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Periodic movements of Greenland turbot *Reinhardtius hippoglossoides* in the eastern Bering Sea and Aleutian Islands

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ABSTRACT

Understanding movement patterns of fish provides a context for making sound management decisions related to these populations; archival tags can provide this information. To better understand the depth-specific behavior of Greenland turbot *Reinhardtius hippoglossoides* in the Bering Sea and Aleutian Islands region, 297 temperature and depth recorders (archival tags) were implanted in fish between 2003 and 2011; 22 tags were subsequently recovered (18 with usable data). Tagged fish were at liberty from 19 to 1859 days, traveled straight line distances from 7.8–513.3 km, experienced mean temperatures from 3.23 to 3.70 °C, and occupied mean depths ranging from 448 to 753 m. Tagged Greenland turbot occupied their maximal depths during January and February, and their shallowest depths from July to September. Six tagged fish that were at liberty more than two years exhibited annual periodicity in depths occupied. Diel vertical migration (DVM, or 24 -h periodicity) was identified for 17 of 18 tagged Greenland turbot, ranging from 4.16 %–60.12 % of an individual fish's time-at-liberty. Activity levels (average rate of depth change and daily depth displacement) were relatively low in the summer and fall and highest in the winter. Four tagged females and no males occupied depths and temperatures consistent with the cold pool (< 2 °C) on the eastern Bering Sea Shelf (< 200 m). Fish at liberty for multiple years showed consistency in depths, activity, and DVM among years. Predictable movements of Greenland turbot in the Bering Sea and Aleutian Islands region may influence the availability and in turn catchability of this species to stock assessment surveys and should be considered by fishery managers.

1. Introduction

Fish can be highly mobile geographically and vertically within the water column. Movement and migration studies on commercially harvested fish species can elucidate seasonal, spawning, and feeding behaviors, and this information can provide a useful context for designing research studies, understanding changes in populations and stock structure, and making sound fishery management decisions (Bowler and Benton, 2005). However, it can be difficult and costly to observe fish movements and migrations, leaving knowledge gaps for many species.

Greenland halibut *Reinhardtius hippoglossoides,* hereafter referred to as Greenland turbot, is a commercially valuable flatfish species in Alaska (e.g., Fissel et al., 2016) with a broad distribution in the northern hemisphere. Greenland turbot in the North Pacific and North Atlantic oceans are considered the same species; however, there is evidence for genetic divergence at the subspecific level such as the population in the Bering Sea and Aleutian Islands (BSAI) (Fairbairn, 1981; Orlova et al., 2017). In the North Pacific Ocean, Greenland turbot spend their first 3–4 years on the continental shelf before moving to the continental slope (Alton et al., 1988; Sohn et al., 2010; Swartzman et al., 1992), and an absence of juveniles around the Aleutian Islands suggests that these adults originate from the Bering Shelf (Bryan et al., 2018). As they grow, larger more mature fish are believed to move towards deeper (> 100 m) and warmer (> 0 °C) waters, while smaller fish remain shallow and are found in colder waters (Bryan et al., 2018). Greenland turbot reach sizes of up to 120 cm and mature around 60–70 cm (Cooper et al., 2007). In the BSAI, Greenland turbot are primarily caught by longline and trawl fisheries; this species was heavily exploited in the 1970s, and more recently catches have declined substantially as a result of catch restrictions following perceived low recruitment (Bryan et al., 2018).

Although Greenland turbot is a flatfish, it is not uncommon for this species to be found in the water column (Merrett and Haedrich, 1997; Vollen and Albert, 2008). Unlike most flatfish, their left eye does not fully migrate to one side which provides a wider range of vision, they

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have well-developed muscles on both their dorsal and ventral sides (Alton et al., 1988), and their blind side is colored (Mecklenburg et al., 2002). These traits all suggest that this species is not confined to a benthic lifestyle. Additionally, the diets of Greenland turbot in the Atlantic Ocean often contain pelagic prey such as capelin *Mallotus villosus* and Atlantic herring *Clupea harengus*, with shifts in prey type in concordance with predator size (Hovde et al., 2002; Solmundsson, 2007); diets of conspecifics in the Bering Sea are dominated by walleye pollock *Gadus chalcogrammus*, unidentified fish, and squid (Bryan et al., 2018). Vertical longlines have been used to capture Greenland turbot throughout the water column, confirming this behavior in the Barents Sea (Vollen and Albert, 2008).

The use of archival tags can provide insight into habitat preferences, vertical and horizontal movements, and spawning behavior, all of which can have implications for effective and sustainable management of the species being observed (Ådlandsvik et al., 2007; Nichol and Somerton, 2002; Sippel et al., 2015). For example, archival tag data were used to infer the vertical migration and nest guarding behavior of Atka mackerel *Pleurogrammus monopterygius* (Nichol and Somerton, 2002), estimate the availability of Pacific cod *Gadus macrocephalus* to bottom trawls in Alaska waters (Nichol et al., 2007), and model horizontal movement pathways of northeast Arctic cod *Gadus morhua* in the Barents Sea (Ådlandsvik et al., 2007). Additionally, diel vertical migration (DVM), a behavior of daily vertical movement often associated with feeding (Neilson and Perry, 1990; Løkkeborg and Ferno, 1999; Nichol and Somerton, 2002), has been documented in deep dwelling species such as sablefish *Anoplopoma fimbria* (Goetz et al., 2018; Sigler and Echave, 2019) and large flatfish such as Pacific halibut *Hippoglossus stenolepis* (Scott et al., 2016). This common fish behavior has been categorized as type I, daily migration that is shallower during nighttime, and type II (i.e., reverse), daily migration that is shallower during daytime (Neilson and Perry, 1990; Nichol et al., 2013).

Vertical movements of Greenland turbot have been well documented in the northern Atlantic Ocean using archival tags (Boje et al., 2014; Peklova et al., 2012). Greenland turbot associated with a glacial fjord along the western coast of Greenland displayed rapid vertical movements, occupied waters ranging from 0 to 4 °C, and underwent a seasonal migration, moving into deeper waters in winter months (Boje et al., 2014). Conversely, Greenland turbot in Cumberland Sound (eastern Baffin Island, Canada) were found to go deeper during the ice-free season (mean depth of 1048 m) compared to the ice-covered season (mean depth of 823 m) occupying temperatures from 1.3 to 2.7 °C (Peklova et al., 2012). Greenland turbot regularly travel hundreds of meters off the seafloor and into the pelagic zone of the Barents Sea, where the most vertical displacement and movement frequency occurs in September and the lowest in February (Vollen and Albert, 2008). Behaviorally, Greenland turbot can spend upwards of 20 % of their time in the pelagic zone, and this has the potential to reduce accuracy of bottom survey indices of abundance (Albert et al., 2011). To date, movements of Greenland turbot into the water column have not been investigated in the BSAI.

Greenland turbot movements have been well researched for stocks in the northern Atlantic Ocean, but comparatively little is known about conspecifics in the northern Pacific Ocean. To expand our understanding of the behavior and ecology of Greenland turbot in the BSAI, archival tags were implanted in individuals in this region. The objectives of this study were to 1) describe horizontal movements between Greenland turbot release and recapture locations, 2) characterize the temperatures and depths inhabited by Greenland turbot while at liberty in the BSAI, and 3) analyze depth-specific periodic behaviors (patterns of depth occupation related to environmental cues) at diel and seasonal scales using signal processing techniques. Although archival tagging studies are limited by the number of tags physically recovered, the results of this multi-year Greenland turbot tagging program in the BSAI region describes information not yet reported for this species in Alaska and provides an ecological context to managers of this stock.

2. Materials and methods

2.1. Data collection

From 2003–2011, Greenland turbot were tagged during the National Marine Fisheries Service Alaska Fisheries Science Center longline survey in the BSAI. Sampling was conducted aboard chartered fishing vessels, and stations covered depths from 150 to 1000 m along the continental shelf break. In the BSAI, longline survey sampling alternates between the Bering Sea (odd years) and the Aleutian Islands (even years). Longline sets consisted of 80 (Aleutian Islands) or 90 (Bering Sea) units of gear (generally referred to as a skate) with each containing 45 size 13/0 circle hooks on 0.4-m gangions spaced 2 m apart. Hooks baited with squid were allowed to soak from 3 to 5 h (Lunsford et al., 2018). Greenland turbot caught in good condition and longer than 50 cm (total length) were gently removed from hooks and placed in a live tank prior to tagging. A total of 297 archival tags were implanted in Greenland turbot between 2003 and 2011; each fish was also tagged with an external spaghetti tag through the right side operculum to identify the internal tag.

