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Temperature and body size affect movement of juvenile Atlantic cod (*Gadus morhua*) and saithe (*Pollachius virens*) at nearshore nurseries

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Abstract

Seasonal migrations of marine fish between shallow summer feeding habitats and deep overwintering grounds are driven by fluctuations in the biotic and abiotic environment as well as by changes in the internal state. Ontogenetic shifts in physiology and metabolism affect the response to environmental drivers and may lead to changes in migration timing and propensity. In this study, we investigated the effect of temperature and body size on migration timing and depth distribution in acoustically tagged Atlantic cod, *Gadus morhua*, and saithe, *Pollachius virens*, during the period of seasonal migration from shallow summer habitats. The results from our study revealed a wide range of horizontal and vertical distribution of age 1 and 2 *G. morhua* within the fjord. Larger *G. morhua* inhabited deeper, cooler waters than smaller juveniles, likely reflecting size-dependent thermal preferences and predation pressure. Conversely, juvenile *P. virens* occupied primarily shallow waters close to land. The variation in depth distribution of *G. morhua* was mainly explained by body size and not, against our predictions, by water temperature. Conversely, the dispersal from the in-fjord habitats occurred when water temperatures were high, suggesting that seasonal temperature fluctuations can trigger the migration timing of *P. virens* and larger *G. morhua* from summer habitats. Partial migration of small juvenile *G. morhua* from in-fjord foraging grounds, likely influenced by individual body condition, suggested seasonal migration as a flexible strategy that individuals may use to reduce predation and energetic expenditure. Predation mortality rates of tagged juveniles were higher than previously suggested and are the first robust predation mortality rates for juvenile *G. morhua* and *P. virens* estimated based on acoustic transmitters with acidity sensors. The results have relevance for climate-informed marine spatial planning as under the scenario of increasing ocean temperatures, increasing summer temperatures may reduce the juveniles' resource utilization in the shallow summer nurseries, resulting in lower growth rates, increased predation pressure, and lower chances of juvenile winter survival.

KEYWORDS
acoustic telemetry, *Gadus morhua*, Iceland, migration timing, nursery grounds, *Pollachius virens*, seasonal migration

1 | INTRODUCTION

Seasonal migrations are common in a wide range of taxa conferring evolutionary advantages through optimal foraging (Hopcraft et al., 2014; Leu et al., 2011), growth (Brönmark et al., 2008), and access to breeding habitats (Miller et al., 2016; Winger et al., 2019). In marine fish, seasonal migrations between shallow summer feeding habitats and deep overwintering grounds are common for early life stages (Cote et al., 2004; Hanson, 1996), allowing access to rich trophic resources in coastal habitats at favorable temperatures (Árnason et al., 2009; Perry et al., 2018). Seasonal migrations have been described for both juvenile Atlantic cod, *Gadus morhua* L. (Cote et al., 2004; Strøm et al., 2023), and saithe, *Pollachius virens* L. (Homrum et al., 2012; MacDonald et al., 1984). Juveniles from both species migrate into shallow coastal waters during spring, where they stay throughout the summer months (Clay et al., 1989; Dunlop et al., 2022; MacDonald et al., 1984). High structural diversity in the shallow water habitats is associated with rich feeding grounds and reduced predation pressure, and, together with warm ambient temperatures, fuel the juveniles' growth and lipid build-up during the summer months (Copeman et al., 2017). With the onset of winter, juveniles may migrate into deeper overwintering grounds (Cote et al., 2004; Homrum et al., 2012). During these migrations, age group 1 and 2 juvenile *G. morhua* can cover horizontal distances of more than 225 km (Hanson, 1996). Large-scale seasonal migration has also been described for 0-group juvenile *G. morhua* in Iceland (Pálsson, 1976) and on the east coast of North America (MacDonald et al., 1984), while juvenile populations (age 1) in Sweden reside within shallow nearshore habitats throughout the year (Pihl & Ulmestrand, 1993).

While multiple intrinsic and extrinsic drivers for the timing of seasonal migration have been proposed for *G. morhua*, little research has been done on migration drivers in *P. virens*. Seasonal changes in the thermal environment may increase the energetic expenditure of fish and consequently drive the vertical migration along a thermal gradient, such as the migration of *G. morhua* and *P. virens* into deeper and relatively warmer overwintering grounds. Other environmental factors, such as changing salinity levels (Riley & Parnell, 1984) and decreasing oxygen concentrations at the summer habitats (Limburg et al., 2011; Skjæraasen et al., 2008), have been discussed as drivers for seasonal migration of *G. morhua*. Intrinsic factors, including hormone levels, also affect fish migration (Birnie-Gauvin et al., 2019). Increased levels of thyroid hormones were suggested cues for seasonal, long-distance migration in adult *G. morhua*, as they enhance swimming capacity, metabolism, and sensory physiology (Comeau et al., 2001). Smaller *G. morhua* in poor condition were observed to stay longer or even throughout winter within the shallow nursery grounds (Comeau et al., 2002; Cote et al., 2004), suggesting body size and condition prior to winter as cues for seasonal migration timing.

At summer feeding grounds, age group 0 *G. morhua* are commonly found in inter- and subtidal habitats (Ólafsdóttir et al., 2023; Swain et al., 1998), but age groups 1 and 2 occupy deeper waters between 10 and 40 m (Dunlop et al., 2022; Grabowski et al., 2018; Pihl & Ulmestrand, 1993). An increase in depth distribution with age and body length has frequently been described in juvenile *G. morhua* (Freitas et al., 2021; Riley & Parnell, 1984; Swain et al., 1998). The depth divergence with age also occurs at deep overwintering grounds in the Gulf of St. Lawrence, where age group 1 and 2 *G. morhua* were found between 100 and 200 m depth, and age groups 3 and 4 at depths greater than 200 m (Hanson, 1996; Swain et al., 1998). Three studies investigated juvenile *P. virens* in the wild and found age groups 0 to 2 distributed within the first few meters of the water column close to land (Clay et al., 1989; Nedreaas, 1985; Olsen et al., 2010). Older juveniles (2+) migrate away from land, and were widely distributed in the water column, even close to the surface (Armannsson & Jónsson, 2012; Cargnelli et al., 1999). The cooccurrence of age 0 *G. morhua* and *P. virens* within the inter- and subtidal areas has been documented in North America, Norway and Iceland (Dunlop et al., 2022; Lazzari et al., 2003; Nickel, 2016), although no study has compared the habitat use of age 1+ juvenile *G. morhua* and *P. virens*.

Although fisheries surveys provide large-scale spatial information at a point in time, they do not provide the continuous positioning data of individual fish available from acoustic telemetry (Nathan et al., 2022). Moreover, most fishing gear is limited in deployment depth or restricted to areas with little habitat structure and therefore may not adequately assess juvenile gadoid abundance across different habitats, extending from the subtidal to depth beyond 50 m. Acoustic telemetry can complement fisheries surveys and has been used to support management and enhance conservation efforts of migratory populations through the study of habitat use (Freitas et al., 2021), identification of migratory pathways (Hayden et al., 2014), and survival estimates (Chaput et al., 2019). Moreover, direct measures of fish movement can help explain the influence of environmental factors and intrinsic conditions such as behavioral type, genetic traits, and parasite infestation (Barth et al., 2019; Uglem et al., 2009; Villegas-Ríos et al., 2018). Only a few studies have used acoustic telemetry to document the movement of *P. virens*, particularly of 2- to 4-year-old *P. virens* around sea cages (Otterå & Skilbrei, 2014; Skilbrei & Otterå, 2016; Uglem et al., 2009), while acoustic telemetry has been widely used to study the movement and migration of *G. morhua*, for example in relation to behavioral types (Monk et al., 2023; Villegas-Ríos et al., 2018), genotypes (Strøm et al., 2023), temperature (Cote et al., 2002; Freitas et al., 2015; Freitas et al., 2021), diel rhythm

(Clark & Green, 1990; Espeland et al., 2010), sound disturbances (Van der Knaap et al., 2021), and artificial aggregates (Reubens et al., 2013). Few studies have investigated young *G. morhua* (<30 cm) (Cote et al., 1998, 2004) and none have acoustically tagged *G. morhua* and *P. virens* smaller than 25 cm in length. Mortality at this age is high and has been associated with high predation pressure and low winter survival (Bogstad et al., 2016; Laurel et al., 2016). Acoustic telemetry has the potential to provide better insights into the causes of juvenile mortality as well as to provide robust mortality estimates.

In the current study, we used acoustic telemetry to monitor the fine-scale movements of juvenile age 1 and 2 *G. morhua* and age 1 *P. virens* during the period of seasonal migration from shallow summer habitats to deeper overwintering grounds. Specifically, our objectives were (1) to assess seasonal changes in the movement of juvenile *G. morhua* and *P. virens* at summer nurseries in relation to body size and water temperature, and (2) to examine how body size and condition, and temperature affect the timing of juveniles of each species leaving the in-fjord nursery grounds. We hypothesized that temperature and fish size were key drivers of both depth distribution in the fjord and timing of seasonal migration in juvenile *G. morhua* and *P. virens*. Understanding these factors can have implications for climate change planning and the protection and conservation of nearshore nursery grounds.

2 | METHODOLOGY

2.1 | Ethics statement

The care and use of experimental animals complied with the Act on Animal Welfare (55/2013, Icelandic legislation), guidelines, and policies as approved by the Icelandic Food and Veterinary Authority (MAST, license reference number: 2019-02-02).

2.2 | Study area

The study was conducted in Seyðisfjörður, a small fjord (11.5 km^2) located in the northwest of Iceland (Figure 1). The fjord is characterized by steep slopes dropping rapidly from 0 to 40 m depth in the east of the fjord, and by gentle slopes and plateaus (20 m depth) on the western side. The shoreline is dominated by rocky shore habitats vegetated by *Ascophyllum nodosum* and *Fucus vesiculosus* in the intertidal and Laminaria sp., *Saccharina latissimi*, and *Alaria esculenta* in the subtidal. The deepest areas of the fjord, with a maximum depth of 55 m, are at the mouth of the fjord. Seyðisfjörður opens into a large fjord system (Ísafjarðardjúp) with an average depth between 50 to 100 m and a maximum depth of 130 m (Hafrannsóknastofnun, n.d.).

