RESEARCH ARTICLE

Atlantic cod individual spatial behaviour and stable isotope associations in a no-take marine reserve

Christopher T. Monk[1,2,3] | Michael Power[4] | Carla Freitas[1,5] | Philip M. Harrison[6] | Michelle Heupel[7] | Anna Kuparinen[8] | Even Moland[1,2] | Colin Simpfendorfer[9] | David Villegas-Ríos[10] | Esben M. Olsen[1,2]

[1]Institute of Marine Research, Flødevigen Marine Research Station, His, Norway; [2]Centre for Coastal Research, Department of Natural Sciences, University of Agder, Kristiansand, Norway; [3]GEOMAR Helmholtz Centre for Ocean Research Kiel, Kiel, Germany; [4]Biology Department, University of Waterloo, Waterloo, Ontario, Canada; [5]MARE, Marine and Environmental Sciences Center, Madeira Tecnopolo, Funchal, Madeira, Portugal; [6]Department of Biology and Faculty of Forestry and Environmental Management, Canadian Rivers Institute, University of New Brunswick, Fredericton, New Brunswick, Canada; [7]Integrated Marine Observing System (IMOS), University of Tasmania, Hobart, Tasmania, Australia; [8]Department of Biological and Environmental Sciences, University of Jyväskylä, Jyväskylä, Finland; [9]College of Science and Engineering, James Cook University, Townsville, Queensland, Australia and [10]Instituto de Investigaciones Marinas, CSIC, Vigo, Pontevedra, Spain

Correspondence
Christopher T. Monk
Email: cmonk@geomar.de

Funding information
Academy of Finland, Grant/Award Number: 317495; Canadian Network for Research and Innovation in Machining Technology, Natural Sciences and Engineering Research Council of Canada; Consejo Superior de Investigaciones Científicas; H2020 European Research Council, Grant/Award Number: 770884; H2020 Marie Skłodowska-Curie Actions, Grant/Award Number: 793627; Norges Forskningsråd, Grant/Award Number: 294926; Spanish Ministry of Science and Innovation (Ramón y Cajal Program), Grant/Award Number: RYC2021-032594-I

Handling Editor: Jean-Michel Gaillard

Abstract

1. Foraging is a behavioural process and, therefore, individual behaviour and diet are theorized to covary. However, few comparisons of individual behaviour type and diet exist in the wild.

2. We tested whether behaviour type and diet covary in a protected population of Atlantic cod, *Gadus morhua*.

3. Working in a no-take marine reserve, we could collect data on natural behavioural variation and diet choice with minimal anthropogenic disturbance. We inferred behaviour using acoustic telemetry and diet from stable isotope compositions (expressed as δ^{13}C and δ^{15}N values). We further investigated whether behaviour and diet could have survival costs.

4. We found cod with shorter diel vertical migration distances fed at higher trophic levels. Cod δ^{13}C and δ^{15}N values scaled positively with body size. Neither behaviour nor diet predicted survival, indicating phenotypic diversity is maintained without survival costs for cod in a protected ecosystem.

5. The links between diet and diel vertical migration highlight that future work is needed to understand whether the shifts in this behaviour during environmental change (e.g. fishing or climate), could lead to trophic cascades.

KEYWORDS
acoustic telemetry, Atlantic cod, individual trophic niche, marine reserves, stable isotopes

1 | INTRODUCTION

Foraging is a behavioural process consisting of multiple stages from searching to recognizing, attacking, capturing, handling and ingesting resources (Holling, 1966; Mangel & Clark, 1986). While foraging, individuals need to trade-off benefits of energy and nutrient consumption with associated costs, such as risks of being preyed upon (Lima & Dill, 1990), excess energy expenditure

(O'Brien et al., 1989) and encountering unsuitable thermal habitats (Freitas et al., 2021). The incorporation of behavioural processes as a nonlinear functional response to model density-dependent consumer-resource interaction strengths (Holling, 1959) was a major advancement in predicting food-web dynamics (Berlow et al., 2004; Wootton & Emmerson, 2005). Given the nonlinear basis of food-web interactions, Jensen's inequality implies that population behavioural averages are insufficient measures to predict food web dynamics and individual variation must be accounted for (Bolnick et al., 2011). Indeed, a number of cases have been made for incorporating the role of the individual into food-web modelling (Bolnick et al., 2011; Des Roches et al., 2018; Gibert & DeLong, 2017; Kalinkat, 2014). Building a clear theoretical understanding for how individual behaviour fits into food-web dynamics will support the prediction of trophic cascades driven by changes in behavioural diversity or, vice versa, changes in behavioural diversity driven by trophic cascades which could conceivably occur when consumption or being predated is consistently coupled with individual behaviour (Laskowski et al., 2022; Sommer & Schmitz, 2020).

Consistently structured behavioural differences among individuals that emerge across time and contexts are observed in nearly every animal population (Bell et al., 2009), implying a degree of inflexibility for individual behaviour. Consistent among-individual differences in behavioural traits over time and across contexts are known as "animal personality" or "behaviour types" and have been described for well-studied behavioural axes such as, activity, boldness, sociability, exploration and aggression (Réale et al., 2007). Additionally, personality traits have also been described for other behaviours measured in the wild (Spiegel et al., 2017) such as home-range size and space-use (Villegas-Ríos et al., 2017) or migration timing (Birnie-Gauvin et al., 2021). Relatedly, "individual resource specialists", that have a substantially narrower individual dietary niche than the population's niche, are frequently observed within overall generalist animal populations (Bolnick et al., 2003). In other words, individual foraging tactics where individuals primarily consume a subset of the prey items consumed by the entire population often coexist (Chavarie et al., 2021), potentially without fitness consequences (Woo et al., 2008).

Despite the structured among-individual variation of diet and behaviour within populations, the links between individual resource specialization and personality are so far insufficiently studied. Toscano et al. (2016) have outlined several potential theoretical mechanisms on which testable hypotheses can be developed. For example, in relation to the "locomotor crossover" hypothesis (Huey & Pianka, 1981) active individuals might be expected to forage on less active prey types while inactive individuals might forage on active prey types. Moreover, bolder individuals may forage in riskier habitats (Klefoth et al., 2017), or dominate access to patches in social groups (Kurvers et al., 2010), and mobile and exploratory individuals may have a wider foraging space resulting in access to alternative prey options (Campos-Candela et al., 2018; Spiegel et al., 2017). Lastly, individual behavioural differences may be linked

to underlying physiological differences, related to fast-slow life histories (Campos-Candela et al., 2018; Spiegel et al., 2017), which in turn may lead to differing foraging tactics (Nakayama et al., 2017). There is, therefore, a reasonable basis to expect that personality and diet could covary in the wild.

Until recently it has been relatively challenging to extract a complete profile of both animal behaviour and diet specialization in the wild over the long term. Diet is often assessed by lethal methods where gut contents are identified and quantified, or by non-lethal methods such as gastric lavage, scat analysis, observations of predator–prey events, or quantifying associations in laboratory environments (Nielsen et al., 2018). However, prey items could easily be missed in the gut based on digestive variability or the timing of sampling, while observations of predation events or predatory behaviour provide only a snapshot of a complete diet, but not a measure of long-term dietary preferences. Fortunately, logging long-term, high-resolution animal behaviour in the wild is rapidly becoming available as biologging technologies advance, and transmitters become smaller and cheaper (Hussey et al., 2015; Kays et al., 2015; Nathan et al., 2022) and long-term diet can be assessed non-lethally in the wild using fatty acids (Budge et al., 2006) or ratios of stable isotopes (Carneiro et al., 2017; Crawford et al., 2008; McKechnie, 2004).

The ratio of the stable isotopes of ^{15}N to ^{14}N (i.e. $\delta^{15}N$ ‰) in organismal tissue can approximate the trophic position of an individual, while the ratio of the stable isotopes ^{13}C to ^{12}C (i.e. $\delta^{13}C$ ‰) can approximate the source (e.g. pelagic, benthic, terrestrial) of primary production for consumed resources (Hobson, 1999; Peterson & Fry, 1987). Both ^{15}N and ^{14}N are taken up by primary producers in proportional amounts to the environmental ratio; however, ^{14}N is preferentially excreted at a relatively predictable rate, enriching $\delta^{15}N$ ‰ with consecutive consumption events. Accordingly, $\delta^{15}N$ ‰ increases with trophic position. Similarly, ^{13}C and ^{12}C are taken up from the environment by primary producers, but ^{13}C is preferentially used during carbon fixation at a rate dependent on the photosynthetic mechanism (Peterson & Fry, 1987). In coastal ecosystems, pelagic phytoplankton, benthic algae (e.g. brown algae, and diatom mats), eelgrass and terrestrial primary production have distinct $\delta^{13}C$ ‰ signatures (Fry & Sherr, 1989). As carbon is transferred up trophic levels, $\delta^{13}C$ ‰, remains relatively constant (fractionation rate of 1‰–2‰) (Barnes et al., 2007; Post, 2002) allowing for original sources of primary production to be traced through the food web. As tissues are rebuilt the isotopic ratios also change, reflecting the current diet. As rebuilding rates vary across tissues, by sampling the appropriate tissue one can assess an animal's diet at an approximate timepoint in the past (Peterson & Fry, 1987).

