

RESEARCH ARTICLE

Movement diversity and partial sympatry of coastal and Northeast Arctic cod ecotypes at high latitudes

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Abstract

1. Movement diversity within species represent an important but often neglected, component of biodiversity that affects ecological and genetic interactions, as well as the productivity of exploited systems.
2. By combining individual tracking data from acoustic telemetry with novel genetic analyses, we describe the movement diversity of two Atlantic cod *Gadus morhua* ecotypes in two high-latitude fjord systems: the highly migratory Northeast Arctic cod (NEA cod) that supports the largest cod fishery in the world, and the more sedentary Norwegian coastal cod, which is currently in a depleted state.
3. As predicted, coastal cod displayed a higher level of fjord residency than NEA cod. Of the cod tagged during the spawning season, NEA cod left the fjords permanently to a greater extent and earlier compared to coastal cod, which to a greater extent remained resident and left the fjords temporarily. Despite this overall pattern, horizontal movements atypical for the ecotypes were common with some NEA cod remaining within the fjords year-round and some coastal cod displaying a low fjord fidelity. Fjord residency and exit timing also differed with spawning status and body size, with spawning cod and large individuals tagged during the feeding season more prone to leave the fjords and earlier than non-spawning and smaller individuals.
4. While our results confirm a lower fjord dependency for NEA cod, they highlight a movement diversity within each ecotype and sympatric residency between ecotypes, previously undetected by population-level monitoring. This new knowledge is relevant for the management, which should base their fisheries advice for these interacting ecotypes on their habitat use and seasonal movements.

KEYWORDS

acoustic telemetry, Atlantic cod, behavioural variation, ecotype interactions, fisheries management

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1 | INTRODUCTION

Movement diversity represents an important component of biodiversity, potentially shaping eco-evolutionary dynamics, ecosystem resilience and harvestable yields (Costa-Pereira et al., 2022; Jeltsch et al., 2013). In aquatic systems, movement diversity between populations has been shown to stabilize the aggregated fish abundance in stochastic environments and enhance food security of exploited systems (Connors et al., 2022; Schindler et al., 2010). This portfolio effect implies that aggregated systems are less volatile than their individual entities and can operate at different component levels. Within populations, movement diversity is often linked to different life-history strategies (Moore et al., 2014). Characterization of movement diversity therefore represents a key step towards biodiversity conservation and management of exploited populations for long-term resilience under environmental change.

The Atlantic cod *Gadus morhua* is a cold-water fish distributed in coastal and shelf habitats in the North Atlantic targeted by fishers for centuries (Eikeset et al., 2013; Rosenberg et al., 2005). Throughout its range, cod function as a keystone predator and there are several examples that the depletion of cod populations can cause trophic cascades at various scales (Frank et al., 2005; Norderhaug et al., 2021). Cod movement diversity ranges from year-round residency within confined coastal habitats to long-distance oceanic migrations (Robichaud & Rose, 2004). Along northern parts of the Norwegian coast, two genetically distinguishable ecotypes are found: the Northeast Arctic cod (NEA cod) and Norwegian coastal cod (Johansen et al., 2018; Skarstein et al., 2007). The general understanding is that these ecotypes differ markedly in offspring dispersal patterns and adult movements. NEA cod eggs and larva drift northwards from the Norwegian coastal banks towards the Barents Sea (Vikebø et al., 2005), where individuals settle and reside for several years until they embark on long-distance migrations towards outer coastal and fjord spawning grounds (Olsen et al., 2010). The coastal cod, in contrast, display more locally oriented behaviours, often confined to specific fjords with limited spatial movements between life-stages (Jakobsen, 1987; but see Michalsen et al., 2014). Despite these differences, both ecotypes spawn during the winter and spring (March–May) in overlapping coastal habitats. Recent genetic studies also suggest that the two ecotypes may hybridise, a process which could play a major role in shaping the coastal cod's overall genetic structure and diversity (Breistein et al., 2022; Jorde et al., 2021). The NEA cod population is comparatively large and productive, supporting the largest cod fishery in the world with recent annual catches as high as 800,000t (ICES, 2023). In contrast, the Norwegian coastal cod has been in a depleted state for decades, with recent annual catches of about 20,000t (Johansen et al., 2018). Hence, resolving issues pertaining to the level of sympatric fjord residency and movement diversity within the two ecotypes are highly important from a management perspective.

Advances in animal-borne telemetry have promoted novel insight into individual behaviour and movement diversity across various taxa (Hussey et al., 2015; Kays et al., 2015; Nathan et al., 2022).

In aquatic systems, acoustic telemetry is a powerful tool for quantifying fish movement by allowing for precise observation of individuals over time and space, through transmission of signals from animal-borne tags to receiver devices (Matley et al., 2022).

Here, we investigate movement diversity of coastal and NEA cod in two high-latitude fjords by combining acoustic telemetry with novel genetic analyses determining ecotype and sex. Tagging was done both during the spawning season in April and May and during the feeding season in September and October. To quantify the movement variation within our sample, each fish was assigned an individual fate as well as a behaviour for their time at liberty. We hypothesise that the level of fjord-resident behaviour differs among these ecotypes and that coastal cod will display a greater fjord fidelity compared to NEA cod. Independent of the ecotype, we also test for the effect of body size and sex on propensity to reside within fjord habitats.

2 | MATERIALS AND METHODS

The handling of experimental animals complied with Norwegian animal welfare laws, guidelines, and policies. The project was approved by the Norwegian Food Safety Authority (permit FOTS ID 19342).

2.1 | Study system

The movement diversity of Atlantic cod was studied in two neighbouring fjords in northern Norway (Figure 1). Frakkfjord is about 10km long and 3km wide at the mouth, facing north. Olderfjord is about 4.5km long and 2km wide at the mouth, facing west. Both fjords have a maximum depth of approximately 90m and relatively steep slopes with rocky habitats along the sides, whereas the central basins and innermost parts are flatter with more soft sediments.