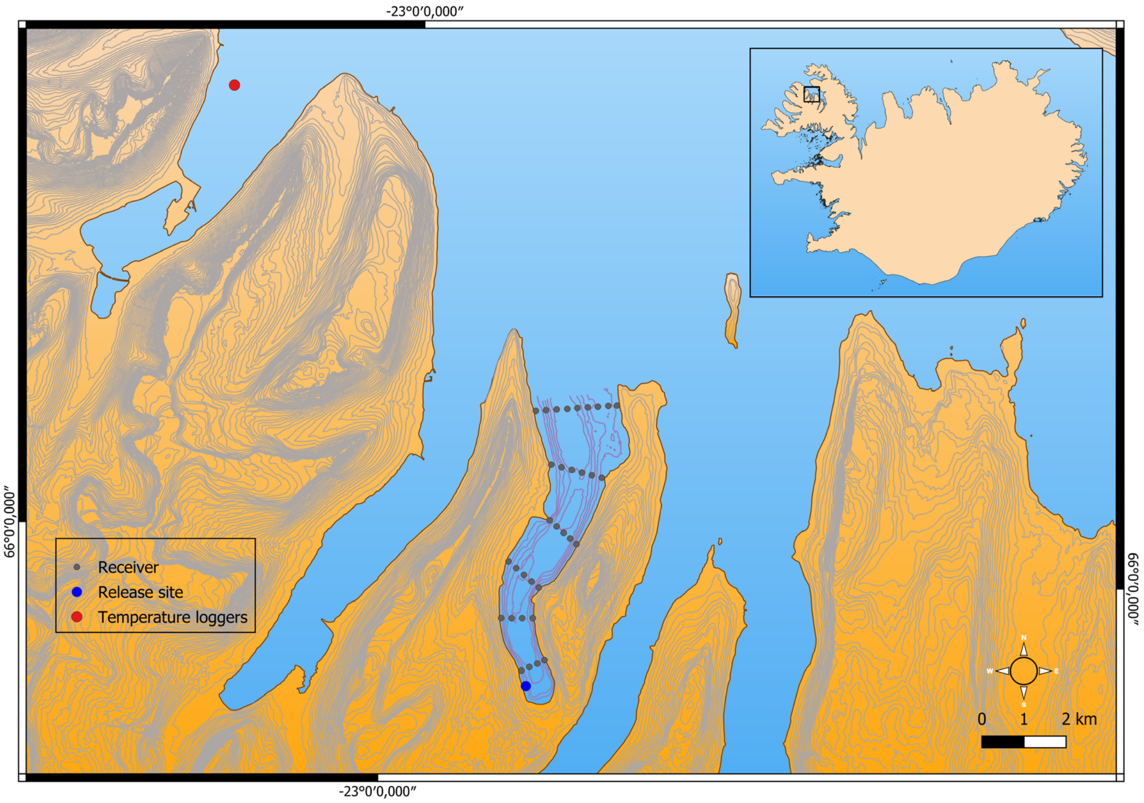

FIGURE 1 Overview map of the study fjord Seyðisfjörður and the surrounding area. Brown points indicate receiver locations in the study area, the blue point indicates the release site, and the red point indicates the location of the temperature loggers. The red lines indicate 10-m depth contours.

2.3 | Acoustic telemetry array

Movement data from an acoustic telemetry system were collected in Seyðisfjörður between July and November in 2020 and 2021. Within the fjord, 33 Vemco VR2W-180 kHz receivers were deployed in six gates across the fjord (Figures 1 and 2). Each receiver was kept at 2 m above the seafloor at a water depth between 5 and 55 m. The receivers were held buoyant with a submerged float 2 m above each device. Each receiver was attached to a mooring, which was connected to a surface float. The receivers' detection range for V5, V5D, and V7TP transmitters was estimated using five VR2W receivers evenly spaced out between 50 and 150 m distance from a V9-2H and a V4-1H transmitter. The range test was conducted over 4 days (103 h) and suggested a minimum detection range of 150 m. Based on these results, the receivers within gates were placed 250 m apart, allowing for overlapping detection ranges. The distance between gates was 840 to 1400 m (mean = 1130 m, standard deviation [SD] = 213 m). No commercial fishing or other commercial boating took place in the fjord during the study periods.

2.4 | Fish handling and tagging

A total of 53 *G. morhua* (21 in 2020, 32 in 2021) and 33 *P. virens* (19 in 2020, 14 in 2021) were tagged and released in Seyðisfjörður. Juveniles were caught between July and September in 2020 and 2021 using gill nets and fyke nets that were deployed in neighboring fjords to avoid recapture of tagged individuals. Juveniles were

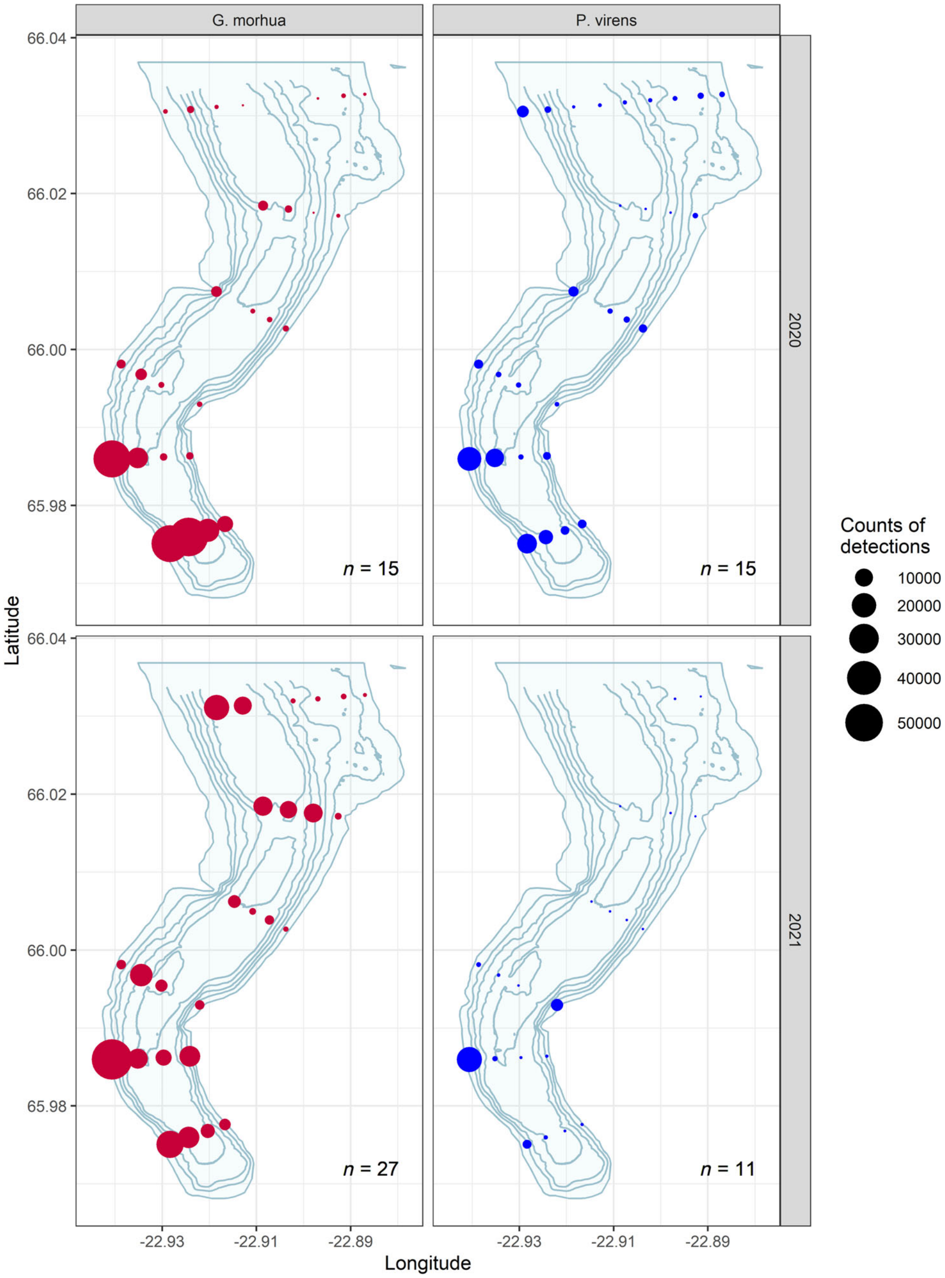

FIGURE 2 The distribution of fish detections in the study fjord. The blue lines indicate 10-m depth contours.

transported to the laboratory and kept for recovery for 6–12 hours before and after surgery. Individuals were anesthetized with MS-222 before (100 mg/L) and during (60 mg/L) the surgical implantation of the transmitter. The transmitter was inserted into the abdominal cavity of the fish through a 1.5-cm incision closed with a suture (Ethicon 8871H 4–0 with a RB-1 17 mm 1/2c taperpoint needle). Tagged fish were released over a period from 24 July until 24 September 2020 and from 9 July until 31 August 2021. The body length of tagged *G. morhua* was between 10.9 and 30.2 cm (mean = 17.8 cm) and weight was between 13.2 and 326.5 g (mean = 76.8 g). *P. virens* were between 11.7 and 22.8 cm long (mean = 17.9 cm) and had weight between 16.4 and 143.5 g (mean = 74.4 g) (Figure S2). The majority of *G. morhua* most likely represented age 1 juveniles but may also have included some age 2 (Jónsdóttir et al., 2019). The *P. virens* tagged in this study most likely belonged to age group 1 (Jónsdóttir, 2023). Fish length and weight were used to calculate the Fulton's body condition factor $K = 100WL^{-3}$ (Fulton, 1904), where W is body weight (g) and L is standard length (cm). The transmitter types used were V5, V5D, and V7TP from Innovasea (Vemco) with a random delay of 30–50 s and an expected battery life of 113, 86, and 118 days, respectively. As this study investigated juvenile gadoids between 11 and 30 cm in length, the smallest Vemco transmitter types available in 2020 (V5, V5D) were chosen. To further collect exact temperature and depth information of individual fish, a subset of 10 juveniles (five *G. morhua*, five *P. virens*) were tagged with V7TP transmitters equipped with depth and temperature sensors. Due to the larger size and weight of the V7TP transmitter, only juveniles larger than 19 cm ($\text{mean}_{G.\ morhua} = 24.2$ cm, $\text{mean}_{P. virens} = 21.1$ g) were selected for carrying the V7TP. The transmitter weight of all types was below 5% of the body weight in all fish.

2.5 | Data preparation

Position data from the receivers were downloaded and time corrected using VUE software (Vemco). Further data preparation, analysis, and visualization were done in the R environment using the RStudio Desktop application (R Core Team, 2016). *G. morhua* ($n = 11$) and *P. virens* ($n = 7$) were excluded from the data analysis when (1) they were detected for less than 24 h (and did not leave the fjord within that time), (2) they stopped moving within 24 h or (3) they did not show any movement post-release. From 86 tagged gadoid juveniles, 17 fish were excluded and 69 individuals were used for further analysis. The excluded fish (mean body length = 16.3 cm) were assumed to have died shortly after tagging (<24 h), which led to an estimated tagging mortality of 19.8%. Moreover, all detections logged after a predation event (indicated by predation sensors on V5D) were excluded from the further data analysis.

Position estimates representing short-term centers of activity were used to adjust for simultaneous detections of one individual at multiple receivers due to overlapping detection ranges. Hourly position estimates (HPEs), reflecting horizontal fish positions, were calculated for individual fish based on weighted means of the number of detections at each receiver during 1-h periods (Simpfendorfer et al., 2002). Consequently, the 546,669 detections used for analysis were reduced to 18,368 HPEs.