Tags were later recovered by commercial fishing vessels (trawl or longline). Lengths, weights, and sex were recorded for some but not all recoveries. The release and recapture locations of each Greenland turbot were the only known locations for the entire period at liberty, providing a straight-line distance (calculated as the great circle distance between these points) of movement as a minimum distance travelled.

2.2. Archival tags

Greenland turbot were internally implanted with Lotek archival tags (Lotek Wireless, Inc., Newmarket, Canada). The model varied by year as follows: in 2003 model LTD-1250 was used, from 2005 to 2008 model LTD-1300 was used, and in 2011 model LAT-2800 was used. The tag, surgical site, and tools were disinfected using 3% betadine. Using a scalpel, a 2-cm long incision was made in the abdominal wall of the right side of the fish through which the tag was inserted into the body cavity. The incision was closed using surgical staples. Fish were then released in close proximity to the site of capture.

2.3. Processing of archival tag data

Recovered tags were sent to Lotek for downloading of the raw data, and all data were subsequently processed in R (R Core Team, 2019). To allow for acclimation of tagged fish post-implantation, the first seven days of data recorded were removed prior to further analysis. In addition to temperature and depth, two derived variables were calculated to characterize daily vertical movement: the first was the rate of vertical displacement (hereafter referred to as activity), which is the change in depth in meters over each time step (m min^{-1}), and the second was daily depth displacement, which is the difference between the minimum and maximum depth (m) over a calendar day. Sunset and sunrise were determined using the R package *suncalc* (Thieurmel and Elmarhraoui, 2019), with the average latitude and longitude from release and recovery sites used as the location for each fish. Seasonal trends were identified by calculating and summarizing the daily mean temperature, mean depth, mean activity rate, and depth displacement. Seasons were designated as winter (December–February), spring (March–May), summer (June–August), and fall (September–November).

Temperature and depth were additionally used to assess whether tagged Greenland turbot were utilizing the cold pool, a known physical oceanographic feature which we will define as water with a temperature of less than 2 °C on the continental shelf or less than 200-m depth (e.g., Stabeno et al., 2012). Water temperatures in the Bering Sea are cooler in the winter and spring, when sea ice reaches near the Bering Slope (Stabeno et al., 2017). Following sea-ice breakup, cold, dense

Table 1
Summary of sampling data from Greenland turbot *Reinhardtius hippoglossoides* recaptured with archival tags in the Bering Sea and Aleutian Islands, showing tag number (ID), sampling interval of data in minutes (Interval), date of tagging/release (Release), number of days the tagged fish was at liberty (Liberty), and fish total length in cm (TL) shown in the form (release TL, recapture TL). Means, and ranges are shown for temperature in °C (Temp) and depth in meters (Depth).

ID	Interval	Release	Liberty	TL	Sex	Temp	Depth
5282	15	6/4/2003	1101	88, 92	F	3.39 (1.39–7.52)[a]	489 (0–1500)[b]
5385	15	6/4/2003	1147	70, 70	M	3.61 (2.06–7.77)	528 (10–1481)[b]
5319	15	6/6/2003	397	67, 68	M	3.33 (2.17–4.07)	709 (53–1438)[b]
5364	15	6/9/2003	408	67, 68	M	3.39 (1.81–4.14)	690 (156–1489)[b]
4122	15	6/10/2003	394	73, 74	M	3.57 (2.31–5.23)	553 (67–1362)
5334	15	6/13/2003	404	69, –	–	3.60 (2.50–4.37)	547 (266–1251)
4126	15	6/15/2003	354	70, 68	M	3.59 (2.05–4.89)	563 (116–1288)[b]
4542	4	6/3/2005	19	86, 85	F	3.49 (3.12–3.68)	624 (516–888)
4551	4	6/4/2005	762	85, 89	F	3.31 (1.60–4.08)[a]	521 (96–1187)
2466	4	6/3/2007	31	79, 81	F	3.54 (3.26–3.96)	629 (402–786)
3883	4	6/6/2008	817	73, 71	M	3.47 (1.89–4.95)	577 (44–1887)
3880	4	6/7/2008	795[c]	94, 94	–	3.32 (1.95–4.21)	753 (279–1906)
387	1	5/30/2011	35	79, –	–	3.66 (3.46–3.84)	550 (396–693)
403	1	5/30/2011	44	68, 70	M	3.60 (2.90–3.84)	580 (398–1011)
390	1	5/30/2011	56	70, 71	F	3.70 (3.54–3.82)	461 (260–620)
386	1	5/30/2011	400	68, 71	F	3.23 (0.90–3.88)[a]	448 (0–971)
406	1	5/30/2011	1176[c]	71, 72	F	3.43 (2.04–5.24)	626 (12–1589)[b]
383	1	5/30/2011	1859[c]	84, –	F	3.56 (0.90–3.96)[a]	565 (4–1502)[b]

[a] Indicates that cold temperatures occurred at depths consistent with the cold pool on the continental shelf.
[b] Indicates that recorded depth reached a maximum value, and actual maximum depth is likely deeper.
[c] Indicates that the archival tag stopped working before the fish was recaptured.

meltwater leads to the formation of the subsurface cold pool on the Bering Shelf, while surface waters begin to warm throughout the summer (Stabeno et al., 2012, 2017). Deeper waters on the continental slope maintain a relatively constant temperature that can be cooler relative to surface waters in the summer and warmer relative to surface waters in the winter (Stabeno et al., 2012, 2017).

2.4. Depth-specific periodic behaviors

A wavelet analysis was conducted to investigate depth-specific periodic movements of Greenland turbot by decomposing time-varying depth into a series of wavelets, also known as a wavelet transform (Torrence and Compo, 1998). The decomposition of time-frequency signals requires a trade-off between time and frequency resolution which can be optimized using a wavelet transform; wavelets can have high time resolution at high frequency (greater variance) and low time resolution at low frequency (less variance) (Cazelles et al., 2008). The Morlet wavelet was chosen to balance the time and frequency resolution, and a non-dimensional frequency (i.e., the number of oscillations within the wavelet) of $\omega_0 = 6$ was used (Cazelles et al., 2008; Torrence and Compo, 1998). To make the analysis more efficient and depth data more comparable from all tags, prior to wavelet analysis, raw temperature-depth data sampled at 1-minute intervals were subsampled to every 15 min, 4-minute intervals were subsampled to every 16 min, and 15-minute intervals were left at that frequency. Each time series was detrended with a LOESS span equivalent of five days to remove stochastic and seasonal trends in the depths occupied while preserving trends of interest (i.e., diel) (Roesch and Schmidbauer, 2018). Additional span sizes of three and seven days were also explored, but results were not sensitive to this change, and thus five days was selected.

To test the null hypothesis of no depth-specific periodicity by Greenland turbot, significance was assessed against a null model created from 2000 simulated time series for each archival tag. Resampling of the observed data was based on a Markov process which preserves the temporal pattern and short time correlation from the original time series (Cazelles and Stone, 2003); this was conducted in R using an adaptation of the *surrogate.ts* function from the R package *synchrony* (Gouhier and Guichard, 2014). A probability transition matrix was built from the observed depths, assuming that the depth at each time step was dependent only upon the depth at the previous time. Depth bins were set to 25-m. Non-random vertical movement (i.e., periodicity) was identified by power spectra values that were greater than the 95 % confidence interval established by the simulated null distribution. Wavelet analysis was carried out in R using modified functions from the package *WaveletComp* (Roesch and Schmidbauer, 2018).

Results from the wavelet analysis were examined at global, local, and scale-averaged forms. Global wavelet power spectra identify the dominant periods present in the depth data for the entire time series. Local wavelet power spectra identify the time-varying dominant periods of depth movement. To correct a bias that underestimates high-frequencies (short periods) present in the raw signal, the raw energy values of the local wavelet power spectra were divided by the scale with which they were associated following Liu et al. (2007). If the global wavelet power spectrum identified 24 h as a significant period, a scale-averaged wavelet spectrum in the range between 22 and 26 h was compared with the null distribution to determine time periods when daily movement was significant; this was considered indicative of DVM.

When Greenland turbot DVM was identified, this behavior was summarized. The overall percentage of DVM for each individual was calculated as the number of records identified with significant DVM divided by the total number of records. For each complete day of data from all fish, the daily percentage of DVM was calculated and cumulatively summarized by month. For each Greenland turbot that exhibited significant DVM for an entire calendar day, the daily mean depth, minimum depth (top of DVM), and maximum depth (bottom of DVM) were determined and associated temperatures and timestamps were extracted. Using this information, monthly summaries were used to examine how DVM varied with the season. Changes in the time of day at the top and bottom of DVM movements was used to interpret changes in DVM type: shallower during the night, type I, and shallower during the day, type II (Neilson and Perry, 1990; Nichol et al., 2013). Monthly mean time of day at the top and bottom of DVM movements was estimated using bootstrap resampling (n = 5000 each month) assuming a von Mises distribution (i.e., a circular normal distribution) in the R package *circular* (Agostinelli and Lund, 2017).