2.2 | Sampling and tagging

Cod were captured in Frakkfjord and Olderfjord during 2019 and 2020 (Table 1). A total of 331 cod, ranging in total length from 35 to 118cm (mean = 67cm) and weighing 210–21,000g (mean = 3918g), were tagged with acoustic transmitters for monitoring of individual behaviour (Table 1). This included 255 cod caught during the spawning season in April and May (mean weight = 4688g), of which 143 were visually assigned on site as spawning cod by the presence of running milt or roe and 76 cod caught during the feeding season in September and October (mean weight = 1332g). Cod from the spawning-season sample were caught by gillnets ($n=163$), hook and line ($n=48$) or traps ($n=44$), whereas all cod from the feeding-season sample were caught in traps. Cod caught by hook and line and cod caught in traps were tagged and released immediately after capture, whereas cod caught using gillnets were kept in a net pen for 1–14 days before tagging. Cod were anaesthetised using an aqueous

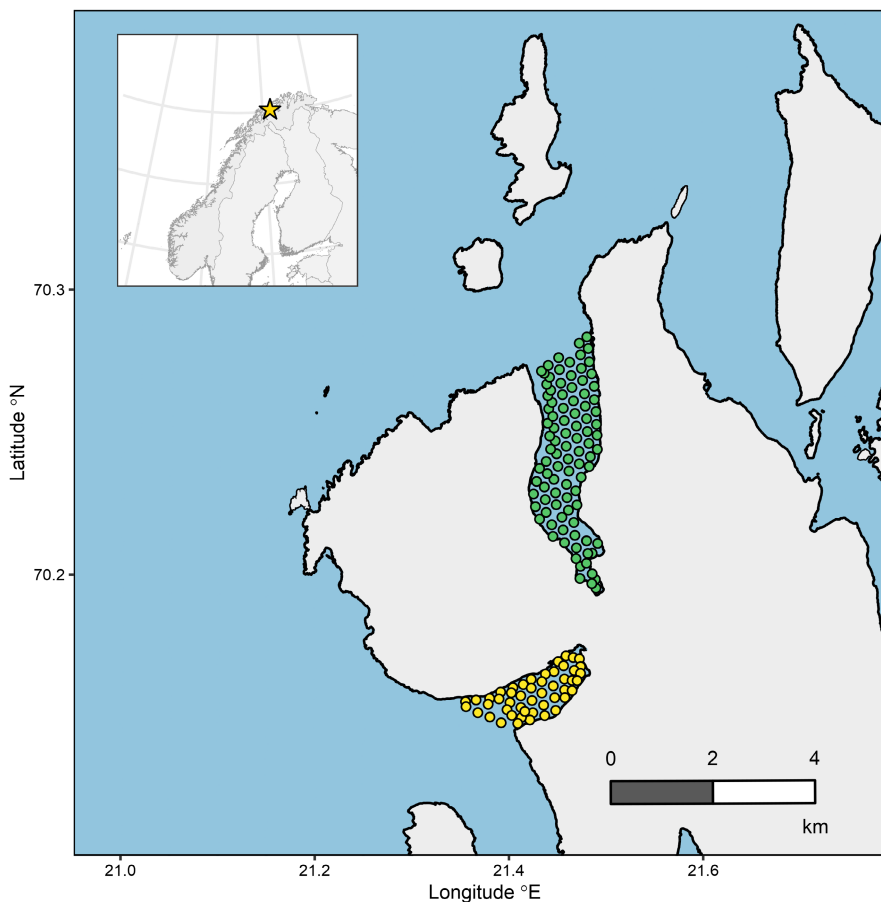


FIGURE 1 Map of the study area with points denoting the positions of acoustic receivers deployed in Frakkfjord ($n=98$, green) and Olderfjord ($n=49$, yellow). Inserted map depicts the location of the study site (yellow star) in Fennoscandia.

TABLE 1 Characteristics of the tagged Atlantic cod. n refers to the number of cod tagged with acoustic transmitters, whereas numbers in parentheses denote individuals detected alive after release.

	n	Length (cm)	Weight (g)
Spawning season (April–May)			
2019	122 (105)	52.4 ± 19.3	2052 ± 3061
2020	133 (93)	90.0 ± 10.4	7106 ± 2555
Feeding season (September–October)			
2019	16 (16)	49.6 ± 8.5	1111 ± 726
2020	60 (59)	50.4 ± 15.4	1391 ± 1663

solution of benzocaine (Benzoak vet. 0.2 mL^{-1}) for ~ 3 – 6 min before an acoustic transmitter was surgically implanted in the abdominal cavity and the incision closed with 2–3 stitches using absorbable suture. Cod smaller than 60 cm were tagged with 13 mm transmitters (V13P; Innovasea Systems; weight in water: 5 g; estimated battery life: 802 days; power output: 152 dB; codespace 9006), whereas cod larger than 60 cm were tagged with 16 mm transmitters (V16P; Innovasea Systems; weight in water: 12 g; estimated battery life: 3650 days; power output: 158 dB; codespace 9002). All transmitters had a random transmission interval with a mean of 250 s (range of

200–300 s) and a built-in pressure sensor (max depth: 136 m; resolution 0.6 m; accuracy: 6.8 m) for transmission of current depth in addition to the identity code. To aid tag returns from fishers, all cod were fitted with an external T-bar tag (Hallprint) placed next to the dorsal fin, which contained a unique identity number and contact information. Before release, a small tissue sample (fin clip) was collected and stored on alcohol for genetic analyses.

2.3 | Genetic assignment

Cod were genetically assigned to either NEA cod or Norwegian coastal cod based on 38 single nucleotide polymorphic markers as described by Johansen et al. (2018). For the genetic assignment of ecotype, the STRUCTURE software version 2.3.4 was used, with ADMIX model, a standard 500,000 burn in, and 1 million MCMC (Pritchard et al., 2000). Of the 331 cod fitted with acoustic transmitters, 67% ($n=222$) were genetically classified as coastal cod, 28% ($n=93$) as NEA cod, and 5% ($n=16$) could not be assigned to ecotype. Overall, 89% of the cod assigned to an ecotype were classified with an 80% certainty or higher, which included 98% of the NEA cod and 85% of the coastal cod. In addition to ecotype assignment, cod were sexed using a modified version of the method presented in Star et al. (2016) using three TagMan SNP

Genotypic Assays (Thermo Fisher Scientific) (T. Johansen, unpublished data). An initial test was performed with the spawning cod caught during the spring-spawning season to quantify the accuracy of this method. Of the 143 cod sexed in the field, the genetically determined sex matched the on-site observation in 94% of the instances, while 2% did not correspond and 4% of the samples failed. The total sample constituted of 56% males ($n=186$), 41% females ($n=135$) and 3% that could not be sexed ($n=10$).