The depth at each HPE was calculated based on bathymetric data, whereby the water depth around each receiver was calculated as the mean of eight points, evenly distributed on a 150-m radius around the receiver (receiver specific detection range). The water depth around each receiver was then used to calculate the hourly depth estimates (HDEs) for individual fish based on weighted means of the number of detections at each receiver during 1-h periods. An HDE represents the estimated water depth at the corresponding HPE.

To test the coherence of HDEs and depth sensor data, HDEs were compared to observed depths from the 10 individuals tagged with V7TP depth-recording tags using a Wilcoxen rank sum test. Separate tests were conducted for each species and 10-cm size classes using the *wilcox. test* function in the Stats package (R Core Team, 2016).

Temperature records were obtained from eight temperature loggers attached to a fish farming pen from Hábrún ehf located in the mouth of the neighboring fjord Skutulsfjörður, 12 km distance from the study fjord. The temperature loggers were deployed at depths between 1.5 ("surface") and 15 m, and the sea temperature was recorded at 10-min intervals. Temperature records from the maximum depth available were considered representative for the benthic (*G. morhua*) and semibenthic (*P. virens*) study species and the daily mean temperature at 15 m depth was used in the statistical model. In addition, temperature data were collected at two locations at 2 m above the seafloor at 13 and 30 m depth in the study area, inside and close to the mouth of the fjord from 12 September until the 07 November 2021. The temperature data from the study fjord were at a similar range and described the same trend as the temperature measured from Skutulsfjörður (Figures 1 and S3).

2.6 | Fish fates

Fish fate was assigned to investigate the emigration and dispersal pattern of juvenile *G. morhua* and *P. virens*. Fish were classed as (1) "left fjord" when their last detection was at one of the two outermost gates, (2) "winter residency" when the individual mean absence period (i.e. temporal absence of detections) was smaller than the period between last detection and retrieval of the receivers, (3) "predation mortality" when predation tags (V5D) were triggered, or (4) "unknown" when last detection occurred within gates 1 to 4 and no other fate applied.

2.7 | Mortality

The instantaneous rate of mortality was determined for each species based on predation events indicated by acidity sensors (V5D). The yearly and daily instantaneous mortality rate (Z) was calculated using $N_t = N_0 e^{-Zt}$ (Anderson & Gregory, 2000), where N_0 is the number of fish carrying V5D tags at beginning of the study period ($N_{0G.morhua} = 3$ and $N_{0P.virens} = 5$ in 2020, $N_{0G.morhua} = 10$ and $N_{0P.virens} = 5$ in 2021), and N_t is the number of untriggered V5D tags ($N_{tG.morhua} = 3$ and $N_{tP.virens} = 5$ in 2020, $N_{tG.morhua} = 7$ and $N_{tP.virens} = 5$ in 2021) at the end of the study period (107 days in 2020, 129 days in 2021). From the instantaneous mortality rate calculated for each study year and species, the weighted mean based on numbers of V5Ds used in each study year was calculated for *G. morhua* and *P. virens*.

2.8 | Statistical analysis

2.8.1 | Seasonal migration

To quantify the effect of fish length, body condition (*k*), year, and species on the likelihood of leaving the study area, a Cox proportional regression model (CPH) was fitted for data on all fish. The event indicator of the hazard function was assigned with score "0" for fish with fate "winter residency", "unknown," and "predation mortality" ($n = 39$), while score "1" was given to individuals with fate "left fjord" ($n = 30$). The last detection day (day of year) of each individual was used as the measure of time from baseline to event or censoring. Model selection with a stepwise reduction by interaction terms and covariates was used to select the best supported model. The starting CPH model was fitted with the covariate "species" and interaction terms for body length and species, body condition and species, and year and species. The model included the interaction terms to account for the expected intraspecific differences within the explanatory variables. The best model indicated by the Akaike information criterion (AIC) was the CPH with an interaction term for body length and species and the two covariates "body condition" and "year" ($\Delta\text{AIC} = 1.1$ to second best model) (see model comparison in Table S2):

$$\text{Surv}(\text{day of last detection}, \text{status} \sim \text{length} : \text{species} + \text{body condition} + \text{year}$$

The CPH was performed in the "survival" package using the *coxph* function (Therneau, 2024).

2.8.2 | Distribution at nearshore nurseries

To account for potential effects on the fish from handling, surgery, and relocation, the movement data collected during the first 48 h post release were excluded in the following analysis. Consequently, the data frame was reduced from 18,368 HPE to 17,318 HPE and the number of fish analyzed decreased from 69 to 62.

The effect of temperature, fish length, diel period, and timing of release on the depth distribution of individual *G. morhua* and *P. virens* was evaluated by fitting a generalized additive mixed model (GAMM) to the HDEs using the *bam* function of the R-package mgcv (Wood, 2017). The statistical family was a gamma distribution with log link function. The model was fitted with species and length as interacting fixed effects, plus five smooth terms. Two smooth terms of class thin plate regression spline were fitted for temperature and day since release. Hour of the day was fitted using a smooth term of class cyclic cubic regression spline and was used to investigate the diel variation in the juveniles' depth distribution. An interaction term between longitude and latitude was included using a Gaussian process smoother. Individuals' ID was included with the random effect smooth term "re":

$$\begin{aligned}\text{depth} \sim \text{species}^{*}\text{length} + \text{s}(\text{temperature}, \text{by} = \text{species})\\ + \text{s}(\text{day since release}, \text{by} = \text{species}) + \text{s}(\text{hour}, \text{by} = \text{species})\\ + \text{s}(\text{longitude}, \text{latitude}) + \text{s}(\text{id})\end{aligned}$$

To account for differences between species, three smooth terms (temperature, day since release, and hour of the day) included the interaction term by species. The smooth term for day since release, that is the count of detection days for individual fish starting with 1 on the release day, was included to account for variation in the release date and hence the potential for different temperature experience among individuals. The interactive smoother between longitude and latitude smooth term was included after spatial correlation was indicated by GAMM residuals. Smoothing parameters in both models were estimated using restricted maximum likelihood.

The model diagnostics included the inspection of fitted residuals and smoothness parameter *k* using the *gam. check* function in mgcv (Wood, 2017). Model dispersion was tested using a simulation-based, nonparametric dispersion test in the R-package Dharma (Hartig, 2022). Fitted residuals were mapped and visually inspected for spatial autocorrelation.

Finally, as tagged fish were released at different times, potentially affecting the detection period and thereby the subsequent analysis, the effect of the release date on the detection period of individuals was tested using a Spearman correlation test. The variables were "day of the year" for the release date and "count of detection days" for individual fish.

3 | RESULTS

Acoustically tagged fish were detected between 24 July to 12 November 2020 and 09 July to 17 November 2021. Mean daily surface temperatures during the study periods were similar between 2020 ($T_{\text{surf}} = 7.2°\text{C}$) and 2021 ($T_{\text{surf}} = 7.8°\text{C}$), as were mean daily temperatures at 15 m ($T_{15} = 8.1°\text{C}$ and $T_{15} = 8.3°\text{C}$, respectively). However, the temperature range in 2021 was greater (Figure 3). Daily mean surface temperatures ranged from 2.5 to 13.1°C in 2020 and from 0.8 to 16.9°C in 2021. Temperatures at 15 m depth ranged between 6.3 and 9.3°C in 2020 and between 4.2 and 11.1°C in 2021.

Based on the exclusion criteria described above, the telemetry data from 43 *G. morhua* and 26 *P. virens* were used for the statistical analysis (Table 1 and S1). Moreover, two *G. morhua* and five *P. virens* with less than a 48-h detection period were excluded from the data modeled in the GAMM. The time spent in the study area differed between individuals and species. *G. morhua* was detected for

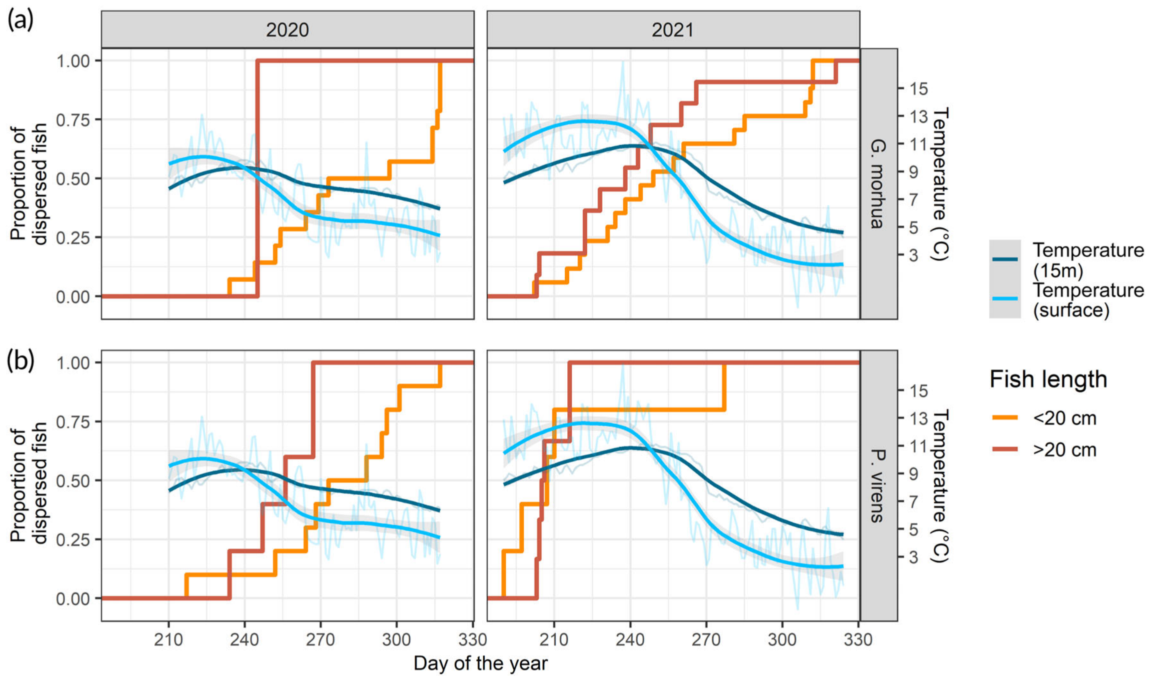

FIGURE 3 Proportion of (a) *Gadus morhua* and (b) *Pollachius virens* dispersing from the fjord during the study period in 2020 and 2021 shown by empirical cumulative distribution functions for 10-cm size classes (stepped lines). Water temperature at surface (light blue) and 15 m depth (dark blue) during the study period is shown on the second *y* axis. Thick blue lines show conditional mean temperatures (smooth method *loess*) and thin lines are observed daily mean temperatures. Shaded areas show the 95% confidence interval.

TABLE 1 Summary data for the 69 acoustically tagged *Gadus morhua* and *Pollachius virens* tagged in the Icelandic Westfjords.