Inter-annual variability of depth-related behavior was examined for Greenland turbot that were at liberty for two or more years (n = 6, Table 1). Daily mean values for temperature (°C), depth (m), and activity (m min^{-1}) were determined for each full day of archival tag records. Additionally, the total daily depth displacement (m) and daily

percent DVM identified were calculated. For each fish, every month with a minimum of 28 days of daily data available was averaged to identify inter-annual differences of individuals by month. To formally test for annual periodicity, daily-mean-depth data were summarized to investigate annual depth-specific patterns using the same wavelet analysis described above, with the time step changed to one day. A null distribution was created using simulated data (n = 5000); no detrending of the time series was needed, and the depth bins were increased to 50-m. A significant period of 365 days in the global wavelet spectrum was considered indicative of annual periodicity.

3. Results

As of November 2018, 22 of the 297 (7.4 %) Greenland turbot implanted with archival tags were recovered. Of the recovered archival tags, 15 contained data that were usable for their entire time at liberty, 3 were partially usable, and 4 were corrupted; hereafter, only the 18 archival tags with usable data are presented and analyzed. Seven tagged Greenland turbot were male, eight were female, and three did not have their sex determined (Table 1).

3.1. Spatial movements

Tagged Greenland turbot were at liberty from 19 to 1859 days, were tagged and recaptured at depths between 200 and 800 m within the BSAI region, and travelled straight-line distances of 7.8–513.3 km (Fig. 1). Of the recaptured fish, six were released along the Bering Slope in 2003, two in 2005, one in 2007, and six in 2011, while three (one in 2003, two in 2008) were released along the continental slope north of the Aleutian Islands (Fig. 1).

Although detailed routes are not inferred from archival tags, similarities and differences of movements among fish can be gleaned. Of six fish released at the same location on the same date in 2011, three fish were at liberty less than 60 days (tags 387, 390, and 403), and three fish were at liberty one year or more (tags 383, 386, and 406). These fish were recaptured in all directions along the slope (Fig. 1), with the shortest horizontal displacement by a fish that was at liberty for over 5 years (tag 383). Two fish with similar straight-line trajectories (tags 386 and 390) have depth profiles that allow for different routes, as tag 386 indicates a period of time spent in depths < 200 m (i.e., on the continental shelf), while tag 390 was not shallower than 250 m the entire time at liberty (Figures S1 & S2 of supplemental materials).

3.2. Temperature and depth preference

Mean recorded temperature per animal ranged from 3.23 to 3.70 °C (overall range 0.90–7.77 °C), and mean recorded depth per animal ranged from 448 to 753 m (overall range 0–1906 m) (Table 1). The greatest observed activity was -52.0 m min^{-1} by tag 386 on January 1, 2012, and the greatest daily depth displacement was 1294 m by tag 3883 on January 11, 2009. The advertised maximum pressure for archival tags (equivalent depth between 1250 m and 2000 m depending on tag type and configuration) was exceeded in some instances, and seven archival tags appeared to repeat a maximum pressure while the temperature continued to change, indicating that the fish was likely exceeding the greatest recorded depth for brief periods; though the temperature records did not appear in error, the actual depths during these short times were presumed deeper than the archival tag reported.

Temperature preference was not apparent in at least one Greenland turbot (tag 5282) that spent three consecutive summers on the continental shelf (2003, 2004, and 2005); this location was deduced from the maximum depths consistently near 100 m (Figure S3 of supplemental material). In the relatively warm year of 2003, this fish experienced warmer than average temperatures while on the shelf, but during 2004 and 2005 when the cold pool was more developed, this fish experienced cooler than normal temperatures.

There were 98 days of data that included shallow excursions to less than 50-m depth (< 1.2 % of the total) and were recorded by six fish (one male and one female were only observed going shallower than 50 m one day). The majority of these rare shallow excursion days (n = 67 days) were observed for two female Greenland turbot presumed to be on the continental shelf (< 200-m depth); one fish was shallow during the winter, and the other was shallow between May and October. The remaining two fish, one male (n = 16 days) and one female (n = 11 days), came from depths greater than 200 m before entering water shallower than 50 m and returned to similarly deep waters.

3.3. Seasonal movements

Daily means of temperature, depth, activity, and depth displacement experienced by Greenland turbot changed synchronously throughout the year. Greenland turbot in the BSAI occupied deeper and colder water during the winter and shallower and warmer water during the summer (Fig. 2). The coolest water temperatures were experienced in the upper 200 m of the water column, the most extreme which occurred during the winter. Deeper than 200 m, temperature decreased with depth across all seasons. Tagged Greenland turbot usually began to transition to deeper depths starting in October and transitioned back towards shallower depths starting in March. Activity levels and daily depth displacement were highest during the winter with a right skewed distribution, and this trend remained through spring, while a decline in activity and daily depth change was evident in the summer, and to a lesser extent in the fall (Fig. 2). Some Greenland turbot presumably moved from the Bering Slope (> 200 m) onto the continental shelf (< 200 m).

Greenland turbot that were at liberty for multiple years provided interannual information on seasonal movements for individuals. Depths and temperatures occupied were consistent for individuals across years, generally following the overall pattern of warmer and shallower in the summer and cooler and deeper in the winter (Fig. 3). The exception to this is the cold temperatures at depths less than 200 m (indicative of the cold pool) in the summer for tag 4551 and tag 5282 (Fig. 3). Activity and depth displacement were also consistent for individuals across years, with an increase in both with depth occupied (Fig. 3). Using a wavelet analysis on mean-daily-depth, all six Greenland turbot that were at liberty two or more years exhibited significant annual cycles ($p < 0.05$; period = 365 days) in the global wavelet spectrum, all exhibiting the largest peak at the period between 350 and 380 days (Fig. 4). This indicates that depth occupied changed on an approximately annual cycle.

3.4. Sex-specific movements

Four of the five female Greenland turbot that were at liberty for an entire year or longer recorded temperatures at depths indicative of Bering Sea cold pool utilization; no males were found to occupy presumed bottom depths < 200 m with temperatures < 2 °C. One female tagged in 2003 (tag 5282) spent several months at depths < 100 m beginning in June 2004 and June 2005, during which this fish experienced water temperatures less than 2 °C. A fish tagged in 2005 (tag 4551) appears to have entered the cold pool early in the summer and slowly moved deeper and off the shelf soon after. A fish tagged in 2011 (tag 386) entered the cold pool in October of that year and remained through January of 2012, with maximum depths for this period of approximately 110–140 m of water. Another fish tagged in 2011 (tag 383) made regular nighttime excursions into cold shallow water during April and May of 2012 and April–June of 2013 but returned to warmer water several hundred meters deeper during the day. It is possible this fish was moving up the slope into the cold pool, but due to the time of year and short time period of the excursion, it is more likely moving vertically in the water column to cooler, shallower waters without moving horizontally to shallower bottom depths; the distinction cannot be