2.4 | Receiver deployment

A total of 98 acoustic receivers were deployed in Frakkfjord March 2019, while 49 acoustic receivers were deployed in Olderfjord in May 2019 (Figure 1). We opted for a grid design with receivers positioned uniformly across the study areas, as this enables an unbiased and near-continuous monitoring of the behaviour of tagged fish (Kraus et al., 2018; Peterson et al., 2021). Receivers were typically separated by about 500m. However, in some locations this spacing was adjusted to fit the fjord topography, especially near the shoreline (Figure 1). In most locations, receivers (Innovasea VR2Tx-69kHz) were moored at fixed positions using an iron mooring (40kg), a rope, and a surface float. In some of the deeper locations and at locations with frequent boat traffic and fishing activity, acoustic release receivers (Innovasea VR2AR-69kHz) with no surface float were deployed. All receivers were moored with the hydrophone pointing up. Receivers moored at locations with a sea-floor depth greater than 50m were deployed approximately 20m above the bottom, whereas receivers moored at shallower locations were deployed 10m above the sea floor.

Detection efficiency was monitored by four stationary transmitters, as well as the internal sync tags in the receivers. Although we observed some variation in detection efficiency during the study period, the overall pattern confirmed that tagged cod would be detected when present within the receiver array. Boat traffic could potentially jam the acoustic frequency and limited the detection efficiency. However, this was considered unlikely as boat traffic is limited in the two fjords for large parts of the year, and most echosounders operates at frequencies far away from the 69kHz that our telemetry system utilises.

The acoustic receiver arrays were designed to provide continuous coverage in both Frakkfjord and Olderfjord. However, due to harsh weather conditions, boat traffic and various commercial fishing activity, the arrays suffered substantial losses of receivers that subsequently had to be recovered or replaced. Thus, to prevent extensive loss of receivers and to avoid conflicts with seasonal fisheries, parts of the arrays were taken out of the water between 27 November 2020 and 12 February 2021. Data were downloaded in August 2019, February 2020, November 2020 and November 2021.

2.5 | Data filtering

The logged raw data consisted of a time stamp, as well as the tag identity code and depth value, and form the basis for quantifying

presence, behaviour and fate of tagged cod within the study arrays. Data preparation first involved a linear time correction to account for receiver clock drift during receiver deployment periods. Second, data were filtered to remove likely false detections that may result from environmental noise or code collisions from simultaneously arriving signals. This filtering procedure omitted (i) all signals from transmitter identity coded that did not belong to any of the cod tagged in this study and (ii) single, isolated detections from a transmitter occurring within a 24-h period at a given receiver.

2.6 | Fate and behaviour assessment

To identify tracking periods relevant for quantifying individual residency, the fate of each cod was determined by investigating the tags' horizontal and vertical profile. To standardise the fate assessment, a procedure based on the dichotomous keys developed by Halttunen et al. (2018) and Villegas-Ríos et al. (2020) was used, which classified cod into the following five fate categories.

1. *Alive* if the cod displayed vertical movements concurring with behaviours observed in previous telemetry studies (e.g. Freitas et al., 2021; Michalsen et al., 2014; Righton et al., 2010).
2. *Tagging mortality* if (i) the tag became stationary at the sea floor within 24 hours after release or (ii) if there was evidence of lethal barotrauma with the cod drifting at the surface before eventually disappearing from the system.
3. *Fishing mortality* if (i) a behavioural change not attributed to any candidate predator preceded the stationary event, (ii) a large spatial gap was present prior the tag becoming stationary or (iii) the tag suddenly disappeared from within the system, that is not seen exiting the fjord on the outer receivers.
4. *Predation* if (i) a known predator behaviour preceded the tag becoming stationary or (ii) a known predator behaviour preceded the tag disappearing from the system.
5. *Unknown mortality* if (i) the tag became stationary without an obvious behavioural change or (ii) the tag became stationary with no spatial gap prior the stationary event.

Following the fate assessment, cod that succumbed to *Tagging mortality* were omitted from further analyses. The remaining individuals were classified into three behavioural categories based on their detection history. This was done by plotting the filtered, raw detections of how individual cod moved through the fjord from the innermost receivers to the outermost part of the array (Figure 2).

1. *Resident* if the cod was continuously detected within its tagging fjord throughout its time at liberty, with no indication of the cod leaving the fjord (Figure 2a).