Year	Species	Number of individuals	Length, cm: M ± SD (min–max)	Weight, g: M ± SD (min–max)	Number of transmitters V5/V5D/V7TP	Counts of HPEs	HDE, m: M ± SD (min–max)
2020	*G. morhua*	15	16.5 ± 2.5 (12.6–22.4)	51.9 ± 28.4 (23.2–141.8)	14/3/0	5554	21.4 ± 5.2 (12.1–28.7)
2021	*G. morhua*	28	19.6 ± 5.3 (13.2–30.2)	105 ± 91.7 (22.3–326.5)	12/11/5	9596	29.2 ± 11.3 (11.2–46.7)
2020	*P. virens*	15	16.6 ± 4.3 (11.7–22.8)	62.0 ± 44.4 (16.4–138.6)	10/5/0	1581	17.0 ± 3.7 (10.2–25.6)
2021	*P. virens*	11	19.5 ± 3.1 (13.7–22.6)	92.5 ± 41.9 (28.5–143.5)	2/5/4	1590	13.8 ± 3.8 (9.2–22.1)

Note: The depth information is based on hourly depth estimates (HDEs).
Abbreviations: HPE, hourly position estimate; M, mean; min–max, minimum–maximum; SD, standard deviation.

significantly longer periods (mean = 41 days, SD = 30.8) than *P. virens* (mean = 16 days, SD = 17.6) (Table S1) (Wilcoxon test, $p < 0.001$). No significant correlation was found between release date and the detection period tested for species or year (Spearman correlation, $p > 0.2$).

Based on a comparison of the V7TP depth sensor data and the HDEs, HDEs were a good indicator of fish depth for *G. morhua* but not for *P. virens*. The vertical distribution from the V7TP depth sensors occurred at a mean depth of 42 ± 0.53 m for *G. morhua* ($n = 5$) and 4.8 ± 0.56 m for *P. virens* ($n = 4$). No significant difference (Wilcoxon test, $p = 0.39$) was found between the observed depth (V7TP) of *G. morhua* and the HDEs, indicating that *G. morhua* were distributed near the sea floor. In contrast, there was a significant difference (Wilcoxon test, $p < 0.001$) between observed depth (V7TP) and HDEs for *P. virens*, with V7TP depth describing a much shallower, near-surface distribution (Figure 5b).

3.1 | Fish fates

Tagged juveniles were assigned to one of four fish fates (Table 2). Out of 43 *G. morhua*, 47% dispersed from the study area ("left fjord") and 26% remained in the fjord until the receiver retrieval ("winter resident"). Predation mortality was assigned to 7% of *G. mohua* based on triggered acidity sensors and 21% had an unknown fate. The fate "winter resident" was only assigned to small *G. morhua* and accounted for 50% of the individuals below 20 cm. Out of 26 *P. virens*, 38.5% left the study fjord and 61.5% were assigned to an unknown fate.

TABLE 2 Summary data on fish fates assigned to 69 acoustically tagged *Gadus morhua* and *Pollachius virens*.

Species	Fish fate	Number of individuals	Length, cm: M ± SD (min–max)	Body condition: M ± SD (min–max)	Days tracked: M ± SD (min–max)	Day of last detection: M ± SD (min–max)	Depth, m: M ± SD (min–max)
G. morhua	Left fjord	20	20.7 ± 5.6 (14.4–30.2)	1.13 ± 0.09 (0.99–1.27)	28 ± 19 (2–88)	242 ± 24 (203–285)	31.5 ± 14.5 (5.3–64.5)
G. morhua	Winter residency	11	16.6 ± 2.3 (13.2–21.9)	1.06 ± 0.06 (0.97–1.13)	80 ± 20 (62–127)	315 ± 4 (309–321)	20.3 ± 13.1 (8.4–61.8)
G. morhua	Predation mortality	3	19.9 ± 4.9 (16.7–25.6)	1.06 ± 0.13 (0.97–1.15)	35 ± 33 (3–69)	231 ± 32 (199–264)	33.3 ± 14.1 (5.7–63.7)
G. morhua	Unknown	9	15.1 ± 2.0 (12.6–18)	1.04 ± 0.09 (0.88–1.16)	21 ± 19 (2–51)	249 ± 26 (202–297)	23.1 ± 6.5 (5.1–46.1)
P. virens	Left fjord	10	19.0 ± 3.8 (13.0–22.8)	1.14 ± 0.09 (0.98–1.27)	19 ± 22 (1–48)	255 ± 19 (216–277)	11.9 ± 5.1 (5.2–57.1)
P. virens	Unknown	16	16.5 ± 4.3 (11.7–22.6)	1.14 ± 0.08 (1.02–1.26)	14 ± 15 (2–71)	248 ± 46 (197–317)	18.1 ± 8.5 (5.2–55.2)

Note: The depth information is based on GAMM predictions.

Abbreviations: M, mean; min–max, minimum–maximum; SD, standard deviation.

Individuals with unknown fates could have left the fjord or died, since receiver losses within the outer gates and close to land in 2021 may have reduced the detections during the out-migration from the fjord, especially for *P. virens*.

3.2 | Mortality

Predation of tagged juveniles was investigated by using 23 V5D transmitters. Of those, three acidity sensors, all carried by *G. morhua*, were triggered in 2021 (note: only two of the three fish were detected for more than 24 h and hence only those two are included in Table 2). The instantaneous mortality rate based on predation of *G. morhua* was 0.78/year (0/year in 2020, 1.01/year in 2021) and 0.0021/day (0/day in 2020, 0.0028/day in 2021). No predation transmitter was triggered in *P. virens*, so the instantaneous mortality rate was estimated as 0.

3.3 | Seasonal migration

In the Cox proportional hazards model, the effect of fish length significantly affected the likelihood of *G. morhua* ($p < 0.01$) and *P. virens* ($p < 0.01$) leaving the fjord (Table 3). Larger fish were more likely to leave the fjord than smaller ones (hazard ratio $[\mathrm{HR}]_{G.mohua} = 1.17$, $\mathrm{HR}_{P.virens} = 1.23$) (Table 3). The model with the best fit (AIC; Table S2) also included body condition and year, suggesting that both covariates impact the likelihood of *G. morhua* and *P. virens* leaving the fjord. Both the likelihood ratio test ($p < 0.01$) and Wald test statistics ($p < 0.01$) for the CPH model were significant.

3.4 | Distribution at nearshore nurseries

The results from the GAMM showed a strong effect of *G. morhua* body length on depth, as inferred receiver depths (Figure 4). Juveniles smaller than 20 cm occupied significantly shallower waters (mean = 20.4 m, SD = 9.7 m) than *G. morhua* larger than 20 cm (mean = 44.1 m, SD = 12.8 m) (Wilcoxon test, $p = <0.001$) (Table 4). Conversely, *P. virens* occupied mainly nearshore, shallow waters with little variation in inferred depth (mean = 15.0 m, SD = 8.2 m) between different body lengths (Figure 4).

Changes in the water temperature mainly affected the depth distribution of juveniles inhabiting the shallow waters of the study area (Figure 5). Individuals smaller than 20 cm moved into slightly shallower waters with decreasing temperatures. The GAMM results indicated a shallow distribution of larger *G. morhua* at temperatures around 8.5°C, but this may represent the distribution of newly tagged individuals after their release into shallow waters (Figure S5). More variation in horizontal distribution was observed in small *G. mohua*

TABLE 3 Summary results of the Cox proportional hazards model evaluating the effect of covariates on the migratory propensity of juvenile *Gadus morhua* and *Pollachius virens*.

Characteristic	Coefficient	HR	95% CI lower	95% CI upper	*p* value
k	3.69	40.14	0.39	4.16E+03	0.12
y	0.95	2.59	0.95	7.08	0.06
G. morhua:length	0.16	1.17	1.08	1.27	<0.01
P. virens:length	0.21	1.23	1.12	1.36	<0.01

Note: The covariates included species, body length, body condition (*k*), and year (*y*).
Abbreviations: CI, confidence interval; HR, hazard ratio.

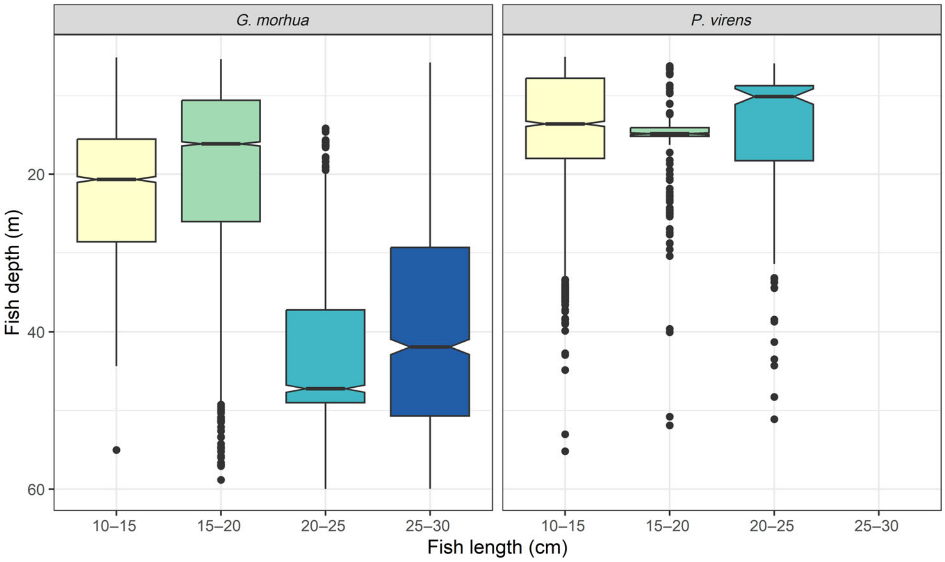

FIGURE 4 Comparisons of the depth distribution of 5-cm size-classes of juvenile *Gadus morhua* and *Pollachius virens* for the entire study period and area. Each box represents 50% of the fish depth predictions (GAMM) distributed between the 1st and 3rd quartiles. The notch on each box indicates the 95% confidence interval of the median. Whisker length is limited to 1.5*interquartile range and points represent individual values outside this range.

TABLE 4 Parameter estimates for the generalized additive mixed model (GAMM) summarize the effect of each predictor on the hourly depth estimates (HDEs) of juvenile *Gadus morhua* and *Pollachius virens*.

Smooth term	Species	Edf	Ref. df	*F* value	*p* value	Parametric coefficient	Estimate	Standard error	*t* value	*p* value
						Intercept	2.82	0.05	42.39	<0.01
						P. virens	−3.19	2.27	−1.41	0.16
						G. morhua: length	1.20E−2	<0.01	3.431	<0.01
						P. virens:length	−1.11E−3	<0.01	−0.16	0.87
s(h, by = species)	*G. morhua*	1.88	2.00	26.82	<0.01					
s(h, by = species)	*P. virens*	1.63	2.00	9.53	<0.01					
s(lon, lat)		16.00	16.00	1.18E+04	<0.01					
s(temp, by = species)	*G. morhua*	8.42	9.26	19.39	<0.01					
s(temp, by = species)	*P. virens*	5.11	6.19	7.48	<0.01					
s(dar, by = species)	*G. morhua*	8.44	9.79	9.44	<0.01					
s(dar, by = species)	*P. virens*	9.97	10.17	14.00	<0.01					

Note: The predictors included species and body length as fixed effects with interaction effect and smooth terms for daytime (h), longitude and latitude (lon, lat), water temperature at 15 m depth (temp) and day after release (dar). All smoothers except "lon, lat" included the interaction term "by species".