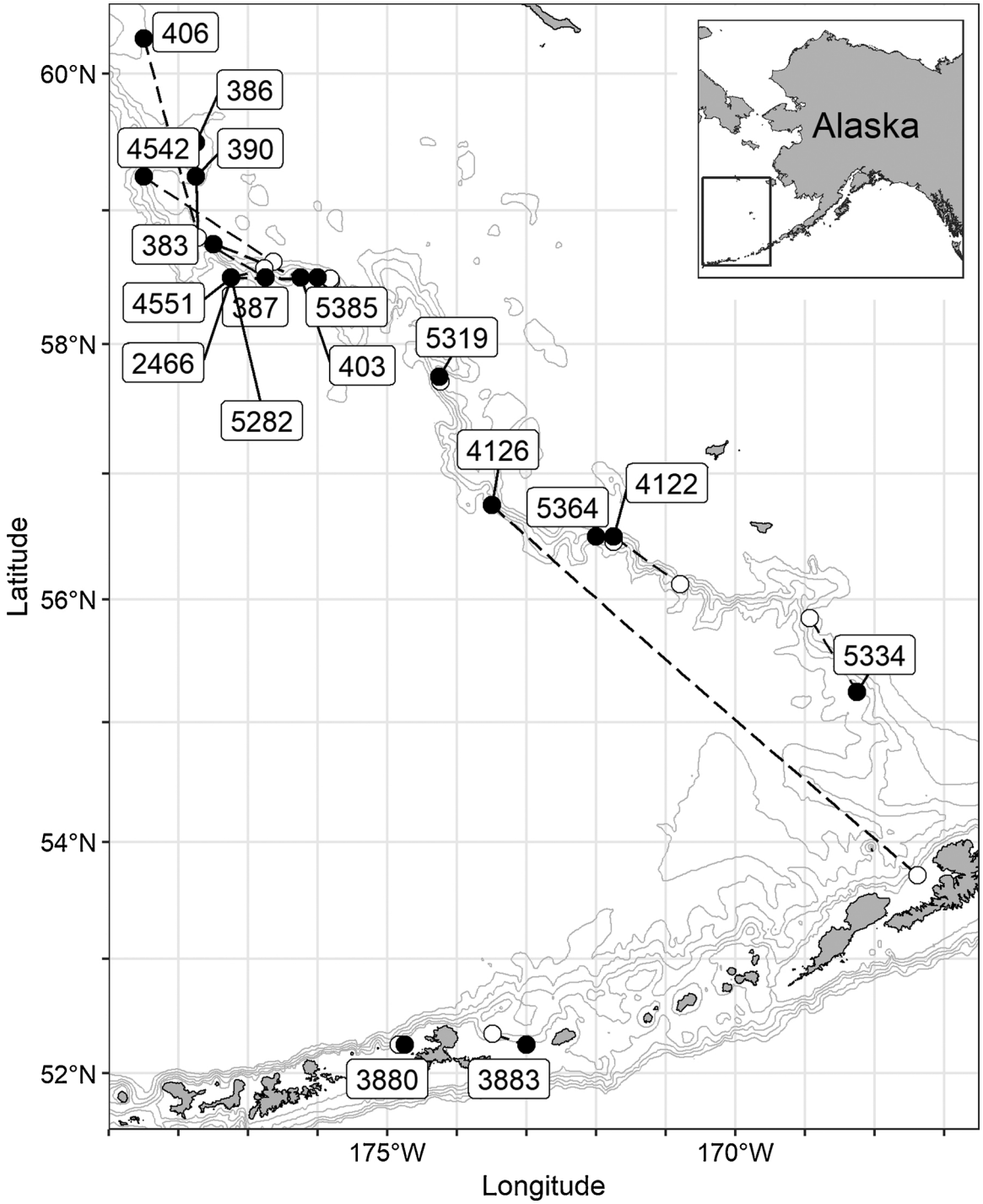

Fig. 1. Map of the study region in the Bering Sea and Aleutian Islands with general location shown in upper right inset. Open circles are release locations of Greenland turbot *Reinhardtius hippoglossoides* with archival tags, closed circles are their recovery locations (with tag number shown), dashed lines are straight-line trajectories, and isobaths (light gray) are 200, 500, 1000, 1500, and 2000 m. Recapture locations have been summarized to the nearest 0.25 degree.

discerned from the archival tag data herein.

3.5. Diel vertical migrations

Diel periodicity in vertical movement was detected for Greenland turbot, though it varied among individual fish in this study. Global wavelet analysis identified a globally significant diel period ($p < 0.05$, period = 24 h) for 17 of 18 fish, and when identified, DVM (period = 22–26 h) for individual fish ranged from 4.16 %–60.12 % of their time at liberty (Fig. 5 & S1–S18 of supplemental material). Local wavelet power spectra showed how DVM varied for individual fish throughout the year (Fig. 5 & S1–S18 of supplemental material). For all fish summarized by month, the mean daily percent of time with significant DVM was between 20 % and 40 %, and the greatest mean daily percent of DVM occurred in April and May with a secondary peak in January and February (Fig. 6).

When DVM was identified, temperature and depth experienced at the top and bottom of these movements were relatively shallower and warmer during the summer and deeper and cooler during the winter. The warmest temperatures were generally experienced when depths

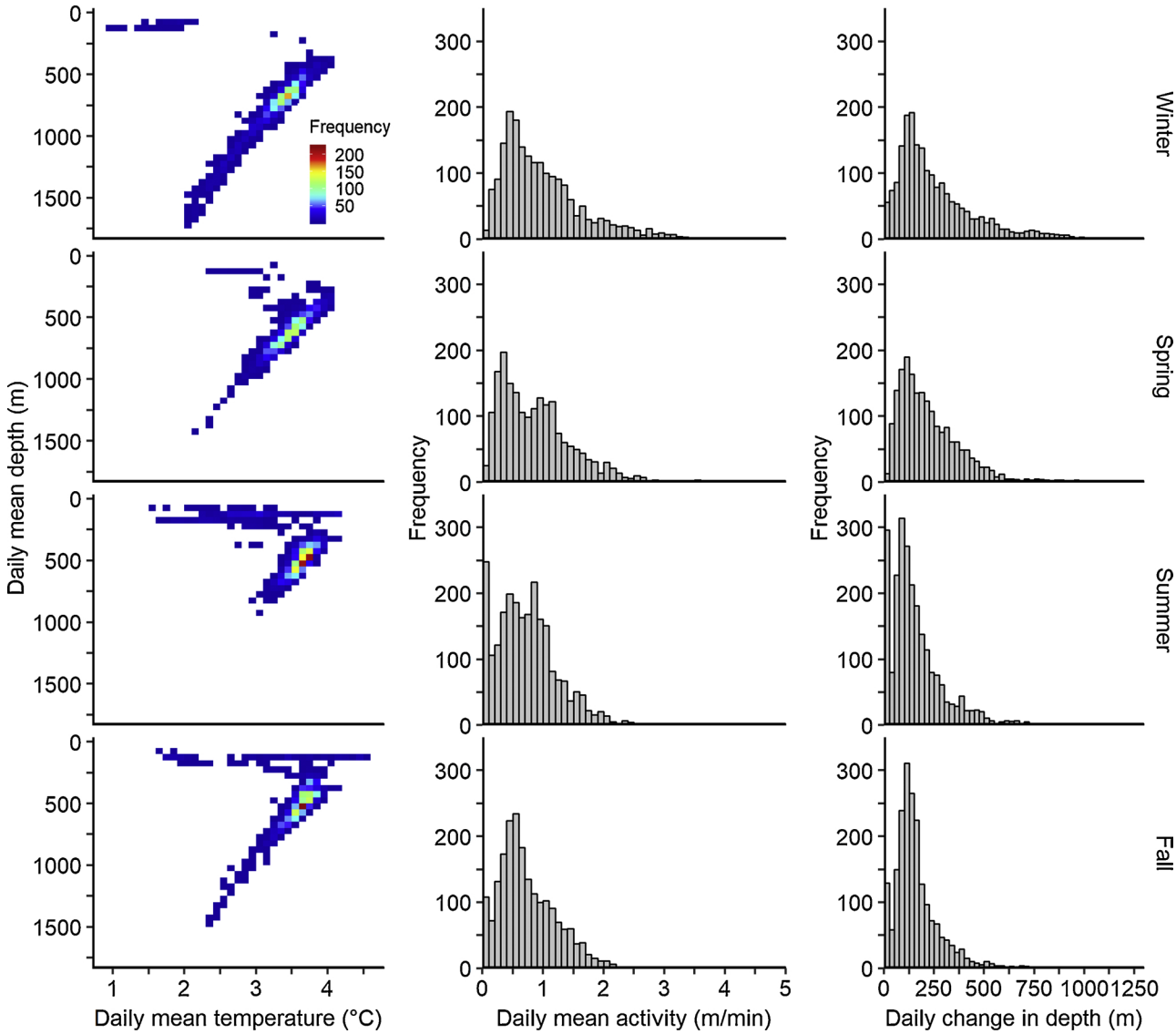

Fig. 2. Histograms summarizing the daily mean temperature (°C) with respect to daily mean depth (m), daily mean activity (m/min), and daily change in depth (m) for tagged Greenland turbot *Reinhardtius hippoglossoides* by season. Colors on the left-hand column two-dimensional histogram reflect the frequency as shown in the legend (upper left panel). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

were shallowest in July, while the coolest temperatures occurred when depths were deepest in January (Fig. 6). The average temperature at the top and bottom of DVM movements in May were both cooler than the mean temperature, suggesting cooler waters, likely associated with melting sea ice, at the top of vertical movements during this month (Fig. 6). The monthly percent of DVM identified varied greatly among Greenland turbot but appeared consistent across years by individual (Fig. 3). DVM was not occurring when tag 4551 and tag 5282 were presumably on the continental shelf (< 200 m) in the summer (Fig. 3).