The few studies to date comparing personality in the wild and diet using stable isotopes do not yield clear or consistent results. Woo et al. (2008) found that repeatable differences in Brünnich's guillemot (*Uria lomvia*) flight time, dive depth and dive shape were correlated with differences in prey selection, where foraging tactics did not result in differences in reproductive success. Exploration in captivity predicted resource acquisition (Ersoy

et al., 2022) by red knots (*Calidris canutus*) and discovery (Herborn et al., 2010) by blue tits (*Cyanistes caeruleus*). In freshwater systems, Eurasian perch (*Perca fluviatilis*) resource consumption from pelagic pathways was higher for individuals that switched more frequently between active and inactive modes (Nakayama et al., 2017), while reliance on benthic pathways for burbot (*Lota lota*) correlated positively with activity at lower trophic levels and negatively with activity at higher trophic levels (Harrison et al., 2017) and bolder sticklebacks were found to forage in more littoral habitats (Theódórsson & Ólafsdóttir, 2022). In a marine coastal system, Dhellemmes et al. (2021) found that the relationship between individual juvenile lemonshark (*Negaprion brevirostris*) exploration and isotopic signatures of foraging in high-risk, exposed eel grass habitats fluctuated in direction and magnitude according to predation pressure. Gharnit et al. (2022) also found sex and resource availability specific relationships between exploration (measured in an open field test) and isotopic signatures in wild eastern chipmunks (*Tamias striatus*). In laboratory and pond environments Kerr and Ingram (2021), Schröder et al. (2016) and Laskowski et al. (2022) observed no impacts of behaviour type on diet, functional response or lower trophic levels, respectively. Hence, some connections between personality and diet have been observed, but no clear pattern has emerged and more effort is required to understand under which circumstances relationships between personality and diet exist, and what mechanisms lie behind the relationships.

Both diet and behaviour are known to be commonly associated with body size, and therefore when investigating associations between personality and diet, body size must be accounted for, unless individuals are restricted to a single size-class. Body size is frequently found to relate to diet, particularly in gape limited predators, where larger individuals can consume larger prey, often at higher trophic levels (Gaeta et al., 2018; Segura et al., 2014). Furthermore, body size is correlated with ontogenetic niche shifts (Kimirei et al., 2013; Scharf et al., 2000), which often involve shifts in diet. Predation risk and metabolic demand both scale allometrically (Krause et al., 1998; Werner & Gilliam, 1984). Larger fish are at lower risk from predation and can therefore access alternative food sources located in previously risky habitats. Larger individuals also have greater absolute energy demand to support a higher resting metabolic rate, and therefore may switch to more energetically profitable food sources. Indeed, positive relationships between body size and diet as indicated by stable isotopes are commonly found in fish (McCormack et al., 2019). Similarly, as fish grow their behaviour is expected to shift as well. Larger individuals can escape predation risk, exploring larger areas (Fuiman & Magurran, 1994; Nilsson & Brönmark, 2000). Larger individuals also may also have greater energy stores allowing higher activity rates (Videler & Wardle, 1991). Moreover, larger fish potentially have altered social interactions, as their place in a size-based dominance hierarchy shifts (Ward et al., 2006). Hence, associations between diet and personality can be missed when body size is the dominant cause for variation in diet or behaviour, unless body size is accounted for.

We focused our investigation in southern Norway on a coastal population of Atlantic cod, *Gadus morhua*, a predatory fish species in North Atlantic marine coastal ecosystems. Cod behaviour has been intensively studied given the species' commercial and cultural importance (Meager et al., 2018) and are known to exhibit consistent behavioural differences along a reactive-proactive spectrum connected to spatial behaviour (home range size) in the wild (Villegas-Ríos et al., 2018). Cod exhibit inter-individual variation in feeding tactics, specializing in specific prey types (e.g. sand eel, flatfishes or crustaceans) (Funk et al., 2021; Hüssy et al., 2016) and, therefore, among-individual differences in diet are likely to be observed. Our main objectives were to test whether these among-individual differences in diet are associated with or independent of cod spatial behaviour and if associations were present, whether they may have fitness impacts in terms of survival. Despite being intensely studied, prey selection in cod is poorly understood, in particular with respect to individual variation (Meager et al., 2018). The cod in the coasts of southern Norway have been observed to have very small home range sizes and remain close to steep rocky edges, making rare excursions into the pelagic (Freitas et al., 2021; Villegas-Ríos et al., 2021). The cod also typically move, on a daily basis, from deeper waters in the daytime to shallower waters at night time during which they are assumed to be foraging (Espeland et al., 2010; Freitas et al., 2021). Foraging cod near the rocky edges of fjords are likely consuming small gobies (*Gobius niger*, *Gobiusculus flavescens*, *Aphia minuta*), sculpins (*Myoxocephalus Scorpius*), amphipods, polychaetes, crustaceans (*Carcinus maenas*) and wrasses (*Ctenolabrus rupestris*, *Symphodus melops*), while cod foraging in the pelagic may consume for example, sprat, herring and other gadids (*Pollachius pollachius*, *Merlangius merlangus*, *Pollachius virens*, *Trisopterus minutus*) (Hop et al., 1993).

In this study we combined high-resolution acoustic telemetry (Nathan et al., 2022) and stable isotope techniques to investigate the relationships between individual behaviour and diet for wild cod in an established no-take marine reserve, with an unexploited food web and cod population. We hypothesized that more active cod with larger activity spaces in shallower habitats and greater diel vertical migration would spend less time foraging on lower trophic organisms such as small gobies and amphipods in benthic habitats and would therefore have a have a more negative $\delta^{13}C$ value and a higher $\delta^{15}N$ value relative to their counterparts, where an activity space is a spatially and temporally defined area in which an individual engages in normal activities. In addition to investigating fundamental ecological principles relating to foraging and behaviour, we also hypothesized based on the findings of Woo et al. (2008) that diet would not have an impact on individual survival during the tracking period. We focused on activity and activity space size, as these behaviours are directly related to the foraging activity and spatial aspects of foraging mechanisms linking personality and diet specialization, as outlined by Toscano et al. (2016). We also considered depth and diel vertical migration distance, because the vertical dimension is an important component of the cod's environment in our study system (Freitas et al., 2015, 2021).

2 | MATERIALS AND METHODS

2.1 | Study region and acoustic telemetry system

Our study was conducted in the Tvedestrand Fjord (52.60282°N, 8.948268°E), located on the Skagerrak Sea's coast in southern Norway (Figure 1; See the Appendix for a full description of the fjord). Importantly, a large portion of the fjord (150 ha) has been designated as a no-take marine reserve since June 2012, where all forms of fishing and trapping are prohibited, in addition to two buffer areas where fixed fishing gear is forbidden (Figure 1). A portion of the cod population is resident in the fjord, thought to remain inside the study area for its lifetime (Villegas-Ríos et al., 2021), and thus are probably largely protected from harvest, though harvest remained possible in the buffer areas outside the no-take area. The study site is therefore advantageous for studying long-term natural cod behaviour in the wild.

Tvedestrand Fjord has been equipped with a high-resolution Innovasea VPS telemetry system since June 2013. The median system accuracy is 1.8–4.4 m (see Freitas et al., 2016). The original VPS system consisted of 31 VR2W receivers (Innovasea, Halifax, Canada)

distributed within the no-take marine reserve. In 2018, the VPS system was expanded to buffer zones located north and south of the no-take reserve, to a total of 55 receivers. Each receiver is fixed at 3 m depth, with moorings and subsurface buoys. The receivers record the time-of-arrival data from unique ultrasonic signals emitted from transmitters surgically implanted into the body cavities of fish. Based on discrepancies in signal arrival times among receivers, the fish positions within the fjord can be calculated by multilateration. Additional transmitters (V16-4X) fastened below each receiver act as "synctags" to correct for clock drift among receivers and four "reference" transmitters (V13-1x & V13T-1x) were placed at fixed locations within the array to measure system performance. The addition of a calibrated pressure sensor inside fish transmitters enabled the addition of a third dimension for each position.