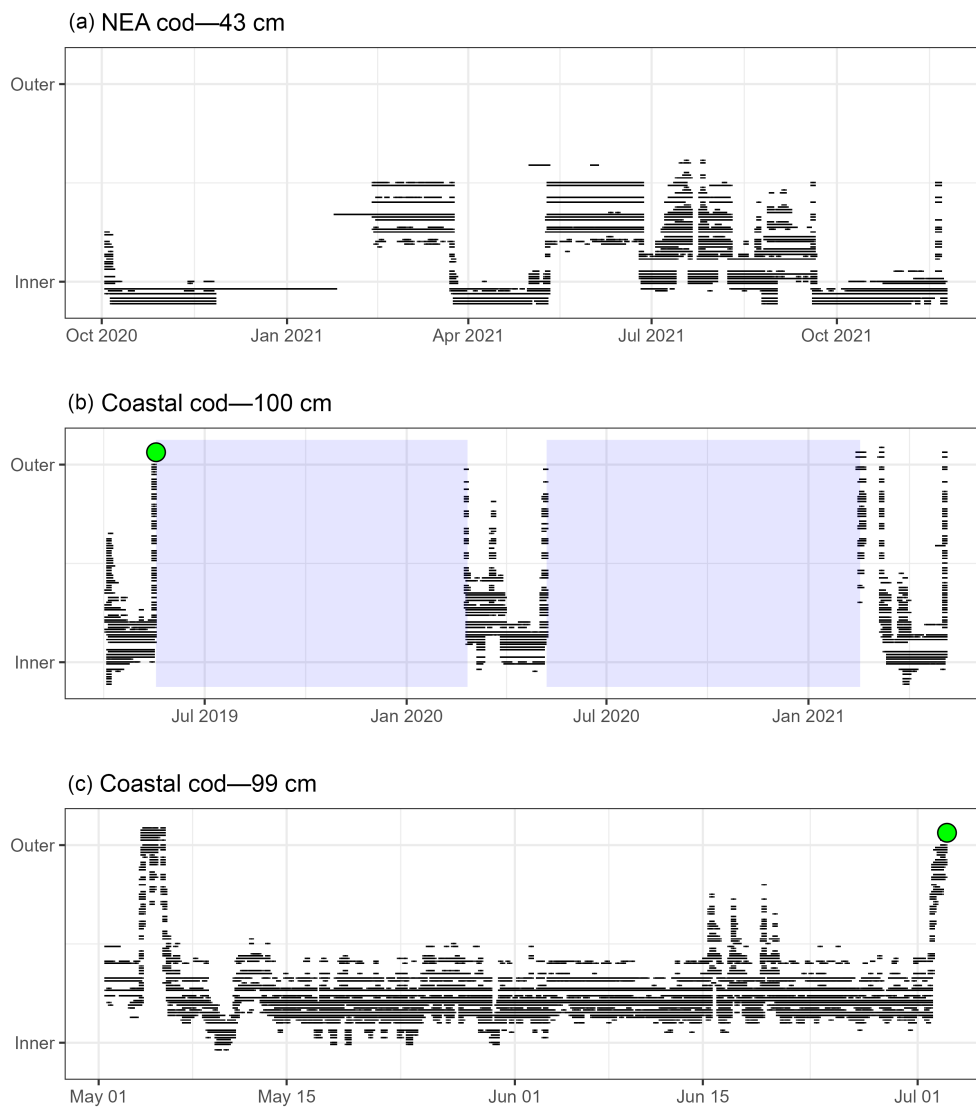


FIGURE 2 Horizontal movement patterns of Atlantic cod classified as *resident* (a), *temporary exit* (b) and *permanent exit* (c). Shaded areas in (b) depict periods when the cod was considered absent. Green points in (b) and (c) denote time of exit from the fjord they were tagged.

2. *Temporary exit* if the cod was observed to temporarily leave their tagging fjord during the tracking period. Cod was inferred to leave its tagging fjord if (i) a temporal gap >30 days followed detections at the outer edges of the receiver arrays (Figure 2b) or (ii) if it was observed in the neighbouring system.
3. *Permanent exit* if the cod left their tagging fjord (i.e. final detections at the outer edges of the receiver arrays) without returning (Figure 2c).

2.7 | Statistical analyses

For the statistical analyses, the complete dataset was divided into a spawning-season sample and a feeding-season sample. This was done to enable the inclusion of *Spawning status* as a covariate. All statistical analyses were conducted using the R version 4.2.2 (R Core Team, 2022).

2.7.1 | Behavioural variability

To determine what influenced the behaviour of cod, multinomial regression models were fitted to the data with behaviour category set as the nominal response variable. For both the spawning-season and feeding-season models, *resident* was set as the reference behaviour:

$$\log(O_i/R) = \alpha_i + \beta_{ni} \times X_{ni},$$

where $\log(O_i/R)$ denotes the log-odds of the outcome O_i (*temporary* or *permanent exit*) compared to the reference level R (*resident*), α_i denotes the intercept of model i , which provides information necessary for estimating the difference in outcome across the baseline level of covariates; β_{ni} denotes the regression coefficients of model i ; and X_{ni} the model covariates.

For the spawning-season sample, the most complex model included *Ecotype*, *Sex* and *Spawning status* as two-way interacting covariates, and *Fjord* and *Year* as main effects. Prior to model formalization *Fish Length* was considered as a candidate covariate. However, it was omitted due to its strong correlation with *Spawning status* (binomial GLM: $Spawning\ status \sim Fish\ length$, $\beta \pm SE = 0.162 \pm 0.022$, p -value $< 10^{-11}$, McFadden's $R^2 = 0.76$). For the feeding-season sample, the most complex model included *Ecotype*, *Sex* and *Fish Length* as two-way interacting terms, in addition to *Fjord* and *Year* as main effects. p -values were estimated by the Wald test and fitting of the multinomial models was done using the *multinom* command from the *nnet* package (Venables & Ripley, 2002).

2.7.2 | Exit timing

To investigate what influenced the timing when cod left their tagging fjord, accelerated failure-time (AFT) models were fitted to the data:

$$\log(\text{Time}) = \alpha + \beta_n \times X_n + W.$$

The AFT model is a parametric survival model, where $\log(\text{Time})$, denotes the logarithm of the time until an observable event, that is cod leaving their tagging fjord; α denotes the model's intercept; β_n denotes the regression coefficients, X denotes the model covariates and W denotes the residuals that are assumed to follow a specific distribution. Like other survival models, the AFT model allows for right censoring, thus accounting for cod that were not observed to experience the event by censoring them at the time of their last relevant observation. We could have opted for a cox proportional hazard model, which allows for simultaneous inference about whether both the occurrence and timing of the event differ among covariates (Whoriskey et al., 2019). However, our objective was specifically to determine what influenced the timing of tagging-fjord exit, which is more easily inferred by using an AFT model.

For the spawning-season sample the full model included *Ecotype*, *Sex* and *Spawning status* as two-way interacting covariates, and *Fjord* and *Year* as main effects. For the feeding-season sample, the most complex model included *Ecotype*, *Sex* and *Fish Length* as two-way interacting terms, in addition to *Fjord* and *Year* as main effects. In both model sets, the underlying distribution of the residuals was proxied by comparing the Akaike information criterion (AIC) values for models with various residual distributions. For both models, a log-normal residual distribution was chosen. Fitting and validation of AFT models were done using the *survreg* and *survfit* commands from the survival package (Therneau, 2020).

2.7.3 | Model selection

Model selection was done using the *dredge* function from the *MuMIn* package (Barton, 2022) with the model producing the lowest conditional AIC (AICc) value considered the most parsimonious.

3 | RESULTS

3.1 | Fate assessment

Of the 331 Atlantic cod fitted with acoustic transmitters, 321 were detected by the acoustic receivers. Of these, 61% ($n=196$) were alive until their last detection, with track durations ranging from 1 to 957 days (mean \pm SD = 294 ± 287 days); 24% ($n=77$) died by either *fishing*, *predation* or for *unknown* reasons; and 15% ($n=48$) experienced tagging mortality. Notably, 98% ($n=47$) of the cod that suffered *tagging mortality* were caught by gillnets during the spawning season (April–May). Only cod detected alive post release ($n=273$) were considered for further analyses.