Both types of DVM, shallower during the nighttime (type I) and shallower during the daytime (type II), were identified but not differentiated between using local wavelet power spectra (Fig. 7). When Greenland turbot were identified as exhibiting DVM, the type of DVM changed throughout the year. Fish displayed type I DVM from May through September during which daily minimum depths occurred on average in the evening between 2200 and 0400 h; the estimated mean timing of the deepest portion of the DVM movement was not as well defined in May or June as it was after that time (Fig. 8). Type II DVM was more prevalent from October to December during which daily maximum depths occurred in the evening between 0200 and 0600; beginning in December the estimated mean timing of the shallowest portion of the DVM movement was less defined (Fig. 8). From January to April, there was not a strong pattern in the type of DVM occurring, and a gradual transition of the timing of and confidence in mean estimates was evident (Fig. 8).

4. Discussion

Adult Greenland turbot in the BSAI region primarily occupy the continental slope, although archival tag data from this study provides evidence that individuals will sometimes occupy shallower depths on the shelf, move throughout the water column, and occupy varying depths throughout the day and year. Depth-specific periodic behaviors were identified on diel and annual scales, indicating the possibility of regularity in the behavior of Greenland turbot. Female Greenland turbot appear more likely to utilize the Bering Sea cold pool than males.

Horizontal displacement of Greenland turbot is variable, and while individuals of this species may travel great distances in a short period of time, some fish may have home ranges or some level of site fidelity. In Cumberland Sound, eight satellite tagged fish at liberty between 70 and 310 days travelled between 3.2 and 27.4 km (Peklova et al., 2012). It is possible that Greenland turbot in nearshore habitats such as fjords

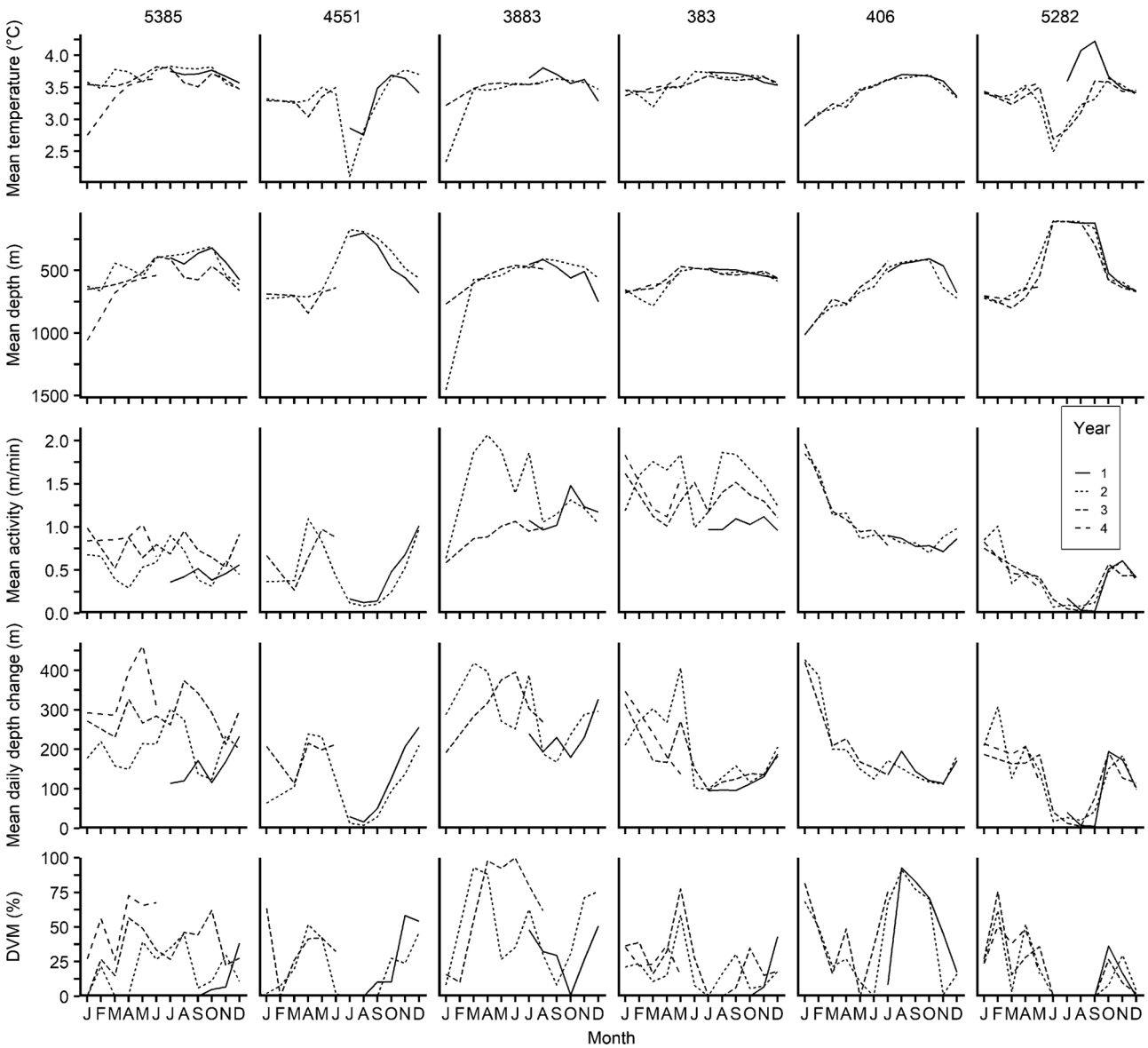

Fig. 3. Monthly mean values of temperature, depth, activity, depth displacement, and percent of diel vertical migration (DVM) for tagged Greenland turbot *Reinhardtius hippoglossoides* at liberty for two or more years. Different line types represent the respective calendar year at liberty as shown in the legend. Constructed from daily means when entire day of data was available, and only includes months with a minimum of 28 days.

exhibit different movements compared to conspecifics in the open ocean of the Bering Sea, as at least one fish travelled over 500 km in this study. A long-term conventional tagging program found limited long distance movements and a high level of site fidelity for Greenland turbot inhabiting fjords in Greenalnd, while fish offshore revealed great migratory pathways of up to 2500 km (Boje, 2002). Connections between fjord and offshore populations have been suggested (Barkley et al., 2017), though it remains unclear what level of transience versus residency, if any, is characteristic for Greenland turbot in the BSAI.

Changes in the magnitude and extent of the cold pool can lead to shifting distributions of fish species and thus varying competition and foraging opportunities (e.g., Hollowed et al., 2012). Generally, as water temperatures warm, there is a northward shift in the distributions of arctic and boreal species in the Bering Sea (Mueter and Litzow, 2008). Walleye pollock are an important food resource for Greenland turbot in the BSAI, with smaller fish targeting age 0–1 and larger fish targeting adults (Bryan et al., 2018; Aydin and Mueter, 2007). Walleye pollock recruitment is expected to be poor with extended warm periods in the Bering Sea (Hunt et al., 2011), and biomass of capelin, another important forage fish, declines during warm years (Andrews et al., 2016). Perhaps the variety of individual strategies, such as inhabiting the continental shelf versus slope in the summer or winter, provides an opportunity for Greenland turbot to better adapt as a species in a changing environment. In the event that the cold pool is poorly formed (as in 2003), or does not form at all as was the case in 2018 (Siddon and Zador, 2018), a Greenland turbot that habitually returns to the continental shelf may find a different thermal environment each year, and thus different foraging opportunities. Understanding these different strategies may also be important for interpreting the distribution of Greenland turbot.