2.2 | Cod sampling

Cod were sampled between May 2018 and December 2020 during five sampling events (spring 2018, spring 2019, fall 2019, spring
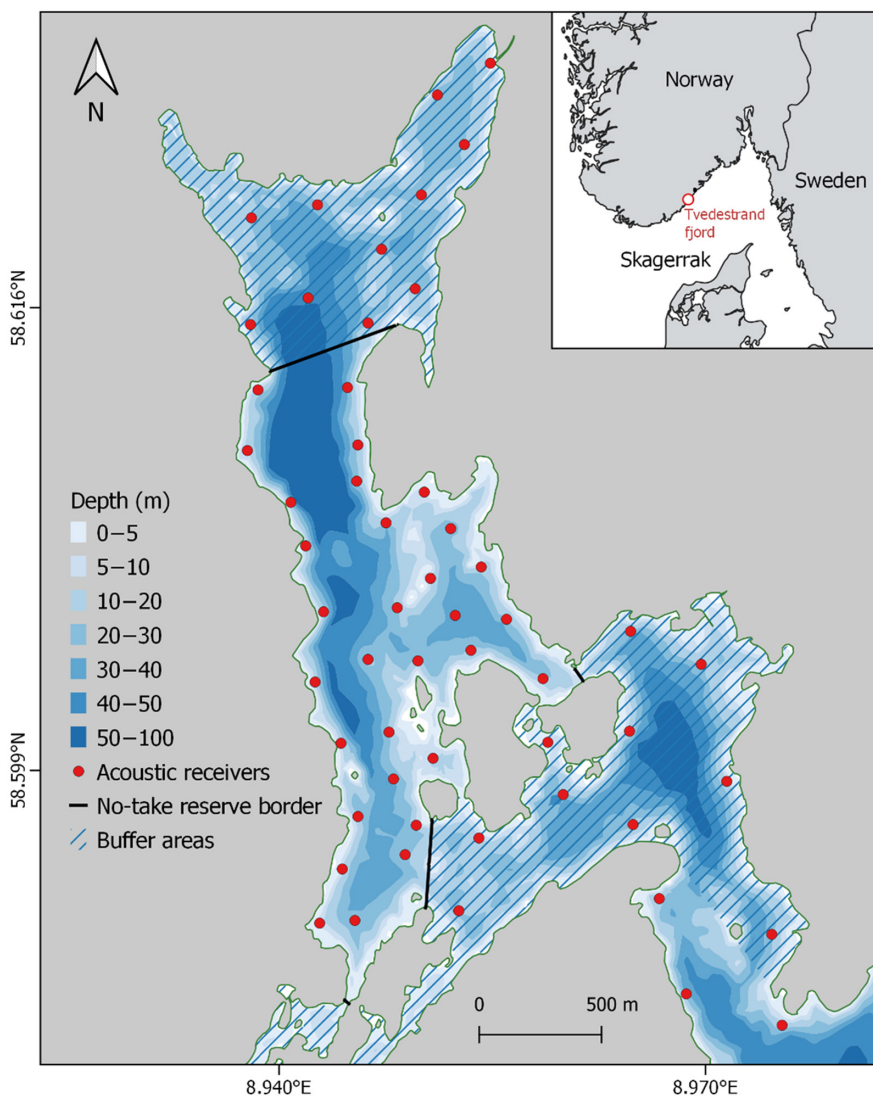

FIGURE 1 Map of the study area showing the location of the 55 acoustic receivers in Tvedestrand Fjord and the location of the full-protected marine reserve and its buffer areas.

2020 and fall 2020, see Figure A1). Cod were captured by fyke-nets distributed along the fjord's coastline between 1 and 10 m depth and soaked for 1–3 days. The captured cods' fork lengths ($n = 184$) were measured, and a 5 mm dermal punch was used to sample the dorsal muscle for stable isotope analysis. Tissue samples were stored at −25°C until processing. A subset of cod ($n = 97$) were taken to the nearest shore for sampling and transmitter implantation and anaesthetised with a 9:1 EtOH: clove oil solution added to water at $0.4\,mL\,L^{-1}$. Transmitters (V13P; Innovasea Systems, Halifax, Canada; weight in water: 5.5 g; estimated battery life: 1285 days; power output: 147 dB) were surgically implanted into the body cavity of these cod, and incisions were closed with two adsorbable sutures. The acoustic transmitters had a random transmission interval with a mean delay of 180 s (range of 130–230 s) and a built-in pressure sensor (maximum depth: 68 m; resolution 0.3 m; accuracy: 3.4 m) for transmission of current depth as well as the identity code. Each cod received an external T-bar anchor tag (TBA-2, 30×2 mm, Hallprint Pty. Ltd, Holden Hill, South Australia) parallel to the anterior dorsal fin. All cod were released at the capture site immediately after recovery from anaesthesia. All cod sampling and tagging was approved by the Norwegian Food Safety Authority (permit 19556).

2.3 | Estimation of behavioural traits

Cod detection data were downloaded from acoustic receivers twice per year. Fine-scale cod positions were subsequently estimated by Innovasea using the VEMCO positioning system and we based our estimation of behavioural traits and mortality on these fine-scale positions. Prior to behavioural analysis, the trajectories of each cod were inspected and subset to filter out unlikely positions (positions with a VPS HPE ≥34 were removed (Freitas et al., 2016)), positions that appeared on land and positions after natural mortality (e.g. that belonged to a preyed cod) to ensure only the live cod behaviour was analysed and used to measure survival. We determined each cod's fate following the methods described by Villegas-Ríos et al. (2020), where cod were classified as surviving, dispersing, or succumbing to natural mortality or harvest, based on the inspection of three-dimensional positions. Natural mortality was assigned when the vertical and horizontal movements stabilize at the same time, harvesting was assigned when detections stop before the end of the transmitter battery life and the last detections were not at the edge of the study system (in which case dispersal is assigned), predation was assigned when a clear change in movement pattern suddenly occurs that resembles known behaviours of a cod predator (e.g. a harbour seal, *Phoca vitulina*), and survival was assigned when the cod displayed the expected vertical and horizontal behaviour throughout the battery life of the transmitter.

We estimated four behavioural traits (activity, activity-space size, depth and diel vertical migration distance) on a daily timescale for each cod throughout the entire study period. Days were considered to be between consecutive sunrises (based on the NOAA

sunrise calculator (www.esrl.noaa.gov/gmd/grad/solcalc/) for all behaviours. Activity was calculated by summing the three-dimensional Euclidean distances between consecutive positions along each trajectory. Euclidean distances below 4.4 m were excluded as they could not be distinguished from the telemetry system error (Freitas et al., 2016) and therefore we could not be reasonably certain that the cod was moving. The 2d activity space size of the cod was calculated using the 95% kernel utilization density (kud) area of the cod positions. The activity space sizes were calculated in R using the adehabitatHR package (Calenge, 2011). The daily individual activity space size was only calculated if more than 30 positions were available. Depth was assessed based on the pressure sensor in the acoustic transmitters and summarized as the mean depth. Diel vertical migration distance was calculated as the difference between the mean depth after sunset and the mean depth before sunset. Note that in the case of diel vertical migration distance negative values indicate cod were shallower at night and deeper during daytime. We excluded measures of diel vertical migration distance between March 1 and May 1 each year, as this is the likely spawning period during which diel vertical migration is not a typical behavioural pattern (Espeland et al., 2007).

2.4 | Stable isotopes analysis

We used dorsal muscle tissue obtained from muscle biopsies known to have no lasting effects on fish (Bøe et al., 2020). Muscle tissue in cod has been found to change very little 90 days after dietary changes (Ankjærø et al., 2012) and, therefore we can safely interpret the $\delta^{13}C$ and $\delta^{15}N$ as representing around 3 months of past consumption. As we have only single measures for $\delta^{13}C$ and $\delta^{15}N$ we considered our isotope measurements to represent individual trophic niche (Dhellemmes et al., 2021; Hussey et al., 2017).

The cod dorsal muscle biopsies were processed at the Environmental Isotope Laboratory at University of Waterloo in Canada. The samples were dehydrated at 50°C for 24 h and then crushed into a powder with a mortar and pestle and weighed in tin capsules (Tin Capsules Pressed Standard Weight 5×3.5 mm, Elemental Microanalysis Ltd., Okehampton, UK) using an analytical balance (XP205 DeltaRange, Mettler-Toledo GmbH, Greifensee, Switzerland). The stable isotope values from each sample were measured using a Delta Plus Continuous Flow Stable Isotope Ratio Mass Spectrometer (Thermo Finnigan, Bremen, Germany) coupled to a 4010 Elemental Analyser (CNSO 4010, Costech Analytical Technologies Inc., Valencia, USA), with results expressed in delta notation as $\delta^{13}C$ and $\delta^{15}N$, relative to the international standards Vienna Pee Dee Belemnite for $\delta^{13}C$ (Craig, 1957) and atmospheric nitrogen for $\delta^{15}N$ (Mariotti, 1983). Measurement repeatability was assessed by reweighing every tenth sample. Analytical precision (±0.2‰ for $\delta^{13}C$ and ±0.3‰ $\delta^{15}N$) was assessed using internal laboratory standards cross-calibrated against the International Atomic Energy Agency standards CH3 and CH6 for carbon and N1 and N2 for nitrogen. The C:N ratios were close to three (3.23 ± 0.12

mean ± SD, 8 samples >3.5), and therefore we did not conduct any lipid extraction. We also did not observe any correlation between C:N ratios and $\delta^{13}C$ values (Figure A2. cor = −0.07, t = −0.96, df = 182, p = 0.34, Pearson's product–moment correlation), and therefore did not correct $\delta^{13}C$ values.