3.2 | Ecotype and sex

Of the 273 cod, 259 were genetically assigned to ecotype, of which 77% ($n=199$) were classified as coastal cod and 23% ($n=60$) as NEA cod (Figure 3). Coastal cod dominated during both sampling periods (spawning season: 70%, feeding season: 81%), with a greater presence of NEA cod in the spawning-season sample (spawning season: 25%, feeding season: 15%) (Figure 3).

In total, 265 of the 273 cod were successfully sexed based on genetic markers. Of these 55% ($n=147$) were males and 45% ($n=118$) were females (Figure 3). Males dominated the spawning-season sample (60%), whereas most cod tagged during the feeding season (September–October) were females (63%) (Figure 3).

3.3 | Cod behaviour—Residency, temporary or permanent exit

Of the 273 cod, 33% ($n=91$) were *resident* and remained within their tagging fjord during the entire tracking period, 23% ($n=61$) *exited temporarily* and 44% ($n=121$) *exited permanently*. Of the fish exiting either *temporarily* or *permanently*, 26% ($n=48$) were observed within the neighbouring fjord at some point during the tracking period. Although the tendency to remain *resident* was greatest for coastal cod (38%), some NEA cod also resided within their tagging fjord throughout the tracking period (20%), including two individuals tracked continuously for 417 (see Figure 2a) and 706 days. NEA cod *exited permanently* to a greater extent than coastal cod (NEA cod=75%, coastal cod=35%), whereas a substantially greater proportion of coastal cod *exited temporarily* (NEA cod=5%, coastal cod=27%). For the cod not genetically classified to ecotype ($n=14$), 29% were *resident*, 21% *exited temporarily* and 50% *exited permanently*.

Of the cod tagged during the spawning season ($n=198$), 28% remained *resident*, 23% *exited temporarily* and 49% *exited permanently*. Multinomial regression revealed effects of *Ecotype* and *Spawning status* on the behaviour of cod but no effect of *Sex*, *Fjord*, *Year* or the interaction terms (Table 2). Overall, the parsimonious model

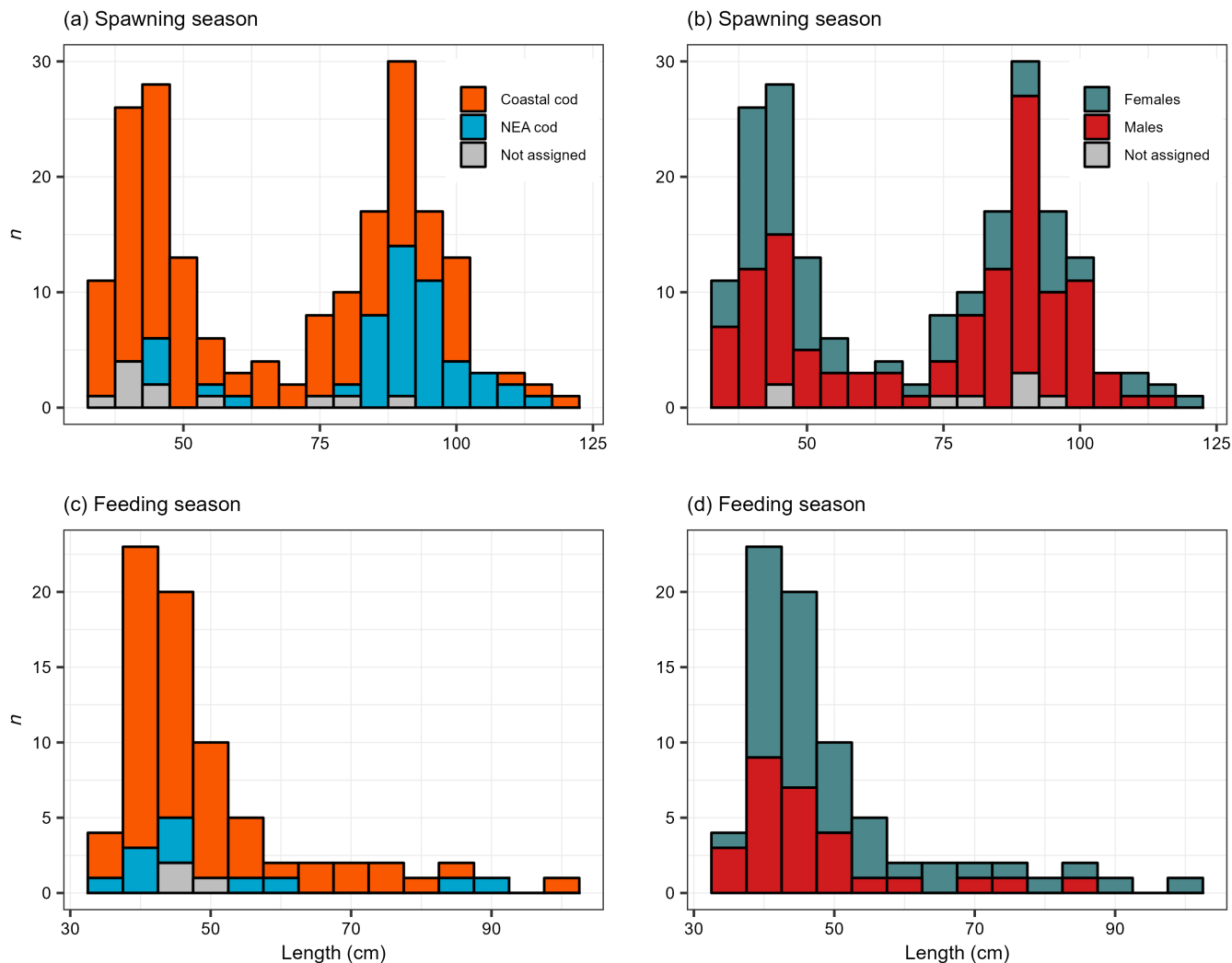


FIGURE 3 Length distribution of Atlantic cod successfully tracked with acoustic transmitters ($n=273$) tagged during the spawning season in April and May (a, b) and during the feeding season in September and October (c, d). Colours correspond to ecotype (a, c) and sex (b, d).