Beyond the general depth and temperature trends that most tagged Greenland turbot shared, tagged fish at liberty for multiple years provided evidence for seasonally habitual movements by individual. These trends indicate that Greenland turbot in the BSAI returned to similar depths annually. This result could be due to seasonal site fidelity, a behavior that has been observed in Pacific halibut tagged in Glacier Bay National Park of Southeast Alaska (Nielsen et al., 2014). Additionally, individuals showed unique patterns in DVM from each other, but

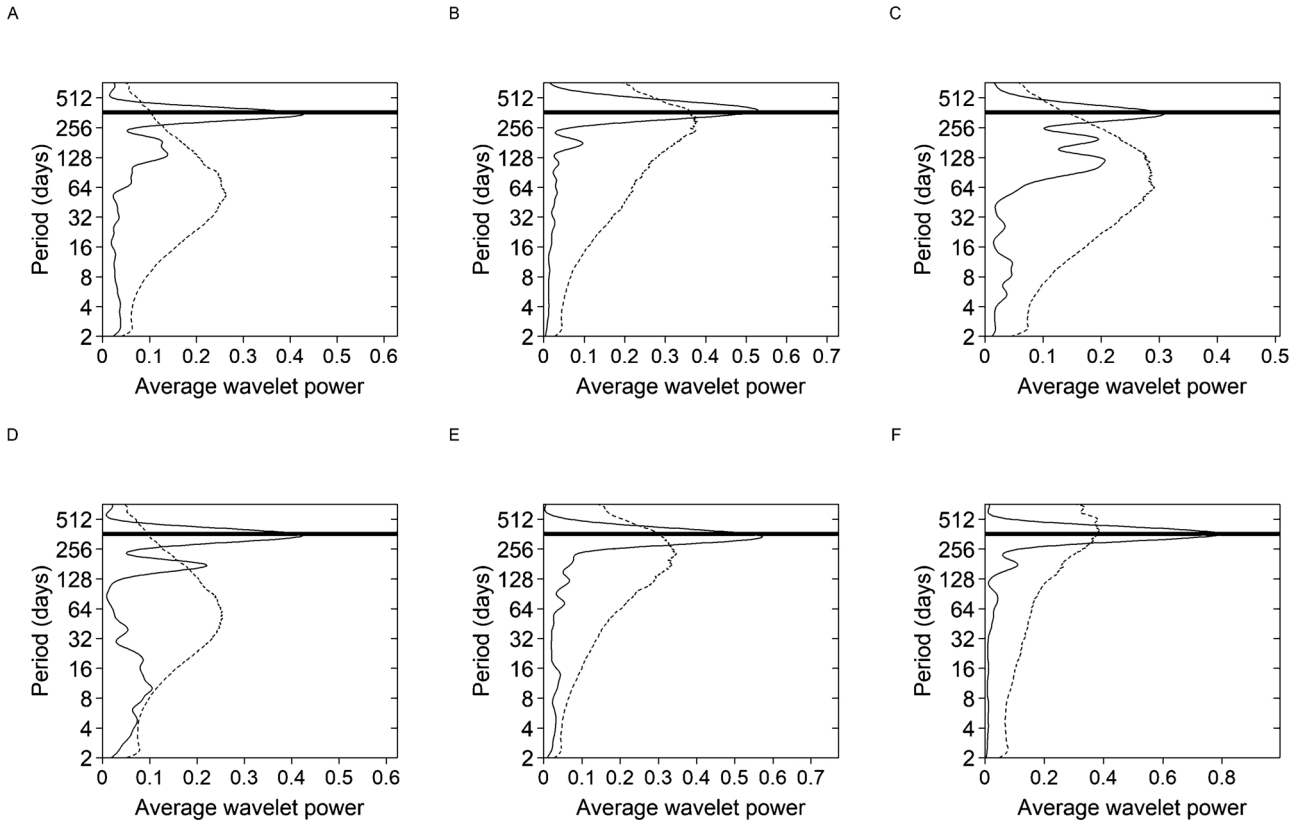

Fig. 4. Global wavelet power spectra from mean-daily-depth data collected using archival tags in Greenland turbot *Reinhardtius hippoglossoides* that were at liberty for multiple years. Tag numbers are as follows: a) 5385, b) 4551, c) 3883, d) 383, e) 406, and f) 5282. Solid line is the global wavelet power spectrum from the raw depth data, dashed line is the 95 % confidence interval from simulated data (n = 5000), and the horizontal gray bar highlights an annual period (350–380 days).

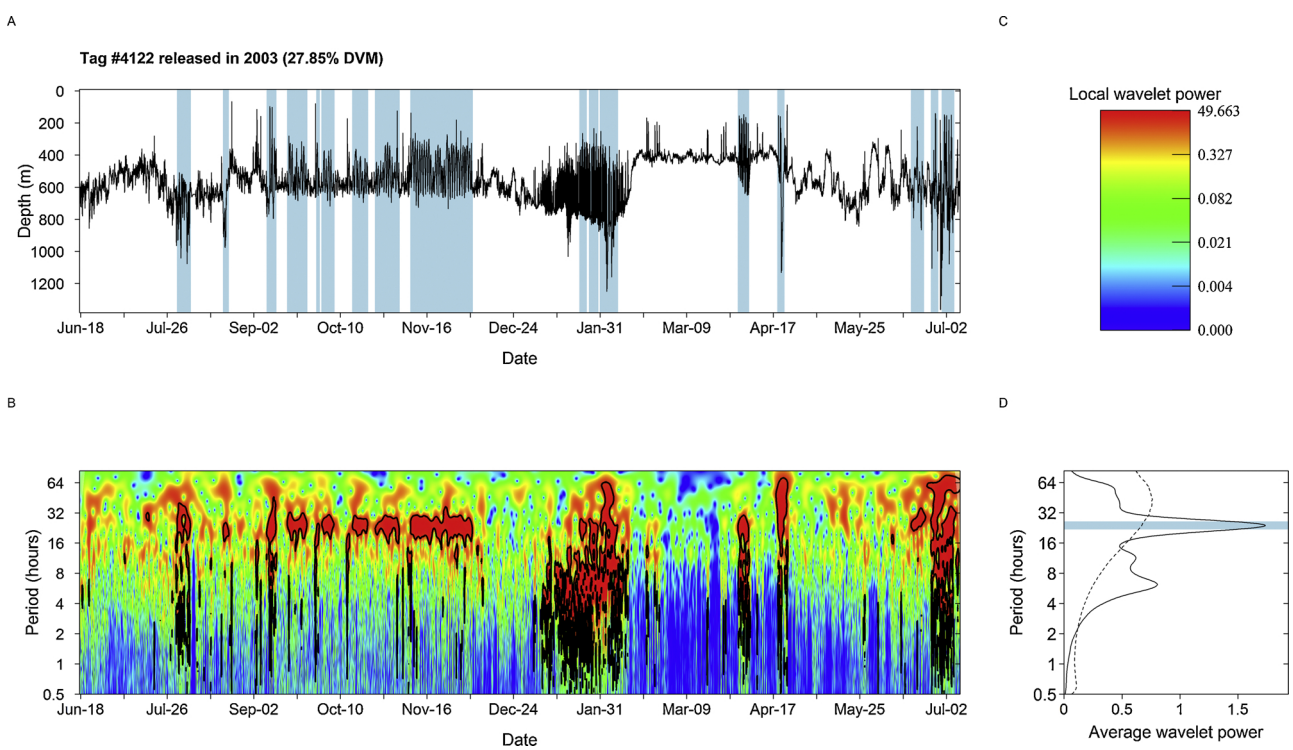

Fig. 5. An example of the wavelet analysis used to assess diel vertical migration (DVM) of Greenland turbot *Reinhardtius hippoglossoides*. (A) The raw depth data, (B) the local wavelet power spectrum with black lines indicating the 95 % confidence interval, (C) the local wavelet power legend (scaled using quantiles), and (D) the global wavelet power spectrum with the dashed line indicating the 95 % confidence interval. When the global wavelet power spectrum exceeded the 95 % confidence interval at a daily period of 24 h (22–26 h highlighted in light blue on panel D), then localized DVM (period = 22–26 h) was highlighted in light blue on panel A. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