2.5 | Stable isotopes context

Our assessment that $\delta^{15}N$ values are indicative of trophic position relies on several assumptions, namely that the baseline $\delta^{15}N$ values in our study system are not heterogeneous across benthic and pelagic modes of primary production, and $\delta^{15}N$ values are evenly distributed in space and time. Further, our assessment that $\delta^{13}C$ values are indicative of primary production source requires verification that benthic and pelagic primary production can indeed be distinguished at lower trophic levels. We therefore opportunistically collected stable isotopes from lower trophic organisms in the Fjord. We collected seven *Ascophyllum nodosum* samples in January 2020 and 6 *Ascophyllum nodosum*, 10 *Cerastoderma edule*, 6 filamentous green algae, 20 *Littorina* spp. and 20 *Mytilus edulis* samples in June 2020 from the study system and measured stable isotopes from these samples using the same methods as we did for cod dorsal muscle samples. We tested for differences in $\delta^{15}N$ values between *Ascophyllum nodosum* and filamentous green algae samples using a *t*-test and visually inspected all samples for homogeneity of $\delta^{15}N$ values across $\delta^{13}C$ values in our samples. We also inspected the spatial distribution of $\delta^{15}N$ values from these samples as runoff points from farmland or sewage may inflate $\delta^{15}N$ value baselines at nearby sample sites (Baker et al., 2017). Further, we inspected for spatial trends along latitude and longitude and temporal trends of $\delta^{15}N$ and $\delta^{13}C$ values from our cod muscle samples.

2.6 | Statistical analysis

We assessed the relationship between fate and individual trophic niche using a cox-proportional hazards model fit to Kaplan–Meier survival curves using the "survival" package (Therneau & Lumley, 2015) in R. In this model we used right censored (survived or dead) survival time. Cod that survived the entire transmitter battery life or dispersed from the study area were considered survivors and right-censored on their last detection day, whereas cod that died from either natural reasons or harvesting were considered dead. The model covariates, $\delta^{13}C$ and $\delta^{15}N$ median activity, median activity space size, median depth and median diurnal migration distance, were standardized (scaled and centred) for comparability of effect sizes. We confirmed that the proportional hazards assumption was met using the "cox.zph" function within the survival package.

To carry over variation in daily behavioural measurements we used multivariate linear mixed effects models to estimate the correlations among cod body size, behaviour and diet (Houslay & Wilson, 2017). Models were fit with Bayesian inference, using the MCMCglmm package in R (Hadfield, 2010). We fit one multivariate model where the sextivariate response included daily measures of individual behaviours (activity, activity space size, depth, diel vertical migration) and single measures of individual $\delta^{13}C$ $\delta^{15}N$ values. As fixed effects we included cod fork length at the level of all response variables, sampling event fit at the level of both isotope response variables and solar elevation (scaled and centred) and fit at the level of the four behaviour response variables. This was done to control for the effect of body size on behaviour and diet, and sampling period on baseline isotope values and seasonal effects on baseline behaviour respectively. We have assumed that shifts in baseline values of $\delta^{15}N$ is homogenous across $\delta^{13}C$ values and vice versa. The solar elevation at midnight each day was calculated in degrees above the horizon using the R package oce (Kelley et al., 2022) based on Michalsky (1988). To understand the associations among behaviour and isotope values, we fit an unstructured covariance matrix in the random effects using ID as the grouping variable. For each model we ran 550,000 iterations, with a burn-in of 50,000 and a thinning interval of 175. The model used an uninformative Inverse-Wishart prior (R1: V = diag(6) + 0.002, nu = 6 + 0.002, R2: V = diag(4), nu = 4 + 0.002). To account for the fact that we had repeated measures of behaviours, but did not have repeated measures for body size, $\delta^{13}C$ and $\delta^{15}N$, we followed the recommendations of Thomson et al. (2017) and Dingemanse et al. (2021) setting "covu = TRUE" in the residual structure of the prior to allow the sets of residuals to covary with the random effects. Activity and activity space size were $\log_{10}$ transformed to meet normality assumptions, and all response variables were scaled and centred to allow for comparable effect sizes. Model assumption violations were assessed by examining trace plots, Geweke diagnostics and posterior autocorrelation. Correlations between the behaviour traits and isotope measurements were estimated from the median and 95% credible intervals (highest probability density intervals) of the posterior distribution of among-individual covariance between behaviour and the isotope value divided by the product of the square root of each trait's among-individual variances (i.e. the product of each trait's among-individual standard deviation) (Houslay & Wilson, 2017). Significance was assessed by whether the 95% credible interval of the correlation's posterior distribution overlapped zero. As the stable isotope data represents diet prior to sampling and our behavioural data is collected after sampling, an assumption of our models is that behaviour and diet remain stable. We therefore also estimated adjusted repeatability (*r*), to assess how consistently different the cod behaviours in our study system were. Accordingly, from the multivariate mixed effects model we estimated a posterior distribution for adjusted repeatability by dividing each posterior draw of among-individual behavioural variance by the sum of within-individual variance and among-individual behavioural variance. We then evaluated the 95% credible interval (highest probability density interval) of the posterior of adjusted repeatability.

3 | RESULTS

The 184 sampled cod (165 unique individuals) ranged between 16 and 72 cm (mean ± SD: 44 ± 13 cm) in fork length. The δ^{13}C values ranged between −19.90‰ and −16.38‰ (mean ± SD: −18.11‰ ± 0.78‰) indicating consumption of varying mixes of prey from both pelagic and benthic pathways in the cod population in Tvedestrand Fjord. The δ^{15}N values ranged over approximately two trophic levels between 12.45‰ and 18.97‰ (mean ± SD: 14.58‰ ± 0.99‰) indicating varying reliance on fish and other higher trophic level prey.

Of the 97 cod fit with acoustic transmitters, six left the study system and were assumed to have survived until the dispersal date, 23 died from natural mortality, 25 were consumed by predators, 15 were harvested, 26 remained and survived through the tracking period, one individual died from tagging mortality and one fate could not be determined. One individual, at the northern study system edge, was never detected by a sufficient number of receivers to generate any fine-scale positions. Accordingly, 94 cod generated

behavioural data ranging from 5 to 901 days of tracking per individual (median = 179 days). The cod swam per day 362 [0, 14,395] m (median [minimum, maximum]) (mean ± SD), and used an activity space of 0.39 [0.17, 22.0] ha (median [minimum, maximum]) each day (Figure 2). The cod were 11.2 [0, 46.9] m ha (median [minimum, maximum]) deep during the tracking period and the cod migrated -0.3 [-28.8 (descent), 38.8 (ascent)] m ha (median [minimum, maximum]) from night to day (Figure 2). No detectable relationships occurred between individual survival and δ^{13}C, δ^{15}N or behaviour (Table 1). Activity ($r=0.66$, 0.58–0.72; mode, 95% CI), activity space size ($r=0.67$, 0.59–0.74; mode, 95% CI) and depth ($r=0.53$, 0.45–0.62; mode, 95% CI) were repeatable behaviours over the study period, but diel vertical migration ($r=0.17$, 0.12–0.24; mode, 95% CI) had lower repeatability. Of the 94 cod generating behavioural data, 78 could be included in our multivariate mixed effects model. This was because behavioural estimates for all four behaviours were required on a daily basis, and for individuals with few detections on a specific day, activity space could not be estimated. Therefore some
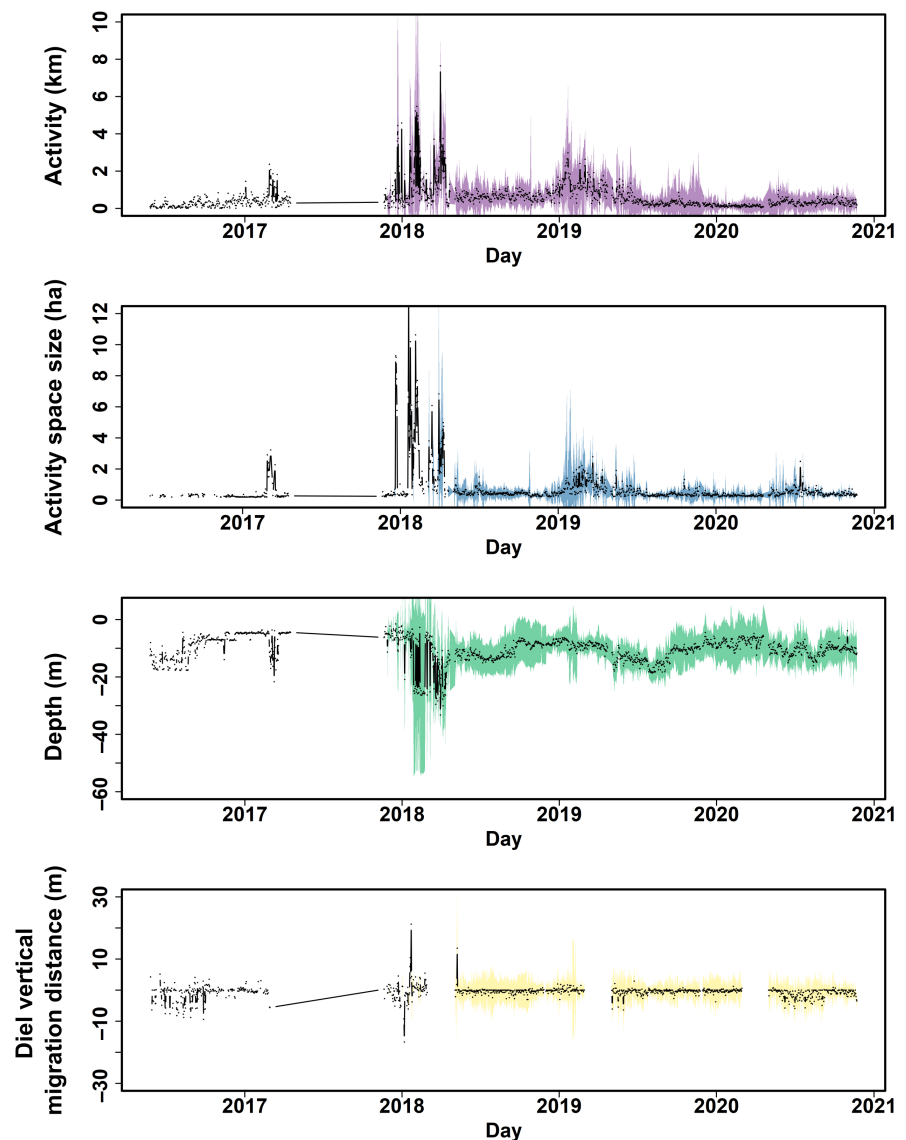

FIGURE 2 Daily population median values (black points) and standard deviations (polygons) of four cod behaviours (n = 94 fish) based on acoustic telemetry data from the Tvedestrand Fjord. Behaviour from only one individual was collected until fall 2017 (see Figure A1) and therefore no standard deviation is shown. Negative diel vertical migration distance indicates cod were deeper during the day and shallower at night.

individuals only present in the study system for a shorter time period and with poorer detectability did not have days with all behaviours estimated simultaneously.