Reference behaviour	Reference behaviour	Model term	Coefficient	SE	p -value	Δ AICc
Resident	Temporary exit	Intercept	-0.786	0.292	0.007	-2.84
		Ecotype	-2.272	1.129	0.044	
		Spawning status	1.805	0.484	$<10^{-3}$	
Permanent exit	Permanent exit	Intercept	-0.713	0.276	0.010	
		Ecotype	1.201	0.531	0.024	
		Spawning status	1.998	0.437	$<10^{-4}$	

TABLE 2 Result from the parsimonious multinomial regression model investigating the behavioural variability of Atlantic cod tagged during the spawning season (April–May). Reference levels for the *Ecotype* and *Spawning status* covariates were coastal cod and non-spawners, respectively. SE denotes the standard error of the model coefficients. Δ AICc denotes the difference in conditional AIC value compared to model that produced the second lowest value.

documented that coastal cod were more likely to remain *resident* and *exit temporarily* than NEA cod, whereas NEA cod *exited permanently* to a greater extent (Figure 4). Spawning cod of both ecotypes were less likely to remain *resident* and more likely to *permanently exit* compared to their non-spawning counterparts (Figure 4).

Of the cod tagged during the feeding season ($n=75$), 47% remained *resident*, 21% *exited temporarily* and 32% *exited permanently*.

The parsimonious model included *Fish length* and *Fjord* as covariates influencing cod behaviour (Table 3). The model documented a positive effect of length on the probability of cod to *exit temporarily* in both fjords, and on the probability of cod *exiting permanently* in Frakkfjord (Figure 5). Independent of body size, the model predicted that cod tagged in Olderfjord were less likely to remain *resident* than cod tagged in Frakkfjord (Figure 5).

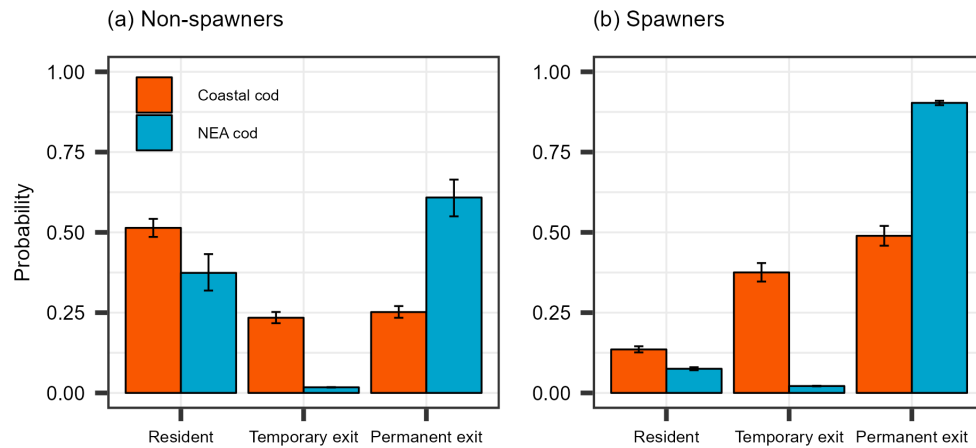


FIGURE 4 Predicted behavioural probabilities of Atlantic cod tagged during the spawning season in April and May, with error bars denoting 95% confidence intervals. Panels depict pairwise comparison of *Ecotype* across *Spawning status*.

TABLE 3 Result from the parsimonious multinomial regression model investigating the behavioural variability of Atlantic cod tagged during the feeding season (September–October). Frakkfjord was set as the reference levels for the *Fjord* covariate. SE denotes the standard error of the model coefficients. Δ AICc denotes the difference in conditional AIC value compared to model that produced the second lowest value.

Reference behaviour	Reference behaviour	Model term	Coefficient	SE	p-value	Δ AICc
Resident	Temporary exit	Intercept	-5.892	1.714	0.001	-2.18
		Fish length (cm)	0.077	0.028	0.006	
		Fjord	2.436	0.805	0.002	
	Permanent exit	Intercept	-3.534	1.324	0.008	
		Fish length (cm)	0.050	0.024	0.040	
		Fjord	1.531	0.614	0.013	

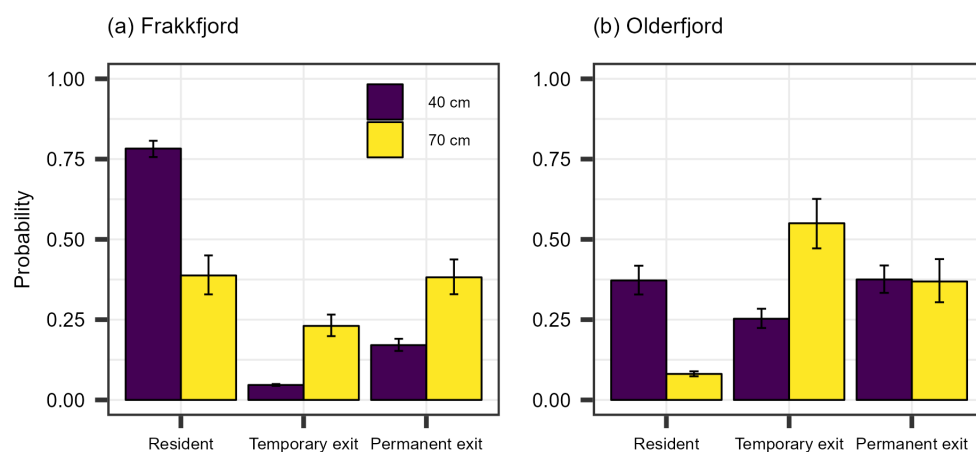


FIGURE 5 Predicted behavioural probabilities of Atlantic cod tagged during the feeding season in September and October, with error bars denoting 95% confidence intervals. Panels depict pairwise comparison of small (40 cm) and large (70 cm) cod across *Fjord*. Small and large individuals correspond to the 10th and 90th percentile *Fish length* of cod tagged during the feeding season.

3.4 | Cod behaviour—Exit timing

In total, 182 cod exited after spending between 1 and 606 days (median=29 days, mean=106 days, SD=143 days) within their

tagging fjord. Cod tagged during the spawning season exited earlier (median=22 days, mean=100 days, SD=151 days) than cod tagged during the feeding season (median=119 days, mean=136 days, SD=110 days). Overall, NEA cod left their tagging fjord earlier

(median = 15 days, mean = 28 days, SD = 48 days) than coastal cod (median = 56 days, mean = 136 days, SD = 154 days).