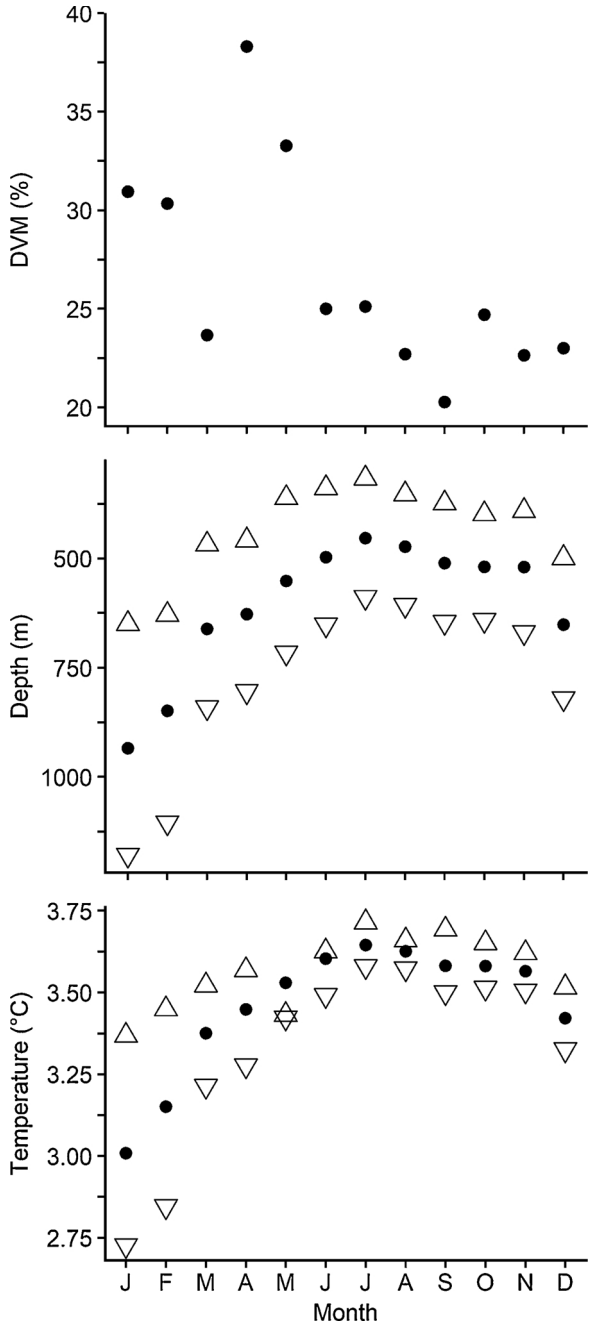

Fig. 6. Monthly summary of diel vertical migrations (DVM) for all tagged Greenland turbot *Reinhardtius hippoglossoides*. Top panel shows the mean daily percent of DVM identified by month. Middle panel shows mean depth (increasing depth towards the x-axis) of days with DVM (circles), mean depth of the top of DVM (upward pointing triangles), and mean depth of the bottom of DVM (downward pointing triangles). Bottom panel shows mean temperature of days with DVM (circles), mean temperature of the top of DVM (upward pointing triangles), and mean temperature of the bottom of DVM (downward pointing triangles). Note the y-axes do not begin at zero.

consistency in their own pattern across years; this observation could be associated with the depths that individual Greenland turbot occupy, where differing levels of DVM are associated with different depths or habitats occupied throughout the year. This variety is highlighted by the different strategies being employed by individuals which is beneficial for a population that exists in a changing environment where diversification may be important to adapting now and into the future.

Archival tags implanted in Greenland turbot occasionally recorded depths at or near the surface (Table 1), which was shallower than expected for adults of this species. Young Greenland turbot have been encountered in surface waters with some regularity, but older conspecifics from the Atlantic are rarely captured in surface waters (Jørgensen, 1997; Vollen and Albert, 2008). After a closer examination of temperature-depth profiles from days when depth was shallower than 50 m, the shallow depths reported herein were deemed not to be erratic or erroneous data; the records gradually decrease in depth with a concordant lagged change in temperature (expected for an internal sensor) before returning to the presumed bottom depth (Figure S19 of supplemental materials). The behaviors associated with these shallow excursions are not known, but possible causes include feeding near the surface or temperature regulation.

For the majority of tagged Greenland turbot, the daily change in depth was greatest in the winter, but it is important to recognize that this metric can increase with the maximum depth occupied by the fish. In other words, a fish that occupies water of 100-m depth is limited by this depth for daily vertical migrations. It remains noteworthy that some Greenland turbot are displaced more than 1000 vertical meters within a day, though archival tag data does not distinguish whether this is along the bottom or off the bottom and into the water column. Although not directly investigated, because this great vertical movement is occurring during winter months, the presumed peak spawning period (Sohn et al., 2010), this behavior may be associated with spawning. Across its distribution, Greenland turbot are believed to migrate to deeper waters to spawn (Serebryakov et al., 1992; Alton et al., 1998; Sundby and Kristiansen, 2015). Consistent with other behaviors observed, activity levels throughout the year are not the same for all tagged Greenland turbot; however, those fish that were at liberty for multiple years did show consistency in the timing of increased vertical displacement.

The wavelet analysis identified diel and annual periods of depth-specific movements by Greenland turbot. There were some cases when diel periodicity appeared to occur, and though relatively higher wavelet power was exhibited, the movements were not deemed significantly different than the null distribution using this analysis (e.g., tag 4126 from October to December of 2003 in Figure S9 of supplemental material). This conservative approach seemed to detect large-scale movements more easily and may not have detected small-scale movements which was similarly noted in Goetz et al. (2018). It is important to consider how varying null models will lead to differing determinations of significance (Cazelles et al., 2014); the resampling technique chosen was deemed appropriate as it maintained the temporal structure of each fish's behavior while allowing for a mean and variance that is not constant. Additionally, the Markov resampling method will be sensitive to the size of the depth bin, so selection of an appropriate sized depth bin for the species and objective is important; detection of a small change in depth such as the tide over a fish resting on the bottom would require an appropriately small depth bin, whereas larger bins are appropriate for larger vertical movements.

Archival tags on Greenland turbot showed both type I and type II DVM. Type I DVM is a common behavior in fish and often related to feeding (Brierley, 2014). Zooplankton such as euphausiids, copepods, and chaetognaths, as well as smaller fish including age-0 walleye pollock and capelin *Mallotus villosus* undergo DVM (Bailey, 1989; Schabetsberger et al., 2000; Davoren et al., 2006). Both type I and type II DVM have been detected for Pacific cod (Nichol et al., 2013), while Atka mackerel mostly exhibit type I DVM (Nichol and Somerton, 2002). For sablefish in Alaska, type I DVM was found to occur from August to December and type II DVM was found to occur from December to March (Sigler and Echave, 2019). The majority of the sablefish in that study were from the Gulf of Alaska, whereas the Greenland turbot in this study are in the Bering Sea, and this geographic difference (further north) could be responsible for an earlier onset of a transition from type I DVM to type II DVM found herein. Type I DVM appears to be occurring when feeding would be the most important behavior (spring/

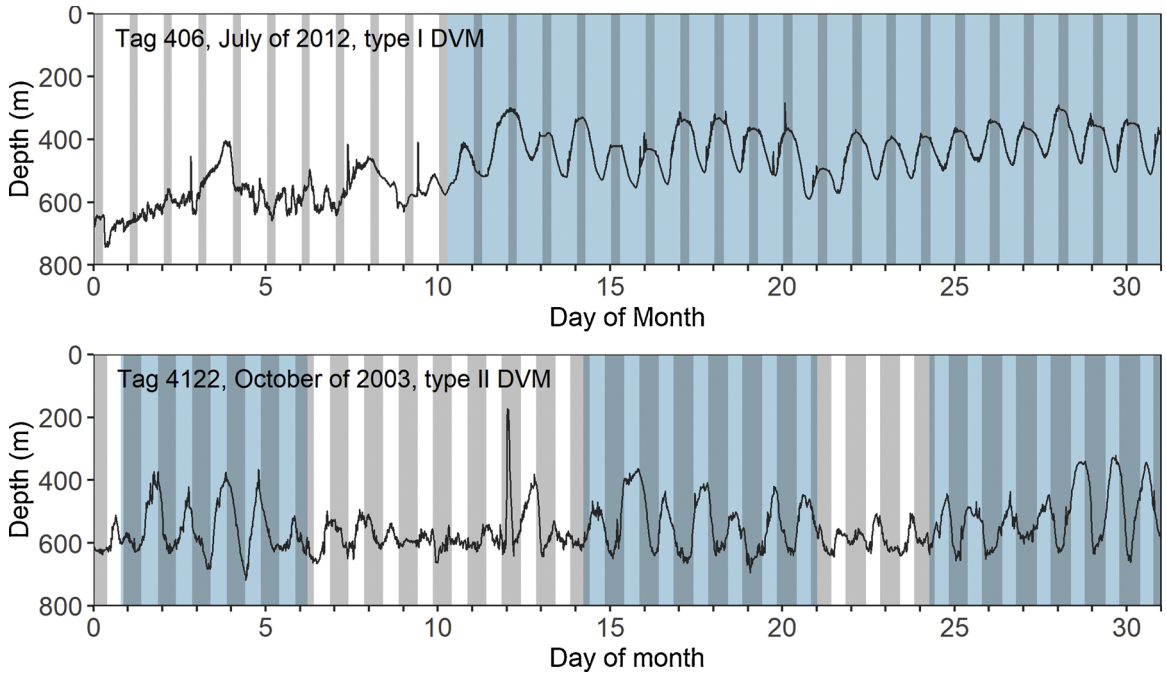

Fig. 7. Examples of raw depth data from tagged Greenland turbot *Reinhardtius hippoglossoides* highlighting significant diel vertical migrations (DVM, period = 22–26 h) in light blue as identified from wavelet analysis. The gray shaded regions mark the time between sunset and sunrise. The top panel shows type I DVM (shallower during the night) occurring in July of 2012, and the bottom panel shows type II DVM (shallower during the day) occurring in October of 2003. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

summer), and the transition to type II DVM could be connected with diminishing light in the fall, as there is an incremental shift from October through December.