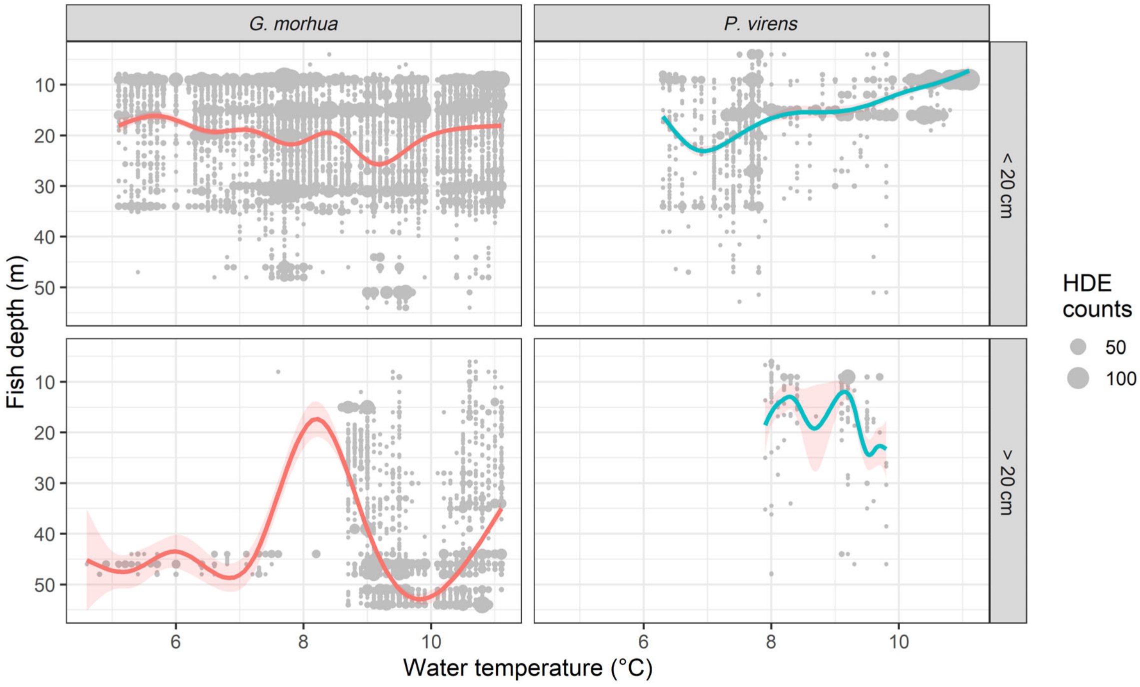

FIGURE 5 Depth distribution of juvenile *Gadus morhua* and *Pollachius virens* as a function of water temperature at 15-m depth and fish length. Solid lines are fish depth estimates from GAMM predictions (smooth method *gam*) and gray points are the observed fish depth weighted by counts of HDEs. Light red areas show the 95% confidence interval.

than in large individuals. *P. virens* smaller than 20 cm increased in depth with decreasing temperatures, from a mean depth at 10.9 m above 8°C to 19.3 m below 8°C, reflecting an increase in their distance to land at lower temperatures (Figure 5).

Diurnal vertical migration was exhibited by *G. morhua*, especially by *G. morhua* smaller than 20 cm (Figure 6a). The juveniles moved from deeper areas during the day into shallower waters closer to land during night. This pattern was described by both the model predictions and the observed depth data from the five *G. morhua* with depth sensors (Figure 6a,b). No diurnal vertical migration was observed for *P. virens*.

The interactive smoother between longitude and latitude in the model, included to correct for spatial correlation, confirmed the distribution of larger *G. morhua* in the central and deeper areas of the fjord

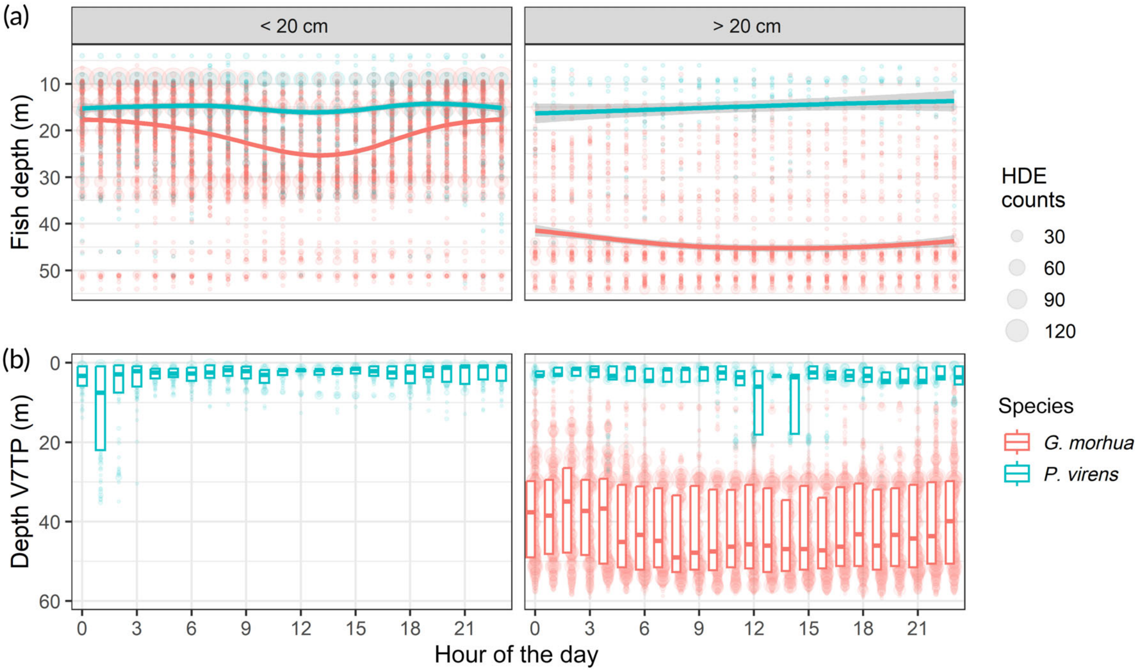

FIGURE 6 Depth distribution of *Gadus morhua* and *Pollachius virens* as a function of fish size and hour of day. (a) Solid lines show the estimated fish depth predicted from the GAMM (smooth method *gam*) and points are calculated hourly depth estimates (HDEs) weighted by their counts. (b) Box plots compare observed values from depth sensors (V7TP) of *G. morhua* ($n = 5$) and *P. virens* ($n = 4$) between hours of the day. Points show depth measurements from depth sensors (V7TP) weighted by their counts.

(Figure S4a). Small *G. morhua* and *P. virens* were closer to land, especially close to the western shore, where the tagged fish were released (Figure 1). The variation in juvenile depth distribution along the fjord increased with latitude, reflecting the fjord's bathymetry. Overall, *G. morhua* went deeper with increasing latitude, while, despite increasing variation in the depth distribution, *P. virens* stayed equally shallow along the fjord (Figure S4b).

GAMM results showed little effect of "day after release" on the depth distribution of small *G. morhua* (Figure S5). For larger *G. morhua*, the model predictions indicated a shallow distribution during the first days after release as well as around 50 days after release. Larger *P. virens* went deeper with time after release, while no clear trend was apparent for smaller *P. virens*.

The covariates and smooth terms in the GAMM explained 97.2% of the variance of the depth distribution of juvenile *G. morhua* and *P. virens* ($R^2 = 0.96$). High significance ($p < 0.001$) of the random effect term in the GAMM indicated high between individual variation (Table 4). The difference between simulated and observed model dispersion was close to 1 (dispersion parameter = 1.05, $p = 0.008$).

4 | DISCUSSION

The results from our study revealed wide horizontal and vertical distribution of age 1 and 2 *G. morhua* within the fjord. Larger *G. morhua* inhabited deeper, cooler waters than smaller juveniles. Ontogenetic shifts to deeper habitats have previously been linked to a decrease in optimal temperatures with *G. morhua* body size (Tirsgaard et al., 2015). Larger juveniles may disproportionately benefit from cooler temperatures that decrease metabolic rates and growth, but also increase longevity (Malek et al., 2004; Valenzano et al., 2006). Conversely, smaller juveniles may benefit more from increased growth rates, fuelled by warmer temperatures, and diverse feeding grounds in the shallowest waters (Árnason et al., 2009; Perry et al., 2018). A wider thermal tolerance may allow small juvenile *G. morhua* to remain within shallow waters despite seasonal temperature fluctuations (Tirsgaard et al., 2015). In contrast to *G. morhua*, *P. virens* of all size classes were mainly observed in shallow waters close to land. This is consistent with previous studies in North America (Cargnelli et al., 1999) and the Faroe Islands (Bertelsen, 1942) where age group 0 and 1 *P. virens* inhabited the inter and subtidal areas during summer and autumn. The cooccurrence of different size classes of juvenile *P. virens* suggested that neither thermal range nor intraspecific competition limited their occurrence in the shallow water habitats.

Predation is another potential driver for the depth segregation of juvenile *G. morhua*. Shallow vegetated rocky shores provide structured habitats suitable for small juvenile fish to hide from predators (Bogstad et al., 2016; Riley & Parnell, 1984). The presence of active predators, including conspecifics, is known to drive juvenile *G. morhua* into structurally more complex habitats (Gotceitas et al., 1995; Rangeley & Kramer, 1995b) and predation pressure is expected to increase with depth because of less vegetation and larger fish (Linehan et al., 2001).

Irrespective of the main driver, segregation by depth, as observed between size classes of *G. morhua* and between *P. virens* and larger *G. morhua*, may reduce resource competition among the gadoids.

Despite ontogenetic niche shifts (Ólafsdóttir et al., 2015), competition for trophic resources between different sized juvenile *G. morhua* prevails as larger individuals feed on small prey items when large prey is absent (Hanson & Chouinard, 2002; Link et al., 2009). Habitat overlap in the current study occurred primarily between small juvenile *G. morhua* and *P. virens*. However, a demersal distribution of *G. morhua* and semi-pelagic distribution of *P. virens* was confirmed by depth sensors (V7TP), suggesting vertical separation between the species within the water column. Again, vertical segregation may reduce niche overlap and facilitate coexistence of different species and cohorts at nurseries.

The observed variation in the depth distribution of *G. morhua* may also be linked to diel migration patterns. Numerous studies suggest that diel migration of *G. morhua* results from nocturnal feeding migrations into relatively shallow waters driven by multiple factors, such as rich feeding resources, predation risk (Espeland et al., 2010), optimal metabolic rate (Árnason et al., 2009; Tirsgaard et al., 2015), and growth (Armstrong et al., 2013). In the current study, the observed diel migration patterns were most pronounced among juvenile *G. morhua* smaller than 20 cm, indicating that vertical diel migration changes with ontogeny. This is in accordance with a study on *G. morhua* in Norway, which showed a stronger vertical diel migration pattern among "small" juveniles (35 cm) than larger ones (75 cm) (Freitas et al., 2015). The absence of a diel horizontal movement in *P. virens* is contrary to a previous beach seining study in the Bay of Fundy where juvenile *P. virens* was more abundant in shallow waters during night than day (Rangeley & Kramer, 1995a). However, most transmitters used in the current study did not include depth sensors, which limited the possibilities to identify very small-scale fish movement as in the case of potential vertical migration of *P. virens* within the shallow waters.