We did not detect any differences between $\delta^{15}N$ values across benthic and pelagic sources of primary production (Figure 3). A *t*-test comparing $\delta^{15}N$ values of filamentous green algae and *Ascophyllum nodosum* was not significant ($t = -1.78$, df = 8.95, $p = 0.11$). Further, we did not observe any locations enriched in $\delta^{15}N$ from our samples of baseline and lower trophic organisms (Figure A2) and we did not observe any spatial patterns in $\delta^{15}N$ or $\delta^{13}C$ values in our cod isotope samples (Figure A3). However, there was a decrease in $\delta^{15}N$ values between 2018 and 2020 sampling dates in our cod samples (Figure A4).

We detected a positive relationship between cod diel vertical migration distance and $\delta^{15}N$ values (Figure 4, Figure A5). As the cod typically exhibited a negative diel vertical migration, moving from deep water during the day to shallow water at night, a positive relationship with distance values indicates that cod exhibiting shorter diel vertical migrations consumed resources from higher trophic

levels. We did not detect any other statistically significant correlations between behaviour and $\delta^{13}C$ or $\delta^{15}N$ as shown by the posterior distributions of the correlations (Figure 4, Figures A6 and A7). Fork length positively predicted $\delta^{13}C$ and $\delta^{15}N$ values, indicating that cod consume prey from increasingly benthic pathways, and/or higher trophic levels as they become larger (Table A1, Figure 5). We also found some significant effects of sampling period on isotope values (Table A1, fixed effects), where $\delta^{15}N$ ‰ was greater in spring 2018 than in other sampling periods. With increasing solar elevation (i.e. in summer) cod increased their activity and depth and reduced their diel vertical migration distance (Table A1, fixed effects).

4 | DISCUSSION

As foraging is a behavioural process, among-individual variation in diet must have a basis in behavioural differences. We found some support for our first hypothesis that more active cod with larger activity spaces in shallower habitats and greater diel vertical migration distance would have a have a more negative $\delta^{13}C$ value and a higher $\delta^{15}N$ value relative to their counterparts, as cod with a shorter diel vertical migration distance consumed prey with a higher contribution from higher trophic levels, suggesting alternative foraging tactics. Our second hypothesis, that diet would not have an impact on individual survival during the tracking period, was also supported as we did not observe any dietary fitness consequences, in terms of fate, suggesting that in our study system prey choices have equivalent costs for survival, or that cod may compensate for any mortality related costs in prey choice. As repeatable cod behaviour was related to diet as measured by stable isotopes, there is a possibility for potential trophic cascades via alterations to the behavioural composition of the population, for example through selective fishing (Audzijonyte et al., 2013; Hočevar & Kuparinen, 2021; Kindsvater & Palkovacs, 2017).

The fact that behavioural variation is consistent and structured among individuals in animal populations has been firmly established (Bell et al., 2009; Dall et al., 2012). However, the ecological consequences of such consistent among-individual variation, i.e. animal personality, remain poorly understood (Toscano et al., 2016; Wolf & Weissing, 2012). The connection between repeatable individual differences in cod diel vertical migration distance and $\delta^{15}N$ underscores that consistent differences in individual behaviour can have linkages to food web ecology and signifies that changes in frequencies of behaviour types within populations could have community level impacts (Wolf & Weissing, 2012). To fully understand the trophic consequences is beyond the scope of this study, as we do not know the specific prey types consumed and we do not know how changes in cod density would affect foraging patterns.

Diel vertical migration is known to be an important cod behavioural pattern (Freitas et al., 2015; Olsen et al., 2012). For coastal cod it may also be a key behaviour underlying diet and body size scaling relationships, as we found diel vertical migration distance was related to both body size and the trophic level of consumed prey. The diel vertical migration patterns we observed

TABLE 1 Coefficient estimates, hazard ratios, coefficient standard errors (SE), *z* values and *p* values for cox proportional hazard models assessing cod survival after tracking with acoustic telemetry. Model coefficients were standardized for comparability.

	Coefficient	Hazard ratio	SE (coef)	z value	p value
$\delta^{13}C$ ‰	−0.088	0.916	0.153	−0.578	0.563
$\delta^{15}N$ ‰	−0.176	0.838	0.159	−1.108	0.268
Activity	0.281	1.325	0.167	1.680	0.093
Activity space size	0.206	1.228	0.147	1.400	0.161
Depth	0.203	1.225	0.130	1.553	0.120
Diel vertical migration distance	0.085	1.088	0.171	0.495	0.621

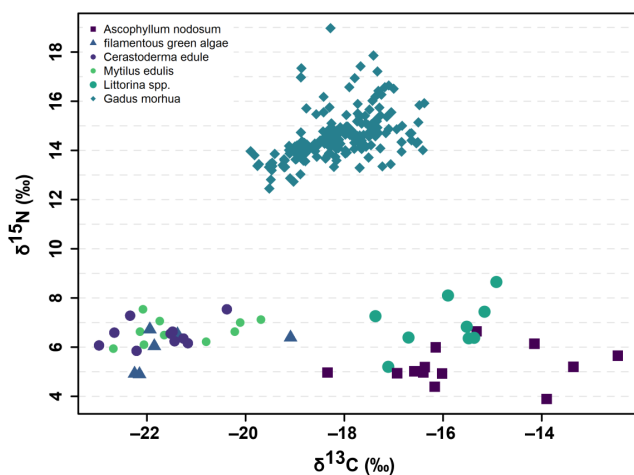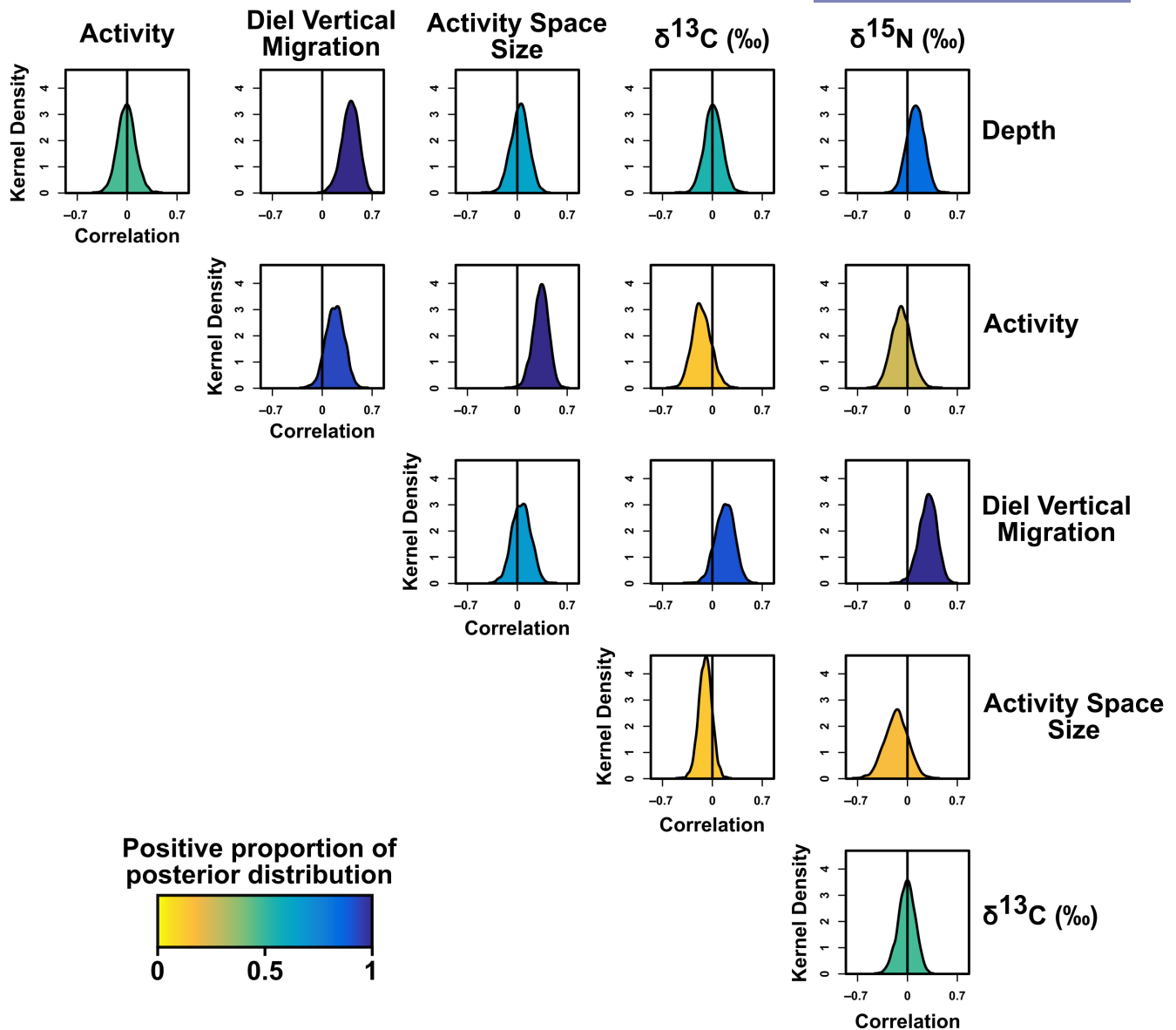**FIGURE 3** The $\delta^{13}C$ and $\delta^{15}N$ values for the 184 cod samples as well as five species indicative of the isotopic baseline in the study system.

