958; Godø and Haug 1988b; Stobo et al. 1988), as do the much-better studied Pacific halibut (Skud 1977; Loher 2008).

Despite the likelihood of seasonal migrations between foraging and spawning grounds, there was little evidence of wide geographic separation between foraging and spawning grounds; indeed, the halibut tagged in this study appeared somewhat more likely to forage in deepwaters along the continental slope as to venture further afield onto the continental shelf. Recapture close to the tagging location has been widely reported for Atlantic halibut (Devold 1938; Godø and Haug 1988a, b; Stobo et al. 1988), much as it has for some other marine fishes (Robichaud and Rose 2001). The results of this study shed only partial light on the question of whether this behavior represents year-long residency or annual homing. Of the halibut identified as potential spawners, roughly half remained deeper than 300 m at all times of the year, apparently never venturing completely onto the shelf, with no distinction between migrants and non-migrants. In addition, the tags of the spawners popped off anywhere between 2 and 350 km from the tagging site, indicating that the full range of migration distances was represented. And although all spawners clearly moved across a substantial depth gradient through the year, the continental slope off the Grand Banks can vary across a depth range of 200–1,400 m in as little as 25–50 km. Therefore, it was not possible to rule out the possibility that some of the spawning halibut remained localized in their movements between foraging and spawning grounds, although some spawners clearly travelled long distances along the slope without straying onto the shelf.

Skud (1977) suggested that the extensive southward movement of juvenile Pacific halibut compensated for the northward drift of eggs and larvae, thus maintaining stock integrity. In the absence of significant collections of halibut ichthyoplankton in the Atlantic, the hypothesis of a compensatory juvenile return migration cannot be tested, although it does seem to have been broadly accepted on both sides of the Atlantic (Stobo et al. 1988; Haug 1990; Kanwit 2007). The absence of tag pop offs over abyssal waters was consistent with the idea of a spawning location over the slope area typically associated with Atlantic and Pacific halibut spawning (Trumble et al. 1993). On the other hand, trans-Atlantic movements have been reported previously for Atlantic halibut, indicating that abyssal waters are not necessarily an impediment to halibut movements (Godø and Haug 1988b; den Heyer et al. 2012).

Previous reports of depth and temperature associations by Atlantic halibut have been based on trawl catches and thus reflect the limitations of fishing activity. Our results indicate that most of the adult halibut spent their time at depths of 400–1,000 m and temperatures of 4–6 °C, although extremes of 1,640 m and 1.2 °C were recorded. Diel vertical migrations were not apparent, presumably due to the minimal light levels at such depths (Campana et al. 2011). The depth and temperature associations were largely consistent with the temperature ranges of 3.5–8 °C reported elsewhere in the Atlantic (McCracken 1958; Haug 1990; Trumble et al. 1993), but somewhat deeper than the 300–700 m depth range associated with trawl catches (Devold 1938; Jakupsstovu and Haug 1986; Trumble et al. 1993; Sigourney et al. 2006). Undoubtedly, the deeper habitat revealed in this study reflects the rarity of trawl catches deeper than 700 m and one of the advantages of PSAT tagging. Pacific halibut tagged with PSAT tags appear to occupy significantly shallower and slightly warmer waters, with median depths of 300–400 m and 5–7 °C, and maximum depths of around 700 m (Loher and Seitz 2006; Loher and Blood 2009) in areas other than the Bering Sea, where maximum depths range to 844 m (Seitz et al. 2011). In both halibut species, summer depths are substantially shallower than winter depths, presumably reflecting foraging and spawning grounds, respectively, although seasonal temperature fluctuations were far more subtle (this study; Loher and Blood 2009).