We hypothesize that on average, DVM (type I and type II combined) occurs about 20–25 % of the time, as seen for June through December and March. During January and February, there is an elevated level of DVM (~30 %) which may be associated with the spawning period (Sohn et al., 2010). This DVM is highly conflated with other shorter periods of significance (e.g., 6, 8, and 12 h periods) and lacks consistent structure of either type I or type II DVM, and these could be rises similar to putative spawning behavior of Atlantic halibut *Hippoglossus hippoglossus* (Murphy et al., 2017). These can be easily identified in the supplemental plots when the depth profiles rapidly and repeatedly cover a broad range of depths (e.g., S5–S9 of supplementary material, panel A) while the local wavelet plots show the dark red extending down into to shorter periods (e.g., S5–S9 of supplementary material, panel B). The highest levels of DVM (~35 %) occur in April and May, which could be associated with the onset of the spring bloom and increased feeding opportunities in the water column during these months (Sigler et al., 2014).

5. Conclusions

Greenland turbot exhibit a variety of movement patterns, some with regular periodicity and others unique in time or to individual fish. Horizontal movements varied from less than ten to hundreds of kilometers. Different behaviors probably cause this result, with site-fidelity being one behavior that would lead to little displacement over long periods of time. General trends suggest movement from relatively shallower depths in the summer to deeper depths in the winter, and activity levels increased with depth. Periodicity was common, with diel and annual periods evident. Beyond common general patterns in the movements of Greenland turbot, there seems to be a high level of consistent movements by individuals occurring at a seasonal periodicity: depth occupied, percentage of DVM, and activity levels inferred from daily vertical displacement. This predictability could be pertinent to stock assessment surveys that are continuously surveying the same regions at the same time of year. Greenland turbot tagged in this study occupied temperatures which were relatively warmer than other Greenland turbot that have been tagged in other regions (Boje et al., 2014; Peklova et al., 2012). With increasing ocean temperatures expected in this region (Hermann et al., 2016; Hunt et al., 2018), and the formation of the cold pool becoming less regular, Greenland turbot distribution may shift deeper or northward (Vestfals et al., 2016); they have been in the Beaufort Sea since at least 1993 (Chiperzak et al., 1995), and continue to be found in the Arctic Ocean (Chernova, 2017; Giraldo et al., 2018). If this happens, current surveys will need to adapt their sampling strategy to effectively assess this population, or stock assessment authors will need to adjust their estimates of catchability/availability.

Future research should include geolocation capabilities to identify where different behaviors are likely occurring between the tagging and recovery of Greenland turbot. Pop-up satellite tags set to release on specific dates to target different behaviors could be used as this method does not require the recapture of the fish, and depths and temperatures recorded by electronic tags may be used to determine probable locations of a fish while at liberty (e.g., Nielsen and Seitz, 2017). Finally, further investigations into the timing and location of spawning behavior should be pursued through tagging and maturity studies, as putative spawning rises are suspected for this species (Loher and Seitz, 2008).

Stock assessment surveys that encounter Greenland turbot in the BSAI region include the Alaska Fisheries Science Center's annual bottom trawl survey which occurs on the shelf (Conner and Lauth, 2017), historically a biennial bottom trawl survey which occurred on the slope (Hoff, 2016), and a longline survey (Lunsford et al., 2018). All survey effort is primarily during the summer and on the bottom. Availability, the number of fish on the fishing grounds, of Greenland turbot will therefore be limited to fish on the bottom. Our results suggest Greenland turbot availability to benthic surveys could vary spatially by sex, with evidence that mature females could be more likely than males to utilize the shelf, and temporally as shifts in DVM timing

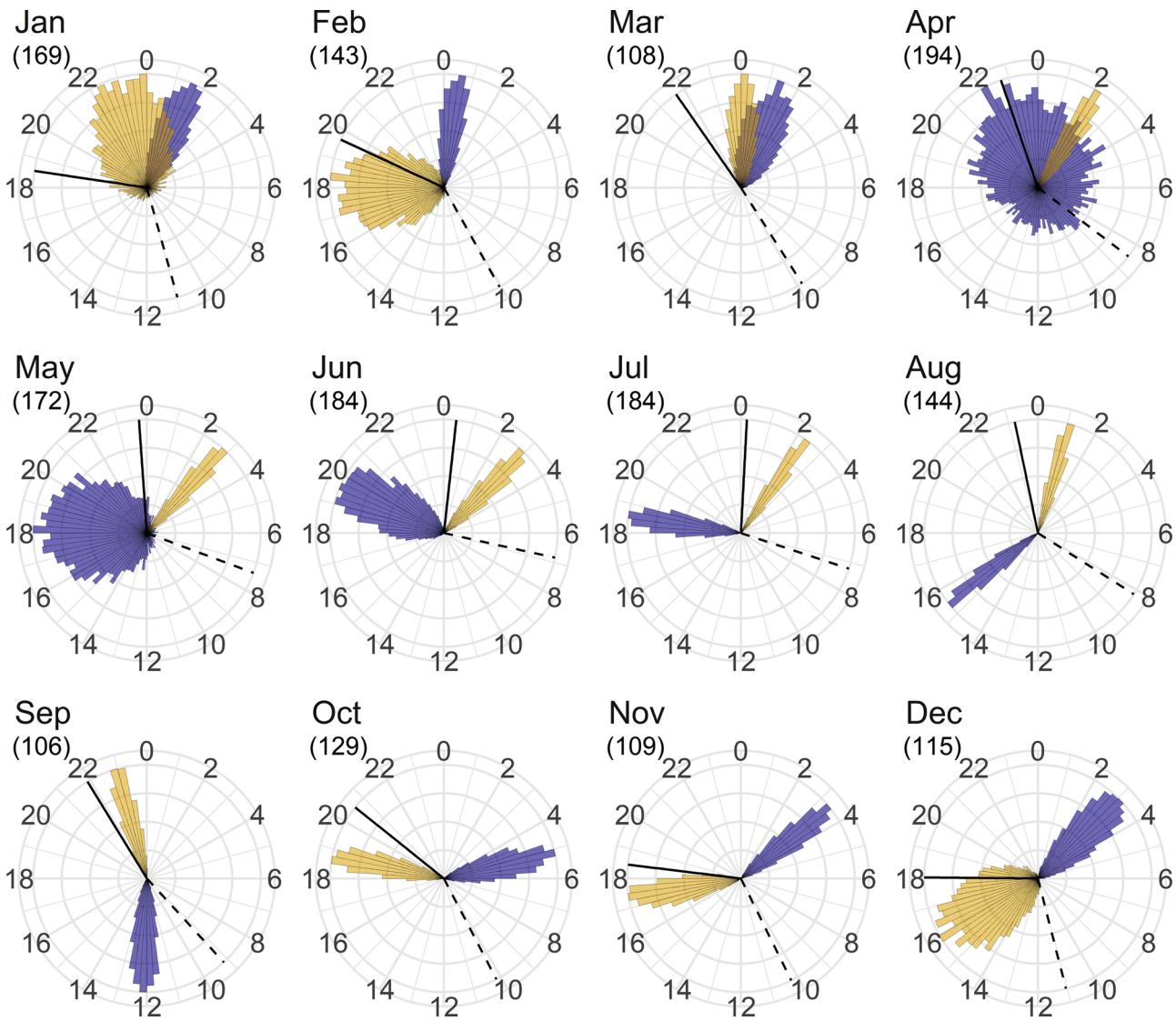

Fig. 8. Circular histograms of the bootstrap resampled mean time (n = 5000 per month) at which tagged Greenland turbot *Reinhardtius hippoglossoides* were at the top (orange) and bottom (blue) of identified diel vertical migrations. Numbers in parentheses under each month indicate the number of days of raw data resampled, and each month is scaled to one. As a proxy of night time, sunset (solid line) and sunrise (dashed line) times are shown from the 15th of each month in 2010 in the middle of the area (56 °N, 174 °W). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

occur. Variation in availability of Greenland turbot to stock assessment surveys can impact catchability, defined as the relationship between catch rates (e.g., catch per unit effort) and the population, thus impacting population estimates from these surveys. Fishery-dependent catch data may be more susceptible to these time-varying parameters because these occur over a greater portion of the year. The observed seasonal shifts in occupied depths and DVM behavior of Greenland turbot could impact the catchability and selectivity of this species over space and time, and this should be considered when interpreting survey and fishery data.

CRediT authorship contribution statement

Kevin A. Siwicke: Conceptualization, Methodology, Software, Formal analysis, Writing - original draft, Visualization. **Karson Coutré:** Conceptualization, Data curation, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the

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