FIGURE 4 Posterior estimates of correlation coefficients among four behaviours, $\delta^{13}C$ values and $\delta^{15}N$ values as estimated by multivariate generalized linear mixed effect models with data from 78 individual cod. Colour indicates the proportion of the posterior distribution above zero, where yellow is a negative correlation with high certainty and dark blue is a positive correlation with high certainty.

are in agreement with previous tracking data from cod, where the smallest individuals underwent the longest diel vertical migrations, while larger individuals generally remained at similar depths for the whole day (Freitas et al., 2015). Diel vertical migrations in coastal Skagerrak seem to occur along the sea floor (where cod follow the bathymetry toward shallower and deeper waters, instead of migrating purely vertically in the water column Freitas et al., 2016, 2021). In general, diel vertical migration may occur because of a trade-off between foraging opportunities and predator avoidance where visual predators can be avoided by refuging in deeper, darker waters during the daytime, and foraging in more productive shallower waters can be conducted more safely during the dark night time (Espeland et al., 2010; Mehner, 2012). Alternatively, predators may show diel vertical migration because

they are following their prey's diel vertical migration patterns (Queiroz et al., 2010) or they may show diel vertical migration because they may regulate their metabolic rate by choosing depths with the optimal ambient temperatures for digestion (i.e. hunt warm and rest cool) (Sims et al., 2006). Therefore, larger cod likely do not undergo diel vertical migrations to the same extent as smaller individuals because they may experience a reduced predation risk. Alternatively, they have switched to consume prey that do not show any diel vertical migration, or they no longer hunt warm and rest cool. Consequently, it is understandable that a behaviour motivated by foraging opportunities is related to the trophic level consumed in the diet. One possible explanation for the trophic level effects of diel vertical migration is that cod remaining shallower during the daytime may have access to alternative prey
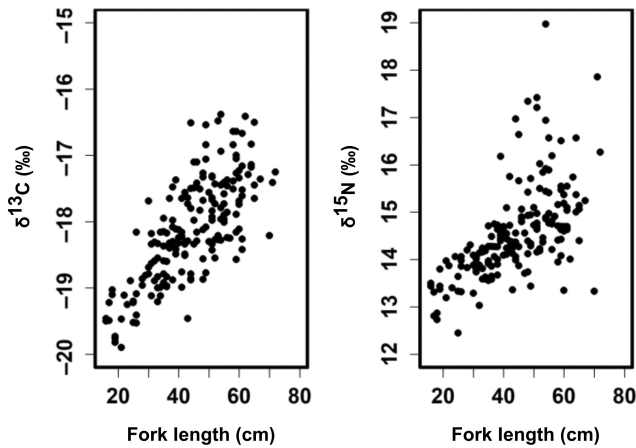
FIGURE 5 Relationship between cod body size (Fork length), and $\delta^{13}C$ and $\delta^{15}N$ values.

options when compared to individuals that only forage in shallower waters during night time. Gape limitation, which scales with body size, also likely contributes to relationship we observed between diel vertical migration and isotope signatures. Diet specialization would not be expected to occur without some fitness advantage over generalists (Bolnick et al., 2003); however, we did not observe any relationship between $\delta^{13}C$ or $\delta^{15}N$ values and survival. We based our hypothesis that there is lack of relationship on a similar study in the wild by Woo et al. (2008) where specialists and generalists Brünnich's guillemets showed no differences in survival or reproductive success. Woo et al. (2008) speculated that this may be driven by slow fluctuations of prey abundance over a decadal scale. Unfortunately, we do not have an indication of the extent to which the cod in our study are specialists or generalists. The variation in both $\delta^{13}C$ and $\delta^{15}N$ isotopes, particularly at large sizes suggests individual variation in feeding strategies, consistent other work with cod diets (Funk et al., 2021; Hüssy et al., 2016). The decade of protected status at our study site means that many prey populations may be reaching carrying capacity at our study site, potentially leading to slow fluctuations in resource abundance. Alternatively, as we did not measure reproductive success it is also possible that the cod's diet does indeed have fitness consequences in our study system, but not in terms of survival.

Body size was related to isotope values, where larger cod consumed resources from higher trophic levels and linked to more benthic primary production sources. Additionally, some of the shifts to a greater $\delta^{13}C$ value with increasing body size may also be driven by consuming prey at a higher trophic level, as $\delta^{13}C$ shows some small fractionation with trophic position (Barnes et al., 2007; Post, 2002). Moreover, some portion of the variance in isotope values with body size could be driven by variation in turnover rate, which can slow down with body size (Vander Zanden et al., 2015; Winter & Britton, 2021). Trophic level typically increases with body size in carnivorous fishes (Keppeler et al., 2020), including in cod (Jennings & Van Der Molen, 2015). Laskowski et al. (2022) found that fish body size (in terms of biomass) over measured

behaviour types caused impacts on lower trophic levels. It is possible, also, that density-dependent processes such as competition may have restricted the foraging opportunities and diet of smaller cod, especially since the study was conducted within a marine reserve. Earlier studies on the Skagerrak cod populations have shown that juvenile growth tends to decrease at higher population densities (Rogers et al., 2011), and that recruitment tends to be relatively poor in years following a strong recruitment episode (Bjørnstad et al., 1999). Decreased recruitment could be explained by inter-cohort cannibalism (Rindorf et al., 2020). Given the behavioural basis of foraging, further work is needed to discover the behavioural mechanism driving body size related differences in prey consumption. Understanding the behavioural mechanisms underlying the body size effects would also clarify under which conditions body size effects can be expected.

While classic ecological principles (Segura et al., 2014) would predict the relationship between body size and diet we observed, cod body size has not always been found to correlate with stable isotope signatures in other studies (Bergstad et al., 2008; Kristensen et al., 2021; but see Jennings & Van Der Molen, 2015). In a fjord system only 11 km northeast along the coast from our study area, a similarly sized cod population showed no change in $\delta^{13}C$ and $\delta^{15}N$ with increasing body size (Kristensen et al., 2021). Moreover, a cod population approximately 40 km northeast along the coast showed an increase in $\delta^{15}N$ with cod body size, but no relationship between body size and $\delta^{13}C$ (Bergstad et al., 2008). These findings suggest cod food web position may be dependent on the local context, which might vary both temporally and spatially between fjords. This local context could partially be driven by heterogeneous values of $\delta^{15}N$ across benthic and pelagic resources. However, due in part to its zoned status as fully and partially protected since 2012, the Tvedestrand Fjord, during the time spanning the present study might have offered a more diverse menu of prey items compared to the neighbouring Sandnes Fjord studied by Kristensen et al. (2021). For example, the absence of a fishery for wrasse has conferred effects on the size structure and density of wrasse species compared to harvested control areas (Halvorsen et al., 2017). A less diverse and possibly miniaturized prey menu might have been less likely to produce a result where body size correlates with trophic position.

We can suggest several mechanisms potentially explaining why relationships between depth, activity or activity space size and individual trophic niche were not observed in our study system. Firstly, it is likely that much of the movement we analysed was motivated by factors aside from foraging. In addition to foraging, movement within a home range may be motivated by factors such as information gathering (Dall et al., 2005), social interactions (Tupper & Boutilier, 1995) and predator avoidance (Ryan et al., 2012). As alternative foraging tactics (Huey & Pianka, 1981) or varying encounter rates while foraging (Toscano et al., 2016) are key mechanisms speculated to link diet and behaviour type, movement data generated by non-foraging related motivations should not correlate with diet unless via other mechanisms. Further, cod have been observed to exhibit ephemeral

gorge feeding events contributing up to 10%–30% of annual energy consumption (Grønkjær et al., 2020). Therefore, the main contributors to the isotopic signatures in cod muscle may be based on relatively rare, but large feeding events and not representative of more general foraging patterns hidden in our movement measurements. Lastly, as stable isotopes can only measure the food types consumed, but not consumption frequency, we could not assess whether individuals with larger activity spaces, or larger diel vertical migration distances benefit from increased consumption rates regardless of prey selection.