The identification of presumed spawning rises in seven of the large halibut is an exciting result of this study, since it provides the first direct evidence of spawning activity in Atlantic halibut. Spawning rises in various flatfish species were first observed by scuba divers, leading Seitz et al. (2005) to hypothesize that similar spawning behavior might also occur in Pacific halibut. Indeed, spawning rises described as seven sequential vertical ascents at intervals of about 5 days were later identified in a single recovered archival tag from a Pacific halibut (Seitz et al. 2005). Loher and Seitz (2008) subsequently used detailed archival data to identify 10 additional Pacific halibut showing regular, repeated spawning rises. Each series consisted of 6–10 individual rises separated by intervals of about 4 days. Each rise spanned a vertical range of about 168 m, initiated at a mean depth of 422 m. All rises took place offshore between late December and March (Loher and Seitz 2008). These rise characteristics for Pacific halibut are remarkably similar to those we identified in Atlantic halibut, even though the details differ. The series we identified occurred in multiples of 2–6 events at 2- to 9-day intervals between October and January, spanning an average vertical extent of 50–100 m at depths of about 800–1,000 m. Although there is no definitive evidence that the vertical ascents represent spawning rises, as opposed to feeding events, the fact that the rises were not evident on the continental shelf or at other times of the year suggests that they were indeed associated with spawning. Atlantic halibut are known to be group synchronous spawners with intermittent spawning; only a proportion of the eggs become hydrated and are released at any one time (Trumble et al. 1993). In addition, experiments on halibut spawning in captivity indicated that they released eggs at more or less regular intervals throughout the spawning season (Haug 1990), with a hydration cycle for the ova lasting about 2 days (Finn et al. 2002). Thus, the presumed spawning rises would be completely consistent with the known reproductive physiology of halibut.

Spawning locations and times have never been definitely identified for Atlantic halibut, but our results indicating a November–January spawning period in 800–1,000 m of water are somewhat different than expectations. Observations of fish captured in spawning condition by otter trawls had suggested that they spawn in winter and spring in deepwater on the continental slope (Haug 1990; Trumble et al. 1993). Deepwater trawl captures off Norway, and the Faroe Islands suggested that mature halibut congregated to spawn in January and February on the continental slope below 700 m (Jakupsstovu and Haug 1986), or in deep fjords (300–700 m) with soft mud or clay bottoms from October onwards (Devold 1938); spawning had apparently finished by April, at which point the halibut migrated to shallow feeding grounds. Based on trawl captures of spent fish, McCracken (1958) speculated that spawning took place in winter and early spring at depths of about 200 m on the Scotian Shelf, and even later in the Gulf of St. Lawrence. However, our results suggest that spawning takes place much earlier than these reports indicate. At first glance, spawning in November and December would seem to be inconsistent with the other studies. However, if spawning does indeed take place at depths between about 800–1,000 m, it is not surprising that trawl captures could provide a misleading perception of spawning time, since few halibut fishermen trawl at such depths. In the only comprehensive, seasonal examination of halibut gonads, Neilson et al. (1993) concluded—as we did—that peak spawning for halibut on the Scotian Shelf took place in November and December. And although the early work of Devold (1938) is often summarized as reporting winter/spring spawning, he actually reports that many halibut spawn off Norway in November and are spent by Christmas. Devold also notes Norwegian fishermen who are well known for landing ripe halibut every year around Christmas, while a January tagging study had both spent and ripe and running halibut on deck in January. Thus, it appears that a November–January spawning period in 800–1,000 m of water would explain many of the previous observations in the northwest Atlantic, if not the northeast Atlantic.

Skud's (1977) hypothesis that Pacific halibut juveniles in Alaskan waters migrate to the southeast to compensate for the northwestward drift of the pelagic eggs and larvae is conceptually appealing, and has often been invoked to explain Atlantic halibut movements, despite the absence of supporting evidence. It is interesting then to test the predictions of the conceptual model against our study results, which suggest that halibut spawn at a depth of about 900 m on the southern slope of the Grand Banks. Halibut eggs have been reported to be neutrally buoyant at salinities of 33.8–35.0 ‰ (Trumble et al. 1993), although Haug (1990) reported that Atlantic halibut eggs may rise for 2–4 days after hatch before reaching a neutral density. Salinity on the continental slope south of Newfoundland is around 34.8 ‰ at depths of 500–1,000 m (Pickart and Smethie 1998), suggesting that prevailing currents at that depth are appropriate for modelling egg and larval drift. The major subthermocline current in the slopewater is the deepwater boundary current (DWBC), which transports water of northern origin toward the south, roughly paralleling the edge of the continental shelf (Pickart et al. 1999). Current velocity at a depth of 900 m is around 2–3 cm s^{-1}. Atlantic halibut eggs hatch after about 18 days at 5 °C (which is the temperature characteristic of a depth of 900 m), but remain pelagic for 6–7 months (Trumble et al. 1993). Thus, the expected drift of the eggs and larvae would be about 300–500 km to the southwest after 6 months. Current velocity at 500 m declines slightly from that at 900 m (Pickart and Smethie 1998), suggesting that slight positive buoyancy of the eggs would not be likely to increase the rate of drift. Similarly, Loder et al. (2001) report that current speeds at a depth of 400–500 m off the edge of the central Scotian Shelf are comparable to those off the Grand Banks, although current velocities increase above 400 m as the Labrador Current takes effect. Using these values as guides, it appears that halibut eggs spawned on the slope south of the Grand Banks would indeed drift toward the center of concentration on the Scotian Shelf, although a drift of 300–500 km would likely not be sufficient to take the progeny as far south as the Browns Bank area implicated as a halibut nursery by Neilson et al. (1993). On the other hand, entrainment in the shallower, faster Labrador Current (which also parallels the edge of the continental shelf) would certainly increase the drift distance. In addition, a significant component of the DWBC penetrates the bottom waters of the Laurentian Channel leading into the Gulf of St. Lawrence (Han et al. 1999), thus providing a possible spawning source for halibut living in the Gulf of St. Lawrence. Under Skud's (1977) hypothesis, juvenile halibut migration in the northwest Atlantic should be oriented to compensate for the southwesterly drift of the larvae, which it is, at least on the Scotian Shelf (Stobo et al. 1988). Therefore, the location of the presumed spawning grounds is consistent with expectations based on Skud's (1977) migration compensation theory, the migratory patterns of the juveniles, the relatively static distribution of the adults off southern Newfoundland, and the prevailing currents at depth. However, a proper test of this hypothesis would require ichthyoplankton collections at depths of 500–1,000 m along the slope edge, as well as some numerical advection modelling (sensu Brickman et al. 2007).