The two species also differed in larger scale migration patterns. Dispersal from the study fjord often occurred when water temperatures were high, suggesting seasonal temperature fluctuations as potential triggers for migration timing of *P. virens* and larger *G. morhua* from summer habitats. Juvenile *P. virens* dispersed from the study area earlier in the warmer year of 2021 when the last detections of *P. virens* occurred before temperatures reached their annual maximum. The dispersal of *G. morhua*, especially larger individuals, occurred during the first half of September. This time reflects decreased thermal stratification usually leading to mixing of warm, surface layers and deeper layers, and consequently to the increase of near-bottom temperatures (Pinet, 2019). The decrease of the thermocline as well as changes in the bottom temperatures have previously been suggested to affect migration timing of demersal *G. morhua* (Comeau et al., 2001; Cote et al., 2004). Changing temperatures are known to trigger migration timing, for example in juvenile salmonids (Teichert et al., 2020; Whalen et al., 1999), and water temperatures exceeding the optimal thermal range can affect the distribution and migration of gadoids on both small (Freitas et al., 2016) and large (Von Leesen et al., 2022) scales.

The optimum thermal range of fish declines with body size (Lindmark et al., 2022), and this has been confirmed in laboratory studies for juvenile *G. morhua* (Árnason et al., 2009; Tirsgaard et al., 2015). No experimental study on the thermal optimum is available for juvenile *P. virens*. However, fisheries surveys in the Gulf of Maine found juvenile *P. virens* (<30 cm) most abundant at water temperatures between 3 and 12°C (Cargnelli et al., 1999). In the current study *P. virens* left the fjord at temperatures exceeding a similar range of 3–11.6°C, supporting the previously reported thermal range. For both species, an early dispersal from summer foraging grounds may lead to a shortened time for energy uptake, growth, and consequently lower amounts of lipid storage. Long-term data from the Skagerrak coast in Norway showed a lower abundance and smaller body sizes of age 0 *G. morhua* during unfavorable hot summer temperatures (>16°C) (Rogers et al., 2011). Hence, increased summer temperatures, due to global climate change, may reduce the feeding period of juvenile *G. morhua* and *P. virens* in the nearshore summer habitats, leading to reduced growth rates and consequently to increased predation pressure and winter mortality.

G. morhua smaller than 20 cm were present in the fjord throughout the study period, across a wide thermal range, suggesting that neither photoperiod nor temperature cued seasonal migration of this group. Intrinsic factors such as body condition or thyroid hormone level have been suggested to determine migration timing between summer and overwintering grounds in adult *G. morhua* (Comeau et al., 2001, 2002). In the current study, body size was the main factor determining the juveniles' migratory propensity as only *G. morhua* smaller than 20 cm stayed until the end of the study period in mid-November. Two previous studies using acoustic telemetry on age 2+ juvenile *G. morhua* found that around 30% of the fish remained within shallow summer nurseries during winter, especially small individuals and individuals with poor body condition (Cote et al., 2004; Strøm et al., 2023). In the current study, body condition was determined during the surgical implantation of the transmitter and may have changed during the study period in summer and autumn, when annual somatic growth rates are highest. Nevertheless, the hazard ratio from the Cox model showed a trend for fish with lower body condition to be less likely to leave the fjord.

Homing behavior could also contribute to the tendency to leave the fjord considering that tagged fish originated from adjacent fjords. High site fidelity and homing behavior have previously been described for different life stages of *G. morhua* (Morris et al., 2014; Svedäng et al., 2007) and *P. virens* (Jónsson et al., 2007; Saha et al., 2015). *G. morhua* were detected for periods up to 127 days (mean = 41), suggesting that the juveniles, especially smaller individuals, settled successfully after translocation. Conversely, *P. virens* stayed for shorter periods but differences of detection periods between years suggested that temperature rather than homing behavior determined the timing of dispersal. Even though homing behavior cannot be excluded, no evidence for instantaneous homing behavior was found for either species.

The partial migration of juvenile *G. morhua* from the in-fjord foraging ground suggested seasonal migration as a flexible strategy, perhaps to reduce predation and optimize energetic expenditure. Small juvenile *G. morhua* benefit from increased levels of antifreeze glycoprotein that allow them to remain within the shallow waters for extended periods (Goddard et al., 1997), thereby avoiding increased predation in deeper waters. Moreover, winter residency might reduce energetic costs and thereby increase winter survival for the smallest fish as small fish burn lipid reserves at higher rates (Bochdansky & Leggett, 2001). Small juvenile *G. morhua* with poor body condition prior to winter are generally at greater risk of winter mortality (Geissinger et al., 2022), therefore winter residency of small juvenile *G. morhua* with poor body condition at the lowest temperatures could be a strategy to reduce the amount of metabolized fat reserves and with that to increase the chance of winter survival. Contrary to juvenile *G. morhua* all the tagged *P. virens* left the study fjord. However, it remains unclear if this reflects a habitat shift since they remained close to land, and in shallow waters, as they dispersed.

The instantaneous mortality rate for *G. morhua* was 0.78/year (0.0021/day), considerably higher than previous estimates for age 1–4 juvenile *G. morhua* (0.3 and 0.6/year), based on bottom trawl surveys (Neuenhoff et al., 2019). Acoustic telemetry can be used to predict mortality rates with high accuracy but assigning the cause of mortality to fish that are not continuously detected can be challenging (Lennox et al., 2023; Vollset et al., 2023). Because fish fates could not be assigned to all fish in the current study, only data from juveniles carrying a predation sensor were used for calculations of the mortality rates, therefore mortality rates only reflect predation from fish or marine mammals, excluding predation events that may have happened out of range of the receivers and avian predation, which may be high in Iceland (Fayet et al., 2021). Moreover, a recent study on the effectiveness of acidity sensors showed that only 50% of predation events were identified by V5D transmitters (Lennox et al., 2021). No predation on *P. virens* was indicated by the sensors, despite more *P. virens* being tagged with predation transmitters than *G. morhua*. This supports the hypothesis that shallow, structurally diverse habitats reduce predation pressure on juvenile fish (Perry et al., 2018). Even though the relatively small sample size of 23 V5D transmitters used in this study does not allow precise estimates of predation mortality, this study provides the first mortality estimates on juvenile *G. morhua* and *P. virens* based on acoustic telemetry.

To conclude, our results highlight the importance of nearshore habitats as nursery grounds for age 1 and 2 *G. morhua* and *P. virens*. Results showed a clear vertical segregation between size groups and species, which were likely driven by size-dependent thermal preferences, predation pressure, and niche differentiation among juvenile gadoids at summer nurseries. Changes in the water temperature affected the distribution of juvenile *G. morhua* and *P. virens* at nurseries and were a major driver for leaving the fjord. Higher temperatures during the second study year led to an early out-migration of *P. virens*, highlighting the effect of temperature on the gadoid juvenile distribution in shallow nurseries. The utilization of nearshore habitats of juvenile *G. morhua* extends from the summer feeding period and into the winter for a subset of the population, potentially enhancing energetic benefits and reducing predation pressure during the winter months. In relation to climate change, our findings suggest that juvenile gadoids will spend less time in the nearshore summer habitats to avoid high water temperatures and consequently may suffer from reduced growth and increased predation pressure, leading to higher juvenile mortality.

AUTHOR CONTRIBUTIONS

Conceptualization: A.K.N., G.A.Ó., and S.E.C. Data collection and curation: A.K.N. and G.A.Ó. Data interpretation and investigation: A.K.N., G.A.Ó., and S.E.C. Data analysis: A.K.N., G.A.Ó., and S.E.C. Writing – original draft: A.K.N. Writing – review and editing: A.K.N., G.A.Ó., and S.E.C. Supervision: G.A.Ó. and S.E.C. Funding: A.K.N. and G.A.Ó.

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REFERENCES

Anderson, J. T., & Gregory, R. S. (2000). Factors regulating survival of northern cod (NAFO 2J3KL) during their first 3 years of life. *ICES Journal of Marine Science*, *57*(2), 349–359.

Armannsson, H., & Jónsson, S. Þ. (2012). Vertical migrations of saithe (*Pollachius virens*) in Icelandic waters as observed with data storage tags. *ICES Journal of Marine Science*, *69*(8), 1372–1381.

Armstrong, J. B., Schindler, D. E., Ruff, C. P., Brooks, G. T., Bentley, K. E., & Torgersen, C. E. (2013). Diel horizontal migration in streams: Juvenile fish exploit spatial heterogeneity in thermal and trophic resources. *Ecology*, *94*(9), 2066–2075.

Árnason, T., Björnsson, B., & Steinarsson, A. (2009). Allometric growth and condition factor of Atlantic cod (*Gadus morhua*) fed to satiation: Effects of temperature and body weight. *Journal of Applied Ichthyology*, *25*(4), 401–406.

Barth, J. M., Villegas-Ríos, D., Freitas, C., Moland, E., Star, B., André, C., Knutsen, H., Bradbury, I., Dierking, J., Petereit, C., Righton, D., Metcalfe, J., Jakobsen, K. S., Olsen, E. M., & Jentoft, S. (2019). Disentangling structural genomic and behavioural barriers in a sea of connectivity. *Molecular Ecology*, *28*(6), 1394–1411.

Bertelsen, E. (1942). Contributions to the biology of the coalfish-Gadus Virens L.-in Faroe waters, with special regard to the youngest age groups. *Meddelelser Fra Kommissionen for Danmarks Fiskeri- Og havundersøgelser*, *XI*, *2*, 3–69.

Birnie-Gauvin, K., Flávio, H., Kristensen, M. L., Walton-Rabideau, S., Cooke, S. J., Willmore, W. G., Koed, A., & Aarestrup, K. (2019). Cortisol predicts migration timing and success in both Atlantic salmon and sea trout kelts. *Scientific Reports*, *9*(1), 2422.

Bochdansky, A. B., & Leggett, W. C. (2001). Winberg revisited: Convergence of routine metabolism in larval and juvenile fish. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*(1), 220–230.

Bogstad, B., Yaragina, N. A., & Nash, R. D. (2016). The early life-history dynamics of Northeast Arctic cod: Levels of natural mortality and abundance during the first 3 years of life. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*(2), 246–256.