5 | CONCLUSIONS

We have found that diel vertical migration distance, assessed with data from 78 individual cod dwelling in a marine reserve, was related to diet, which implies that consistent individual differences in cod behaviour can have community level impacts. This work reinforces the call by Toscano et al. (2016) to better integrate animal personality and individual diet specialization. However, more work needs to be done to understand the circumstances in which relationships between behaviour and diet exist. Further, we conclude that at least in some systems, a lack of mortality risks impacts may allow for multiple combinations of behaviour and foraging tactics to coexist. A better ability to quantify foraging from movement data, perhaps through statistical classification, or by complimentary use of underwater video cameras, would help to tease apart the behavioural mechanisms behind prey selection, in particular the mechanisms behind the body size and diet relationship we observed. Trophic cascades from behaviourally selective fishing based on space-use or depth appear unlikely in coastal populations of cod. Importantly, preconditions for trophic impacts from behavioural selective fishing, or size selective fishing are present in at least some fjord systems, and should be considered in management of coastal ecosystems.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.pk0p2ngv6 (Monk et al., 2023).

ORCID

Christopher T. Monk https://orcid.org/0000-0002-1647-4740
Philip M. Harrison https://orcid.org/0000-0002-4791-3232
Anna Kuparinen https://orcid.org/0000-0002-7807-8946
Even Moland https://orcid.org/0000-0002-6521-2659
Colin Simpfendorfer https://orcid.org/0000-0002-0295-2238
David Villegas-Ríos https://orcid.org/0000-0001-5660-5322
Esben M. Olsen https://orcid.org/0000-0003-3807-7524

REFERENCES

Ankjærø, T., Christensen, J. T., & Grønkjær, P. (2012). Tissue-specific turnover rates and trophic enrichment of stable N and C isotopes in juvenile Atlantic cod *Gadus morhua* fed three different diets. *Marine Ecology Progress Series*, *461*, 197–209. https://doi.org/10.3354/meps09871

Audzijonyte, A., Kuparinen, A., Gorton, R., & Fulton, E. A. (2013). Ecological consequences of body size decline in harvested fish species: Positive feedback loops in trophic interactions amplify human impact. *Biology Letters*, *9*(2), 20121103. https://doi.org/10.1098/rsbl.2012.1103

Baker, D. M., Murdoch, T. J., Conti-Jerpe, I., & Fogel, M. (2017). Investigating Bermuda's pollution history through stable isotope analyses of modern and museum-held gorgonian corals. *Marine Pollution Bulletin*, *114*(1), 169–175.

Barnes, C., Sweeting, C. J., Jennings, S., Barry, J. T., & Polunin, N. V. (2007). Effect of temperature and ration size on carbon and nitrogen stable isotope trophic fractionation. *Functional Ecology*, *21*(2), 356–362.

Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: A meta-analysis. *Animal Behaviour*, *77*(4), 771–783. https://doi.org/10.1016/j.anbehav.2008.12.022

Bergstad, O. A., Jørgensen, T., Knutsen, J. A., & Berge, J. A. (2008). Site fidelity of Atlantic cod *Gadus morhua* L. as deduced from telemetry and stable isotope studies. *Journal of Fish Biology*, *72*(1), 131–142. https://doi.org/10.1111/j.1095-8649.2007.01693.x

Berlow, E. L., Neutel, A., Cohen, J. E., De Ruiter, P. C., Ebenman, B. O., Emmerson, M., Fox, J. W., Jansen, V. A. A., Iwan Jones, J., & Kokkoris, G. D. (2004). Interaction strengths in food webs: Issues and opportunities. *Journal of Animal Ecology*, *73*(3), 585–598.

Birnie-Gauvin, K., Koed, A., & Aarestrup, K. (2021). Repeatability of migratory behaviour suggests trade-off between size and survival in a wild iteroparous salmonid. *Functional Ecology*, *35*(12), 2717–2727. https://doi.org/10.1111/1365-2435.13917

Bjørnstad, O. N., Fromentin, J.-M., Stenseth, N. C., & Gjøsæter, J. (1999). Cycles and trends in cod populations. *Proceedings of the National Academy of Sciences of the United States of America*, *96*(9), 5066–5071. https://doi.org/10.1073/pnas.96.9.5066

Bøe, K., Robertson, M. J., Fleming, I. A., & Power, M. (2020). Evaluating the effect of dorsal muscle biopsies on adult Atlantic salmon growth and

marine return rates. *Conservation Physiology*, 8(1), coz099. https://doi.org/10.1093/conphys/coz099

Bolnick, D. I., Amarasekare, P., Araujo, M. S., Buerger, R., Levine, J. M., Novak, M., Rudolf, V. H. W., Schreiber, S. J., Urban, M. C., & Vasseur, D. A. (2011). Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, 26(4), 183–192. https://doi.org/10.1016/j.tree.2011.01.009

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The ecology of individuals: Incidence and implications of individual specialization. *American Naturalist*, 161(1), 1–28. https://doi.org/10.1086/343878

Budge, S. M., Iverson, S. J., & Koopman, H. N. (2006). Studying trophic ecology in marine ecosystems using fatty acids: A primer on analysis and interpretation. *Marine Mammal Science*, 22(4), 759–801.

Calenge, C. (2011). *Home range estimation in R: The adehabitatHR package*. Office National de La Classe et de La Faune Sauvage.

Campos-Candela, A., Palmer, M., Balle, S., Álvarez, A., & Alós, J. (2018). A mechanistic theory of personality-dependent movement behaviour based on dynamic energy budgets. *Ecology Letters*, 22, 213–232. https://doi.org/10.1111/ele.13187

Carneiro, A. P. B., Bonnet-Lebrun, A. S., Manica, A., Staniland, I. J., & Phillips, R. A. (2017). Methods for detecting and quantifying individual specialisation in movement and foraging strategies of marine predators. *Marine Ecology Progress Series*, 578, 151–166. https://doi.org/10.3354/meps12215

Chavarie, L., Howland, K. L., Harris, L. N., Gallagher, C. P., Hansen, M. J., Tonn, W. M., Muir, A. M., & Krueger, C. C. (2021). Among-individual diet variation within a lake trout ecotype: Lack of stability of niche use. *Ecology and Evolution*, 11(3), 1457–1475. https://doi.org/10.1002/ece3.7158

Craig, H. (1957). Isotopic standards for carbon and oxygen and correction factors for mass-spectrometric analysis of carbon dioxide. *Geochimica et Cosmochimica Acta*, 12(1–2), 133–149.

Crawford, K., McDonald, R. A., & Bearhop, S. (2008). Applications of stable isotope techniques to the ecology of mammals. *Mammal Review*, 38(1), 87–107.

Dall, S. R. X., Bell, A. M., Bolnick, D. I., & Ratnieks, F. L. W. (2012). An evolutionary ecology of individual differences. *Ecology Letters*, 15(10), 1189–1198. https://doi.org/10.1111/j.1461-0248.2012.01846.x

Dall, S. R. X., Giraldeau, L. A., Olsson, O., McNamara, J. M., & Stephens, D. W. (2005). Information and its use by animals in evolutionary ecology. *Trends in Ecology & Evolution*, 20(4), 187–193. https://doi.org/10.1016/j.tree.2005.01.010

Des Roches, S., Post, D. M., Turley, N. E., Bailey, J. K., Hendry, A. P., Kinnison, M. T., Schweitzer, J. A., & Palkovacs, E. P. (2018). The ecological importance of intraspecific variation. *Nature Ecology & Evolution*, 2(1), 57–64. https://doi.org/10.1038/s41559-017-0402-5

Dhellemmes, F., Smukall, M. J., Guttridge, T. L., Krause, J., & Hussey, N. E. (2021). Predator abundance drives the association between exploratory personality and foraging habitat risk in a wild marine meso-predator. *Functional Ecology*, 35(9), 1972–1984. https://doi.org/10.1111/1365-2435.13874

Dingemanse, N. J., Araya-Ajoy, Y. G., & Westneat, D. F. (2021). Most published selection gradients are underestimated: Why this is and how to fix it. *Evolution*, 75(4), 806–818. https://doi.org/10.1111/evo.14198

Ersoy, S., Beardsworth, C. E., Dekinga, A., van der Meer, M. T. J., Piersma, T., Groothuis, T. G. G., & Bijleveld, A. I. (2022). Exploration speed in captivity predicts foraging tactics and diet in free-living red knots. *Journal of Animal Ecology*, 91(2), 356–366. https://doi.org/10.1111/1365-2656.13632

Espeland, S. H., Gundersen, A. F., Olsen, E. M., Knutsen, H., Gjøsaeter, J., & Stenseth, N. C. (2007). Home range and elevated egg densities within an inshore spawning ground of coastal cod. *ICES Journal of Marine Science*, 64(5), 920–928.