Acknowledgments This work was funded by the Department of Fisheries and Oceans International Governance Strategic Funding and the Atlantic Halibut Council. The authors acknowledge and appreciate the support of commercial halibut fishermen Frank Reyno and Andrew Locke for successfully deploying the tags. Warren Joyce and Anna MacDonnell provided expert technical assistance. We also thank Dave Brickman for helpful perspectives on the deepwater circulation patterns. Andrew Seitz, David Righton, and two anonymous reviewers provided helpful comments on the manuscript.

References

Armsworthy SL, Campana SE (2010) Age determination, bomb-radiocarbon validation and growth of Atlantic halibut (*Hippoglossus hippoglossus*) from the Northwest Atlantic. Environ Biol Fishes 89:279–295

Block BA, Dewar H, Blackwell SB, Williams TD, Prince ED et al (2001) Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. Science 293:1310–1314

Bowering WR (1986) The distribution, age and growth and sexual maturity of Atlantic halibut (*Hippoglossus hippoglossus*) in the Newfoundland and Labrador area of the Northwest Atlantic. Can Tech Rep Fish Aquat Sci 1432:34p

Brickman D, Marteinsdottir G, Logemann K, Harms IH (2007) Drift probabilities for Icelandic cod larvae. ICES J Mar Sci 64:49–59

Campana SE, Dorey A, Fowler M, Joyce W, Wang Z, Wright D (2011) Migration pathways, behavioural thermoregulation and overwintering grounds of blue sharks in the Northwest Atlantic. PLoS ONE 6(2):e16854. doi:10.1371/journal.pone.0016854

den Heyer CE, Armsworthy A, Wilson S, Wilson G, Bajona L, Bond S, Trzcinski MK (2012) Atlantic halibut all-sizes tagging program summary report for 2006 to 2011. Can Tech Rep Fish Aquat Sci 2992:vii+34p

den Heyer CE, Schwarz CJ, Trzcinski MK (2013) Fishing and natural mortality rates of Atlantic halibut estimated from multiyear tagging and life history. Trans Am Fish Soc 142:690–702

Devold F (1938) The North Atlantic halibut and net fishing. Fiskeri Dir Skr Ser Havundersr 5:1–47

Finn RN, Ostby GC, Norberg B, Fyhn HJ (2002) In vivo oocyte hydration in Atlantic halibut (*Hippoglossus hippoglossus*); proteolytic liberation of free amino acids, and ion transport, are driving forces for osmotic water influx. J Exp Biol 205:211–224

Godø OR, Haug T (1988a) Tagging and recapture of Atlantic halibut (*Hippoglossus hippoglossus*) in Norwegian waters. J Cons Int Explor Mer 44:169–179

Godø OR, Haug T (1988b) Tagging and recapture of Atlantic halibut (*Hippoglossus hippoglossus* L.) on the continental shelves off eastern Canada, and off western and eastern Greenland. J Northwest Atl Fish Sci 8:25–31

Han G, Loder JW, Smith PC (1999) Seasonal-mean hydrography and circulation in the Gulf of St Lawrence and on the eastern Scotian Shelf and southern Newfoundland shelves. J Phys Oceanogr 29:1279–1301