Brönmark, C., Skov, C., Brodersen, J., Nilsson, P. A., & Hansson, L. A. (2008). Seasonal migration determined by a trade-off between predator avoidance and growth. *PLoS One*, *3*(4), e1957. https://doi.org/10.1371/journal.pone.0001957

Cargnelli, L. M., Griesbach, S. J., Packer, D. B., Berrien, P., Johnson, D. L., & Morse, W. W. (1999). Essential fish habitat source document. Pollock, *Pollachius virens*, life history and habitat characteristics. NOAA technical memorandum NMFS-NE; 131. Available at: https://repository.library.noaa.gov/view/noaa/3117

Chaput, G., Carr, J., Daniels, J., Tinker, S., Jonsen, I., & Whoriskey, F. (2019). Atlantic salmon (*Salmo salar*) smolt and early post-smolt migration and survival inferred from multi-year and multi-stock acoustic telemetry studies in the Gulf of St. Lawrence, northwest Atlantic. *ICES Journal of Marine Science*, *76*(4), 1107–1121.

Clark, D. S., & Green, J. M. (1990). Activity and movement patterns of juvenile Atlantic cod, *Gadus morhua*, in Conception Bay, Newfoundland, as determined by sonic telemetry. *Canadian Journal of Zoology*, *68*(7), 1434–1442.

Clay, D., Stobo, W. T., Beck, B., & Hurley, P. C. F. (1989). Growth of juvenile pollock (*Pollachius virens* L.) along the Atlantic coast of Canada with inferences of inshore-offshore movements. *Journal of Northwest Atlantic Fishery Science*, *9*(1), 37–43.

Comeau, L. A., Campana, S. E., & Chouinard, G. A. (2002). Timing of Atlantic cod (*Gadus morhua* L.) seasonal migrations in the southern gulf of St Lawrence: Interannual variability and proximate control. *ICES Journal of Marine Science*, *59*(2), 333–351.

Comeau, L. A., Campana, S. E., Chouinard, G. A., & Hanson, J. M. (2001). Timing of Atlantic cod *Gadus morhua* seasonal migrations in relation to serum levels of gonadal and thyroidal hormones. *Marine Ecology Progress Series*, *221*, 245–253.

Copeman, L. A., Laurel, B. J., Spencer, M., & Sremba, A. (2017). Temperature impacts on lipid allocation among juvenile gadid species at the Pacific Arctic-boreal interface: An experimental laboratory approach. *Marine Ecology Progress Series*, *566*, 183–198.

Cote, D., Moulton, S., Frampton, P. C. B., Scruton, D. A., & McKinley, R. S. (2004). Habitat use and early winter movements by juvenile Atlantic cod in a coastal area of Newfoundland. *Journal of Fish Biology*, *64*(3), 665–679.

Cote, D., Ollerhead, L. M. N., Gregory, R. S., Scruton, D. A., & McKinley, R. S. (2002). Activity patterns of juvenile Atlantic cod (*Gadus morhua*) in Buckley Cove, Newfoundland. In *Aquatic Telemetry: Proceedings of the Fourth Conference on Fish Telemetry in Europe* (pp. 121–127). Springer.

Cote, D., Scruton, D. A., Niezgoda, G. H., & McKinley, R. S. (1998). A coded acoustic telemetry system for high precision monitoring of fish location and movement: Application to the study of nearshore nursery habitat of juvenile Atlantic cod (*Gadus morhua*). *Marine Technology Society Journal*, *32*(1), 54.

Dunlop, K., Staby, A., van der Meeren, T., Keeley, N., Olsen, E. M., Bannister, R., & Skjæraasen, J. E. (2022). Habitat associations of juvenile Atlantic cod (*Gadus morhua* L.) and sympatric demersal fish communities within shallow inshore nursery grounds. *Estuarine, Coastal and Shelf Science*, *279*, 108111.

Espeland, S. H., Thoresen, A. G., Olsen, E. M., Stige, L. C., Knutsen, H., Gjøsæter, J., & Stenseth, N. C. (2010). Diel vertical migration patterns in juvenile cod from the Skagerrak coast. *Marine Ecology Progress Series*, *405*, 29–37.

Fayet, A. L., Clucas, G. V., Anker-Nilssen, T., Syposz, M., & Hansen, E. S. (2021). Local prey shortages drive foraging costs and breeding success in a declining seabird, the Atlantic puffin. *Journal of Animal Ecology*, *90*(5), 1152–1164.

Freitas, C., Olsen, E. M., Knutsen, H., Albretsen, J., & Moland, E. (2016). Temperature-associated habitat selection in a cold-water marine fish. *Journal of Animal Ecology*, *85*(3), 628–637.

Freitas, C., Olsen, E. M., Moland, E., Ciannelli, L., & Knutsen, H. (2015). Behavioral responses of Atlantic cod to sea temperature changes. *Ecology and Evolution*, *5*(10), 2070–2083.

Freitas, C., Villegas-Ríos, D., Moland, E., & Olsen, E. M. (2021). Sea temperature effects on depth use and habitat selection in a marine fish community. *Journal of Animal Ecology*, *90*(7), 1787–1800.

Fulton, T. W. (1904). On the spawning of the cod (*Gadus morrhua* L.) in autumn in the North sea. *Sea*, *6*(6.51), 6–53.

Geissinger, E. A., Gregory, R. S., Laurel, B. J., & Snelgrove, P. V. (2022). High site-fidelity and low mortality of juvenile Atlantic cod (*Gadus morhua*) in subarctic coastal habitat during their first winter. *ICES Journal of Marine Science*, *79*(4), 1408–1418.

Goddard, S. V., Morgan, M. J., & Fletcher, G. L. (1997). Influence of plasma antifreeze glycoproteins on temperature selection by Atlantic cod (*Gadus morhua*) in a thermal gradient. *Canadian Journal of Fisheries and Aquatic Sciences*, *54*(S1), 88–93.

Gotceitas, V., Fraser, S., & Brown, J. A. (1995). Habitat use by juvenile Atlantic cod (*Gadus morhua*) in the presence of an actively foraging and non-foraging predator. *Marine Biology*, *123*, 421–430.

Grabowski, J. H., Conroy, C. W., Gittman, R. K., Kelley, J. T., Sherman, S., Sherwood, G. D., & Wippelhauser, G. (2018). Habitat associations of juvenile cod in nearshore waters. *Reviews in Fisheries Science & Aquaculture*, *26*(1), 1–14.

Hafrannsóknastofnun. (n.d.). Grunnsævi við nokkra firði. https://www.hafogvatn.is/is/midlun/fyrirskola/fjardarannsoknir/vestfirdir/isafjardardjup/seydisfjordur

Hanson, J. M. (1996). Seasonal distribution of juvenile Atlantic cod in the southern gulf of St Lawrence. *Journal of Fish Biology*, *49*(6), 1138–1152.

Hanson, J. M., & Chouinard, G. A. (2002). Diet of Atlantic cod in the southern gulf of St Lawrence as an index of ecosystem change, 1959–2000. *Journal of Fish Biology*, *60*(4), 902–922.

Hartig, F. (2022). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models (R Package Version 0.4 5). 2022. Available at: https://cran.r-project.org/web/packages/DHARMa/DHARMa.pdf

Hayden, T. A., Holbrook, C. M., Fielder, D. G., Vandergoot, C. S., Bergstedt, R. A., Dettmers, J. M., Krueger, C. C., & Cooke, S. J. (2014). Acoustic telemetry reveals large-scale migration patterns of walleye in Lake Huron. *PLoS One*, *9*(12), e114833. https://doi.org/10.1371/journal.pone.0114833

Homrum, E. Í., Hansen, B., Steingrund, P., & Hátún, H. (2012). Growth, maturation, diet and distribution of saithe (*Pollachius virens*) in Faroese waters (NE Atlantic). *Marine Biology Research*, *8*(3), 246–254.

Hopcraft, J. G. C., Morales, J. M., Beyer, H. L., Borner, M., Mwangomo, E., Sinclair, A. R. E., Olff, H., & Haydon, D. T. (2014). Competition, predation, and migration: Individual choice patterns of Serengeti migrants captured by hierarchical models. *Ecological Monographs*, *84*(3), 355–372.

Jónsdóttir, I. G. (2023). *Unpublished raw data collected during the MFRI shrimp survey in Ísafjarðardjúp from 2016 until 2021*. Marine and Freshwater Research Institute of Iceland.

Jónsdóttir, I. G., Woods, P., Jakobsdóttir, K. B., Jónasson, J. P., Elvarsson, B., & Sólmundsson, J. (2019). Life history of juvenile cod. *Hafrannsóknastofnun, HV2019-61. Available at:* https://www.hafogvatn.is/static/research/files/hv2019-61.pdf

Jónsson, S. Þ., Neilson, J. D., & Marteinsdottir, G. (2007). Distribution and migration of saithe (*Pollachius virens*) around Iceland inferred from mark-recapture studies. *ICES Journal of Marine Science*, *64*, 1006–1016.

Laurel, B. J., Knoth, B. A., & Ryer, C. H. (2016). Growth, mortality, and recruitment signals in age-0 gadids settling in coastal Gulf of Alaska. *ICES Journal of Marine Science*, *73*(9), 2227–2237.

Lazzari, M. A., Sherman, S., & Kanwit, J. K. (2003). Nursery use of shallow habitats by epibenthic fishes in Maine nearshore waters. *Estuarine, Coastal and Shelf Science*, *56*(1), 73–84.

Lennox, R. J., Dahlmo, L. S., Ford, A. T., Sortland, L. K., Vogel, E. F., & Vollset, K. W. (2023). Predation research with electronic tagging. *Wildlife Biology*, *2023*(1), e01045. https://doi.org/10.1002/wlb3.01045

Lennox, R. J., Nilsen, C. I., Nash, A., Hanssen, E. M., Johannesen, H. L., Berhe, S., Berlaup, B., & Vollset, K. W. (2021). Laboratory and field experimental validation of two different predation sensors for instrumenting acoustic transmitters in fisheries research. *Fisheries*, *46*(11), 565–573.

Leu, E., Søreide, J. E., Hessen, D. O., Falk-Petersen, S., & Berge, J. (2011). Consequences of changing sea-ice cover for primary and secondary producers in the European Arctic shelf seas: Timing, quantity, and quality. *Progress in Oceanography*, *90*(1–4), 18–32.

Limburg, K. E., Olson, C., Walther, Y., Dale, D., Slomp, C. P., & Høie, H. (2011). Tracking Baltic hypoxia and cod migration over millennia with natural tags. *Proceedings of the National Academy of Sciences*, *108*(22), E177–E182. https://doi.org/10.1073/pnas.1100684108

Lindmark, M., Ohlberger, J., & Gårdmark, A. (2022). Optimum growth temperature declines with body size within fish species. *Global Change Biology*, *28*(7), 2259–2271.

Linehan, J. E., Gregory, R. S., & Schneider, D. C. (2001). Predation risk of age-0 cod (Gadus) relative to depth and substrate in coastal waters. *Journal of Experimental Marine Biology and Ecology*, *263*(1), 25–44.

Link, J. S., Bogstad, B., Sparholt, H., & Lilly, G. R. (2009). Trophic role of Atlantic cod in the ecosystem. *Fish and Fisheries*, *10*(1), 58–87.

MacDonald, J. S., Dadswell, M. J., Appy, R., Melvin, G., & Methven, D. A. (1984). Fishes, fish assemblages, and their seasonal movements in the lower bay of Fundy and Passamaquoddy Bay, Canada. *Fisheries Bulletin*, *82*, 121–139.