For the spawning-season sample, the parsimonious AFT model included effects of *Ecotype*, *Spawning status*, *Fjord* and *Year* in addition to significant interaction between *Ecotype* and *Spawning status* (Table 4). The model predicted an 85% reduction in time until fjord exit for NEA cod compared to coastal cod and a 93% reduction in residency for spawning coastal cod compared to non-spawning coastal cod (Table 4). However, the *Ecotype*–*Spawning status* interaction coefficient meant that the effect of *Spawning status* was absent for NEA cod (Table 4; Figure 6). Furthermore, cod from Olderfjord left earlier than cod from Frakkfjord and cod tagged in 2020 left earlier than cod tagged in 2019 (Table 4).

For the feeding-season sample, *Fish length* had a negative effect on exit time, with time spent within the tagging fjord decreasing with 7% per cm (Table 5). The parsimonious model also included a

detectable effect of *Fjord*, with cod from Olderfjord leaving earlier than cod from Frakkfjord (Table 5).

4 | DISCUSSION

By continuously monitoring the fjord residency of individual Atlantic cod of different life stages using acoustic telemetry, in combination with genetic classification of ecotype and sex, we document movement diversity previously hidden from population-level monitoring. As expected, cod belonging to the coastal ecotype displayed the highest level of fjord residency and a greater tendency to return to the fjords after exiting. However, a proportion of the oceanic migratory NEA cod ecotype was also present within the fjords for extended periods. While it is possible that these results may represent behavioural anomalies present in the specific fjord systems, we argue that the observed movement diversity challenge the classical description of a distinct separation between coastal and NEA cod, and reveal how between-individual variation in fjord residency promotes sympatry between the ecotypes.

4.1 | Residency of ecotypes

During the spawning season (April–May), coastal cod displayed the highest level of fjord residency, whereas NEA cod were more likely to leave the fjord earlier in the season as well as permanently. While this overall pattern supports the perception of a spatial segregation of the ecotypes (Bergstad et al., 1987; Olsen et al., 2010), we also observed that some NEA cod remained within the fjords. This shows that the migration patterns of the two ecotypes are not as rigid as previous population-level monitoring would indicate, which is further supported by our feeding-season sample (September–October) where we found no difference in fjord residency between coastal

TABLE 4 Result from the parsimonious accelerated failure time model investigating the exit timing of Atlantic cod tagged during the spawning season (April–May). Reference levels for the *Ecotype*, *Spawning status*, *Fjord* and *Year* covariates were coastal cod, non-spawners, Frakkfjord, and 2019, respectively. SE denotes the standard error of the model coefficients. Δ AICc denotes the difference in conditional AIC value compared to model that produced the second lowest value.

Predictor variables	Coefficient	SE	p-value	Δ AICc
<i>Ecotype</i>	-1.922	0.563	$<10^{-3}$	-0.50
<i>Spawning status</i>	-2.636	0.336	$<10^{-14}$	
<i>Fjord</i>	-1.470	0.287	$<10^{-6}$	
<i>Year</i>	-0.871	0.327	0.008	
<i>Ecotype</i> × <i>Spawning status</i>	1.761	0.609	0.004	

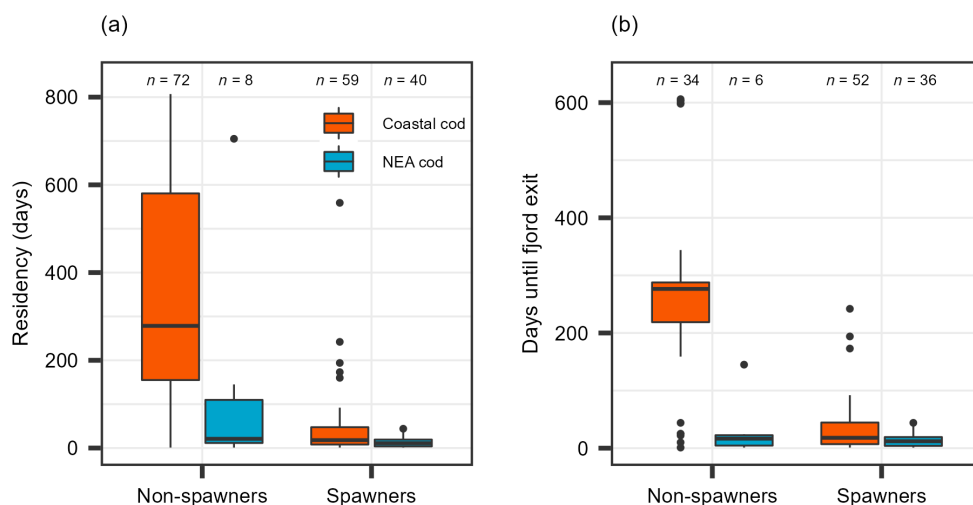


FIGURE 6 Time spent in the tagging fjord for Atlantic cod tagged during the spawning season in April and May, colour coded by ecotype. (a) Days spent in the fjord prior to exiting and total number of days for cod that remained resident. (b) Days spent in the fjord prior to exiting. Numbers above boxes denote the number of fish in each category.

TABLE 5 Result from the parsimonious accelerated failure time model investigating the exit timing of Atlantic cod tagged during the feeding season (September–October). Frakkfjord was set as the reference levels for the *Fjord* covariate. SE denotes the standard error of the model coefficients. Δ AICc denotes the difference in conditional AIC value compared to model that produced the second lowest value.

Predictor variables	Coefficient	SE	p-value	Δ AICc
<i>Fish length</i> (cm)	-0.072	0.014	$<10^{-6}$	-2.01
<i>Fjord</i>	-1.588	0.426	$<10^{-3}$	

and NEA cod. While this lack of an ecotype effect on the behaviour of cod tagged during the feeding season could be attributed to the low occurrence of NEA cod in this sample, the fact that NEA cod of various sizes were observed, including presumably juvenile fish, confirms that different movement tactics are present. NEA cod is expected to first settle in offshore Barents Sea habitats (Olsen et al., 2010). However, by studying the population genetic structure of 0-group juveniles along the North Norwegian coast, Fevolden et al. (2012) documented the presence of both ecotypes in several fjord systems, with NEA cod occasionally dominating the samples. This indication that also the spatial distribution of juveniles may deviate from the perceived patterns is strengthened by our observation that juvenile NEA cod from various size-groups were present within the fjords year-round, adding to the spatial and temporal complexity of how these ecotypes interact.