Haug T (1990) Biology of the Atlantic halibut, *Hippoglossus hippoglossus* (L. 1758). Adv Mar Biol 26:1–70

Jakupsstovu SH, Haug T (1986) Spawning of Atlantic halibut (*Hippoglossus hippoglossus*) in deep waters on the continental slope south west of the Faroe Islands. Frodskaparriti 34–35:76–90

Jensen AG, Wise JP (1961) Movement of tagged halibut off New England—II. Trans Am Fish Soc 90:489–490

Kanwit JK (2007) Tagging results from the 2000-2004 federal experimental fishery for Atlantic halibut (*Hippoglossus hippoglossus*) in the eastern Gulf of Maine. J Northwest Atl Fish Sci 38:37–42

Kohler AC (1964) Movements of halibut on the Nova Scotian and Grand Banks. J Fish Res Board Can 21:837–840

Loder JW, Shore JA, Hannah CG, Petrie BD (2001) Decadal-scale hydrographic and circulation variability in the Scotia-Maine region. Deep Sea Res Part II 48:3–35

Loher T (2008) Homing and summer feeding site fidelity of Pacific halibut (*Hippoglossus stenolepis*) in the Gulf of Alaska, established using satellite-transmitting archival tags. Fish Res 92:63–69

Loher T, Blood CL (2009) Seasonal dispersion of Pacific halibut (*Hippoglossus stenolepis*) summering off British Columbia and the US Pacific Northwest evaluated via satellite archival tagging. Can J Fish Aquat Sci 66:1409–1422

Loher T, Seitz A (2006) Seasonal migration and environmental conditions of Pacific halibut *Hippoglossus stenolepis*, elucidated from pop-up archival transmitting (PAT) tags. Mar Ecol Prog Ser 317:259–271

Loher T, Seitz AC (2008) Characterization of active spawning season and depth for eastern Pacific halibut (*Hippoglossus stenolepis*), and evidence of probable skipped spawning. J Northwest Atl Fish Sci 41:23–36

McCracken FD (1958) On the biology and fishery of the Canadian Atlantic halibut *Hippoglossus hippoglossus* L. J Fish Res Board Can 15:1269–1311

Neilson JD, Kearney JF, Perley P, Sampson H (1993) Reproductive biology of Atlantic halibut (*Hippoglossus hippoglossus*) in Canadian waters. Can J Fish Aquat Sci 50:551–563

Pickart RS, Smethie WM (1998) Temporal evolution of the deep western boundary current where it enters the sub-tropical domain. Deep Sea Res Part I 45:1053–1083

Pickart RS, McKee TK, Torres DJ, Harrington SA (1999) Mean structure and interannual variability of the slopewater system south of Newfoundland. J Phys Oceanogr 29:2541–2558

Robichaud D, Rose GA (2001) Multiyear homing of Atlantic cod to a spawning ground. Can J Fish Aquat Sci 58:2325–2329

Seitz AC, Norcross BL, Wilson D, Nielsen JL (2005) Identifying spawning behavior in Pacific halibut, *Hippoglossus stenolepis*, using electronic tags. Environ Biol Fishes 73:445–451

Seitz AC, Loher T, Norcross BL, Nielsen JL (2011) Dispersal and behavior of Pacific halibut *Hippoglossus stenolepis* in the Bering Sea and Aleutian Islands region. Aquat Biol 12:225–239

Sigourney DB, Ross MR, Brodziak J, Burnett J (2006) Length at age, sexual maturity and distribution of Atlantic halibut, *Hippoglossus hippoglossus*, off the Northeast USA. J Northwest Atl Fish Sci 36:81–90

Skud BE (1977) Drift, migration, and intermingling of Pacific halibut stocks. Inter Pac Halibut Comm Sci Rep 66:42 p

Stobo W, Neilson JD, Simpson P (1988) Movements of Atlantic halibut (*Hippoglossus hippoglossus*) in the Canadian North Atlantic: inference regarding life history. Can J Fish Aquat Sci 45:484–491

Trumble RJ, Neilson JD, Bowering WR, McCaughran DA (1993) Atlantic halibut (*Hippoglossus hippoglossus*) and Pacific halibut (*H. stenolepis*) and their North American Fisheries. Can Bull Fish Aquat Sci 227:84 p

Wise JP, Jensen AC (1959) Movement of tagged halibut off New England. Trans Am Fish Soc 88:357–358