Malek, R. L., Sajadi, H., Abraham, J., Grundy, M. A., & Gerhard, G. S. (2004). The effects of temperature reduction on gene expression and oxidative stress in skeletal muscle from adult zebrafish. *Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology*, *138*(3), 363–373.

Miller, A. S., Shepherd, G. R., & Fratantoni, P. S. (2016). Offshore habitat preference of overwintering juvenile and adult black sea bass, *Centropristis striata*, and the relationship to year-class success. *PLoS One*, *11*(1), e0147627. https://doi.org/10.1371/journal.pone.0147627

Monk, C. T., Power, M., Freitas, C., Harrison, P. M., Heupel, M., Kuparinen, A., Moland, E., Simpfendorfer, C., Villegas-Ríos, D., & Olsen, E. M. (2023). Atlantic cod individual spatial behaviour and stable isotope associations in a no-take marine reserve. *Journal of Animal Ecology*, *92*(12), 2333–2347.

Morris, C. J., Green, J. M., Snelgrove, P. V., Pennell, C. J., & Ollerhead, L. N. (2014). Temporal and spatial migration of Atlantic cod (*Gadus morhua*) inside and outside a marine protected area and evidence for the role of prior experience in homing. *Canadian Journal of Fisheries and Aquatic Sciences*, *71*(11), 1704–1712.

Nathan, R., Monk, C. T., Arlinghaus, R., Adam, T., Alós, J., Assaf, M., Baktoft, H., Beardsworth, C. E., Bertram, M. G., Bijleveld, A. I., Brodin, T., Brooks, J. L., Campos-Candela, A., Cooke, S. J., Gjelland, K. Ø., Gupte, P. R., Harel, R., Hellström, G., Jeltsch, F., … Jarić, I. (2022). Big-data approaches lead to an increased understanding of the ecology of animal movement. *Science*, *375*(6582), eabg1780. https://doi.org/10.1126/science.abg1780

Nedreaas, K. H. (1985). Food and feeding habits of young saithe (*Pollachius virens* L.) on the coast of western Norway. *Demersal Fish Committee. ICES, C.M. 1985/G:22*. Available at: https://imr.brage.unit.no/imr-xmlui/bitstream/handle/11250/104030/CM_1985_G_22.pdf?sequence=1

Neuenhoff, R. D., Swain, D. P., Cox, S. P., McAllister, M. K., Trites, A. W., Walters, C. J., & Hammill, M. O. (2019). Continued decline of a collapsed population of Atlantic cod (*Gadus morhua*) due to predation-driven Allee effects. *Canadian Journal of Fisheries and Aquatic Sciences*, *76*(1), 168–184.

Nickel, A. K. (2016). *Trophic vulnerability of 0-group Atlantic cod (Gadus morhua) and saithe (Pollachius virens): A case study investigating the juveniles' feeding pattern and identifying valuable nursery habitats in the Icelandic Westfjords* (Master's thesis. University of Akureyri. Available from https://skemman.is/

Ólafsdóttir, G. Á., Gunnarsson, G. S., & Karlsson, H. (2015). More rapid shift to a benthic niche in larger *Gadus morhua* juveniles. *Journal of Fish Biology*, *87*(2), 480–486.

Ólafsdóttir, G. Á., Turnbull, S., Jónsdóttir, I. G., Nickel, A., Karlsson, H., Henke, T., Nielsen, E. E., & Pálsson, S. (2023). Genetic assignment predicts depth of benthic settlement for 0-group Atlantic cod. *PLoS One*, *18*(10), e0292495. https://doi.org/10.1371/journal.pone.0292495

Olsen, E., Aanes, S., Mehl, S., Holst, J. C., Aglen, A., & Gjøsæter, H. (2010). Cod, haddock, saithe, herring, and capelin in the Barents Sea and adjacent waters: A review of the biological value of the area. *ICES Journal of Marine Science*, *67*(1), 87–101.

Otterå, H., & Skilbrei, O. T. (2014). Possible influence of salmon farming on long-term resident behaviour of wild saithe (*Pollachius virens* L.). *ICES Journal of Marine Science*, *71*(9), 2484–2493.

Pálsson, Ó. K. (1976). Um líffræði fiskungviðis í Ísafjarðardjúpi. *Hafrannsóknir*, *8*, 5–56. Available at: https://www.hafogvatn.is/is/midlun/utgafa/hafrannsoknir/um-liffraedi-fiskungvidis-i-isafjardardjupi-smaludan-veidiadferdir-og-veidarfaeri-vid-raekjuveidar

Perry, D., Staveley, T. A., & Gullström, M. (2018). Habitat connectivity of fish in temperate shallow-water seascapes. *Frontiers in Marine Science*, *4*, 440.

Pihl, L., & Ulmestrand, M. (1993). Migration pattern of juvenile cod (*Gadus morhua*) on the Swedish west coast. *ICES Journal of Marine Science*, *50*(1), 63–70.

Pinet, P. R. (2019). *Invitation to oceanography*. Jones & Bartlett Learning.

R Core Team. (2016). *R: A language and environment for statistical computing*. Austria. Available from: https://www.R-project.org/

Rangeley, R. W., & Kramer, D. L. (1995a). Use of rocky intertidal habitats by juvenile pollock *Pollachius virens*. *Marine Ecology Progress Series*, *126*, 9–17.

Rangeley, R. W., & Kramer, D. L. (1995b). Tidal effects on habitat selection and aggregation by juvenile pollock *Pollachius virens* in the rocky intertidal zone. *Marine Ecology Progress Series*, *126*, 19–29.

Reubens, J. T., Pasotti, F., Degraer, S., & Vincx, M. (2013). Residency, site fidelity and habitat use of Atlantic cod (*Gadus morhua*) at an offshore wind farm using acoustic telemetry. *Marine Environmental Research*, *90*, 128–135.

Riley, J. D., & Parnell, W. G. (1984). The distribution of young cod. *Flødevigen Rapportserie*, *1*(1984), 563–580.

Rogers, L. A., Stige, L. C., Olsen, E. M., Knutsen, H., Chan, K. S., & Stenseth, N. C. (2011). Climate and population density drive changes in cod body size throughout a century on the Norwegian coast. *Proceedings of the National Academy of Sciences*, *108*(5), 1961–1966.

Saha, A., Hauser, L., Kent, M., Planque, B., Neat, F., Kirubakaran, T. G., Huse, I., Homrum, E. Í., Fevolden, S., Lien, S., & Johansen, T. (2015). Seascape genetics of saithe (*Pollachius virens*) across the North Atlantic using single nucleotide polymorphisms. *ICES Journal of Marine Science*, *72*(9), 2732–2741.

Simpfendorfer, C. A., Heupel, M. R., & Hueter, R. E. (2002). Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. *Canadian Journal of Fisheries and Aquatic Sciences*, *59*(1), 23–32.

Skilbrei, O. T., & Otterå, H. (2016). Vertical distribution of saithe (*Pollachius virens*) aggregating around fish farms. *ICES Journal of Marine Science*, *73*(4), 1186–1195.

Skjæraasen, J. E., Nilsen, T., Meager, J. J., Herbert, N. A., Moberg, O., Tronci, V., Johansen, V., & Salvanes, A. G. V. (2008). Hypoxic avoidance behaviour in cod (*Gadus morhua* L.): The effect of temperature and haemoglobin genotype. *Journal of Experimental Marine Biology and Ecology*, *358*(1), 70–77.

Strøm, J. F., Bøhn, T., Skjæraasen, J. E., Gjelland, K. Ø., Karlsen, Ø., Johansen, T., Hanebrekke, T., Bjørn, P. A., & Olsen, E. M. (2023). Movement diversity and partial sympatry of coastal and Northeast Arctic cod ecotypes at high latitudes. *Journal of Animal Ecology*, *92*(10), 1966–1978.

Svedäng, H., Righton, D., & Jonsson, P. (2007). Migratory behaviour of Atlantic cod *Gadus morhua*: Natal homing is the prime stock-separating mechanism. *Marine Ecology Progress Series*, *345*, 1–12.

Swain, D. P., Chouinard, G. A., Morin, R., & Drinkwater, K. F. (1998). Seasonal variation in the habitat associations of Atlantic cod (*Gadus morhua*) and American plaice (*Hippoglossoides platessoides*) from the southern gulf of St. Lawrence. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*(12), 2548–2561.

Teichert, N., Benitez, J. P., Dierckx, A., Tétard, S., De Oliveira, E., Trancart, T., Feunteun, E., & Ovidio, M. (2020). Development of an accurate model to predict the phenology of Atlantic salmon smolt spring migration. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *30*(8), 1552–1565.

Therneau, T. (2024). A package for survival analysis in R. R package version 3.5–8. Available at: https://CRAN.R-project.org/package=survival

Tirsgaard, B., Svendsen, J. C., & Steffensen, J. F. (2015). Effects of temperature on specific dynamic action in Atlantic cod *Gadus morhua*. *Fish Physiology and Biochemistry*, *41*, 41–50.

Uglem, I., Dempster, T., Bjørn, P. A., Sanchez-Jerez, P., & Økland, F. (2009). High connectivity of salmon farms revealed by aggregation, residence and repeated movements of wild fish among farms. *Marine Ecology Progress Series*, *384*, 251–260.

Valenzano, D. R., Terzibasi, E., Cattaneo, A., Domenici, L., & Cellerino, A. (2006). Temperature affects longevity and age-related locomotor and cognitive decay in the short-lived fish Nothobranchius furzeri. *Aging Cell*, *5*(3), 275–278.

Van der Knaap, I., Reubens, J., Thomas, L., Ainslie, M. A., Winter, H. V., Hubert, J., Martin, B., & Slabbekoorn, H. (2021). Effects of a seismic survey on movement of free-ranging Atlantic cod. *Current Biology*, *31*(7), 1555–1562.

Villegas-Ríos, D., Réale, D., Freitas, C., Moland, E., & Olsen, E. M. (2018). Personalities influence spatial responses to environmental fluctuations in wild fish. *Journal of Animal Ecology*, *87*(5), 1309–1319.

Vollset, K. W., Dohoo, I., & Lennox, R. J. (2023). The paradox of predation studies. *Biology Letters*, *19*(10), 20230354. https://doi.org/10.1098/rsbl.2023.0354

Von Leesen, G., Bogstad, B., Hjörleifsson, E., Ninnemann, U. S., & Campana, S. E. (2022). Temperature exposure in cod driven by changes in abundance. *Canadian Journal of Fisheries and Aquatic Sciences*, *79*(4), 587–600.

Whalen, K. G., Parrish, D. L., & McCormick, S. D. (1999). Migration timing of Atlantic salmon smolts relative to environmental and physiological factors. *Transactions of the American Fisheries Society*, *128*(2), 289–301.

Winger, B. M., Auteri, G. G., Pegan, T. M., & Weeks, B. C. (2019). A long winter for the red queen: Rethinking the evolution of seasonal migration. *Biological Reviews*, *94*(3), 737–752.

Wood, S. N. (2017). *Generalized additive models: An introduction with R*. chapman and hall/CRC.

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