The observed movement diversity of cod ecotypes falls in line with other studies based on repeated observations on individual cod behaviour, where between-individual variation has been reported both in relation to ecotype and environmental change (e.g. Kristensen et al., 2021; Villegas-Ríos et al., 2018). While it is possible that this movement diversity may simply represent noise around an average movement tactic, it is generally perceived that diversification of movement tactics within animal populations represents an important component of diversity linked to how populations cope with environmental change in both the short and long term (Dingemans et al., 2010; Dochtermann et al., 2014). Among fishes, the ecological effects of movement diversity are perhaps best studied in Pacific salmonids *Oncorhynchus* spp, where variability in migratory traits has been estimated to reduce population-size fluctuations in steelhead *Oncorhynchus mykiss* and stabilise the meta-population abundance of Chinook salmon *Oncorhynchus tshawytscha* (Connors et al., 2022; Moore et al., 2014). For the depleted coastal cod, it is possible that the large-scale movement diversity observed here may enhance these populations' resilience and stabilise their biomass through portfolio effects by reducing their exposure to external stressors, such as fisheries and environmental stochasticity. However, the diverse portfolio of movement tactics may also reduce the effectiveness of conservation efforts, such as marine protected areas, because these areas are usually limited in size and hence sensitive to organisms that migrate out of the protected range (Villegas-Ríos et al., 2021).

4.2 | Residency of life-stages

Spawning cod of both ecotypes exited the fjords to a greater extent than non-spawning individuals, and for coastal cod a difference between life-stages was also evident in the exit timing, with spawning individuals leaving earlier. The presence of this life-stage dependent behaviour across ecotypes does not only highlight the tendency of mature coastal cod to utilise other areas during other parts of the year but also demonstrate some degree of spatiotemporal overlap of ecotypes during the spawning period. Recent population genetics studies have suggested that geographic variation in gene flow from NEA cod into local coastal cod populations could maintain the large-scale genetic cline present in the latter (Breistein et al., 2022; Jorde et al., 2021). To what extent this observed sympatry represents genetic introgression is beyond the scope of this manuscript and requires a far more comprehensive description of the behaviour and space use of spawning individuals. In a recent study describing the co-occurrence of coastal and NEA cod in a marine protected area during the spawning period, Johansen et al. (2018) documented that the proportion of NEA cod caught in the commercial fishery exceeded their representation in the egg samples, suggesting that many of the visiting NEA cod did not spawn within the fjord. Furthermore, a closer scrutiny of the data may also provide insight into the number of spawning sites used within a spawning period, whether mature cod utilise the same spawning sites in consecutive years, and the connectivity between the fjords within spawning periods. Temporary residency during spawning, accompanied with interannual spawning site fidelity, has been demonstrated throughout the geographical range of cod and it is likely that the magnitude of such homing behaviour plays a major role in shaping cod populations (Dean et al., 2014; Skjæraasen et al., 2011).

The finding that spawning cod displayed a lower fjord residency than non-spawning individuals coincides with the size-dependent behaviour observed in the feeding-season sample, where larger cod were more likely to exit the fjords and remained resident for shorter time periods than their smaller conspecifics. Space use in animals is strongly linked to body size, both within and among species, with larger animals moving over larger spatial extents (Hopcraft et al., 2012; Rosten et al., 2016; Udyawer et al., 2023). Although we do not explicitly address the effect of body size on space use, it is likely that the negative correlation between fish length and fjord residency reflects greater movement capacity of larger individuals, due to greater swimming ability, greater energy demand, and higher trophic position than smaller cod.

4.3 | Residency of males and females

Patterns of sex-dependent dispersal are often linked to mating system characteristics (Li & Kokko, 2019). For marine mammals or fish with some level of maternal care, males are commonly found to be the more dispersive sex (e.g. Lyrholm et al., 1999; Pardini

et al., 2001). Such male-biased dispersal is also observed in fish with no parental care, where males typically have a greater reproductive potential than females (e.g. Hutchings & Gerber, 2002). However, for some fishes with such reproduction characteristics, females may be the more dispersive of the sexes (e.g. Morita et al., 2012). Previous studies on the habitat use of spawning cod have documented several sex-specific behaviours, both related to residency, with males spending more time at spawning sites than females (Skjæraasen et al., 2021), and to aggregation, with females aggregating over smaller areas than males during daytime (Dean et al., 2014). We observed no effect of sex on cod behaviour and while it is possible that this is caused by random noise in our spawning-season data, we argue that it is more likely that this aspect is inhibited by the spatial resolution of the analyses and further scrutiny of the within fjord movements would be necessary to determine if the behaviour of males and females differ during the spawning period.

5 | CONCLUSIONS

In conclusion, this study provides evidence of extensive movement diversity within both coastal and NEA cod, leading to extended sympatry between the ecotypes. According to the existing dogma, no NEA cod should be found among the cod sampled during the feeding season nor should mature NEA cod remain within the fjord outside of the spawning season. This was clearly not the case and, given the observed spatiotemporal overlap between the ecotypes, it is imperative to understand how they interact, how genetic diversity is maintained and to what level hybridization occurs.

Given the contrasting states of the ecotypes, with NEA cod supporting the world's largest remaining commercial cod fishery and coastal cod being in a depleted state, the observed overlap in habitat use poses stern challenges for the management. Locally, real-time genetic monitoring of NEA cod fisheries may reduce by-catch of coastal cod and mitigate the impact for vulnerable populations (Johansen et al., 2018). However, at a larger scale, by-catch is likely difficult to avoid in the absence of detailed knowledge of the degree of sympatry, including information of individual behaviour and movement diversity. Furthermore, detailed understanding of this movement diversity is not only crucial in management and conservation of the ecotypes themselves but also in the management of the marine ecosystems they inhabit due to their role as a keystone predator in the food web (Frank et al., 2005; Norderhaug et al., 2021).

AUTHOR CONTRIBUTIONS

Pål Arne Bjørn, Thomas Bøhn, Karl Øystein Gjelland, Jon Egil Skjæraasen, Ørjan Karlsen and Esben Moland Olsen designed the study and collected the data. Torild Johansen and Tanja Hanebrekke were responsible for the genetic analyses. John Fredrik Strøm analysed the data and led the writing of the manuscript. All co-authors contributed to the interpretation of the data, the writing of the manuscript and gave their final approval for publication.

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.cnp5hqc9n> (Strøm et al., 2023).

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