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. https://doi.org/10.3354/meps08524

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. https://doi.org/10.1111/1365-2656.12458

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. https://doi.org/10.1002/ece3.1496

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. https://doi.org/10.1111/1365-2656.13497

Fry, B., & Sherr, E. B. (1989). $\delta^{13}C$ measurements as indicators of carbon flow in marine and freshwater ecosystems. In P. W. Rundel, J. R. Ehleringer, & K. A. Nagy (Eds.), *Stable isotopes in ecological research*. Ecological studies (Vol. 68, pp. 196–229). Springer. https://doi.org/10.1007/978-1-4612-3498-2_12

Fuiman, L. A., & Magurran, A. E. (1994). Development of predator defences in fishes. *Reviews in Fish Biology and Fisheries*, 4(2), 145–183. https://doi.org/10.1007/BF00044127

Funk, S., Frelat, R., Möllmann, C., Temming, A., & Krumme, U. (2021). The forgotten feeding ground: Patterns in seasonal and depth-specific food intake of adult cod *Gadus morhua* in the western Baltic Sea. *Journal of Fish Biology*, 98(3), 707–722. https://doi.org/10.1111/jfb.14615

Gaeta, J. W., Ahrenstorff, T. D., Diana, J. S., Fetzer, W. W., Jones, T. S., Lawson, Z. J., McInerny, M. C., Santucci, V. J., & Vander Zanden, J. M. (2018). Go big or … don't? A field-based diet evaluation of freshwater piscivore and prey fish size relationships. *PLoS One*, 13(3), e094092. https://doi.org/10.1109/ICPR.1992.201868

Gharnit, E., Dammhahn, M., Garant, D., & Réale, D. (2022). Resource availability, sex, and individual differences in exploration drive individual diet specialization. *The American Naturalist*, 200(1), 1–16. https://doi.org/10.1086/719669

Gibert, J. P., & DeLong, J. P. (2017). Phenotypic variation explains food web structural patterns. *Proceedings of the National Academy of Sciences of the United States of America*, 114(42), 11187–11192. https://doi.org/10.1073/pnas.1703864114

Grønkjær, P., Ottosen, R., Joensen, T., Reeve, L., Nielsen, E. E., & Hedeholm, R. (2020). Intra-annual variation in feeding of Atlantic cod *Gadus morhua*: The importance of ephemeral prey bursts. *Journal of Fish Biology*, 97(5), 1507–1519. https://doi.org/10.1111/jfb.14520

Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software*, 33(2), 1–22.

Halvorsen, K. T., Larsen, T., Sørdalen, T. K., Vøllestad, L. A., Knutsen, H., & Olsen, E. M. (2017). Impact of harvesting cleaner fish for salmonid aquaculture assessed from replicated coastal marine protected areas. *Marine Biology Research*, 13(4), 359–369.

Harrison, P. M., Gutowsky, L. F. G., Martins, E. G., Ward, T. D., Patterson, D. A., Cooke, S. J., & Power, M. (2017). Individual isotopic specializations predict subsequent inter-individual variation in movement in a freshwater fish. *Ecology*, 98(3), 608–615. https://doi.org/10.1002/ecy.1681

Herborn, K. A., Macleod, R., Miles, W. T. S., Schofield, A. N. B., Alexander, L., & Arnold, K. E. (2010). Personality in captivity reflects personality in the wild. *Animal Behaviour*, 79(4), 835–843. https://doi.org/10.1016/j.anbehav.2009.12.026

Hobson, K. A. (1999). Tracing origins and migration of wildlife using stable isotopes: A review. *Oecologia*, 120, 314–326.

Hočevar, S., & Kuparinen, A. (2021). Marine food web perspective to fisheries-induced evolution. *Evolutionary Applications*, 14(10), 2378–2391. https://doi.org/10.1111/eva.13259

Holling, C. S. (1959). A model of the functional response of predator to prey density involving the hunger effect. *The Canadian Entomologist*, 91, 385–398.

Holling, C. S. (1966). The functional response of invertebrate predators to prey density. *The Memoirs of the Entomological Society of Canada*, 98(S48), 5–86.

Hop, H., Danielssen, D., & Gjøsæter, J. (1993). Winter feeding ecology of cod (*Gadus morhua*) in a fjord of southern Norway. *Journal of Fish Biology*, 43(1), 1–18.

Houslay, T. M., & Wilson, A. J. (2017). Avoiding the misuse of BLUP in behavioural ecology. *Behavioral Ecology*, 28(4), 948–952. https://doi.org/10.1093/beheco/arx023

Huey, R. B., & Pianka, E. R. (1981). Ecological consequences of foraging mode. *Ecology*, 62(4), 991–999.

Hussey, N. E., DiBattista, J. D., Moore, J. W., Ward, E. J., Fisk, A. T., Kessel, S., Guttridge, T. L., Feldheim, K. A., Franks, B. R., Gruber, S. H., Weideli, O. C., & Chapman, D. D. (2017). Risky business for a juvenile marine predator? Testing the influence of foraging strategies on size and growth rate under natural conditions. *Proceedings of the Royal Society B: Biological Sciences*, 284(1852), 20170166. https://doi.org/10.1098/rspb.2017.0166

Hussey, N. E., Kessel, S. T., Aarestrup, K., Cooke, S. J., Cowley, P. D., Fisk, A. T., Harcourt, R. G., Holland, K. N., Iverson, S. J., Kocik, J. F., Mills Flemming, J. E., & Whoriskey, F. G. (2015). Aquatic animal telemetry: A panoramic window into the underwater world. *Science*, 348(6240), 1255642. https://doi.org/10.1126/science.1255642

Hüssy, K., Andersen, N. G., & Pedersen, E. M. (2016). The influence of feeding behaviour on growth of Atlantic cod (*Gadus morhua*, Linnaeus, 1758) in the North Sea. *Journal of Applied Ichthyology*, 32(5), 928–937. https://doi.org/10.1111/jai.13160

Jennings, S., & Van Der Molen, J. (2015). Trophic levels of marine consumers from nitrogen stable isotope analysis: Estimation and uncertainty. *ICES Journal of Marine Science*, 72(8), 2289–2300. https://doi.org/10.1093/icesjms/fsv120

Kalinkat, G. (2014). Bringing animal personality research into the food web arena. *Journal of Animal Ecology*, 83(6), 1245–1247. https://doi.org/10.1111/1365-2656.12284

Kays, R., Crofoot, M. C., Jetz, W., & Wikelski, M. (2015). Terrestrial animal tracking as an eye on life and planet. *Science*, 348(6240), aaa2478. https://doi.org/10.1126/science.aaa2478

Kelley, D. E., Richards, C., & Layton, C. (2022). oce: An R package for oceanographic analysis. *Journal of Open Source Software*, 7(71), 3594.

Keppeler, F. W., Montaña, C. G., & Winemiller, K. O. (2020). The relationship between trophic level and body size in fishes depends on functional traits. *Ecological Monographs*, 90(4), e01415. https://doi.org/10.1002/ecm.1415

Kerr, N. R., & Ingram, T. (2021). Personality does not predict individual niche variation in a freshwater fish. *Behavioral Ecology*, 32(1), 159–167.

Kimirei, I. A., Nagelkerken, I., Trommelen, M., Blankers, P., van Hoytema, N., Hoeijmakers, D., Huijbers, C. M., Mgaya, Y. D., & Rypel, A. L. (2013). What drives ontogenetic niche shifts of fishes in coral reef ecosystems? *Ecosystems*, 16(5), 783–796. https://doi.org/10.1007/s10021-013-9645-4

Kindsvater, H. K., & Palkovacs, E. P. (2017). Predicting eco-evolutionary impacts of fishing on body size and trophic role of Atlantic cod. *Copeia*, 105(3), 475–482. https://doi.org/10.1643/OT-16-533

Klefoth, T., Skov, C., Kuparinen, A., & Arlinghaus, R. (2017). Towards a mechanistic understanding of vulnerability to hook-and-line fishing: Boldness as the basic target of angling-induced selection. *Evolutionary Applications*, 10(10), 994–1006. https://doi.org/10.1111/eva.12504

Krause, J., Loader, S. P., McDermott, J., & Ruxton, G. D. (1998). Refuge use by fish as a function of body length–related metabolic expenditure and predation risks. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 265(1413), 2373–2379.

Kristensen, M. L., Olsen, E. M., Moland, E., Knutsen, H., Grønkjær, P., Koed, A., Källo, K., & Aarestrup, K. (2021). Disparate movement behavior and feeding ecology in sympatric ecotypes of Atlantic cod. *Ecology and Evolution*, 11(16), 11477–11490. https://doi.org/10.1002/ece3.7939

Kurvers, R. H. J. M., Prins, H. H. T., Van Wieren, S. E., Van Oers, K., Nolet, B. A., & Ydenberg, R. C. (2010). The effect of personality on social foraging: Shy barnacle geese scrounge more. *Proceedings of the Royal Society B: Biological Sciences*, 277(1681), 601–608. https://doi.org/10.1098/rspb.2009.1474

Laskowski, K. L., Alirangues Nuñez, M. M., Hilt, S., Gessner, M. O., & Mehner, T. (2022). Predator group composition indirectly influences food web dynamics through predator growth rates. *The American Naturalist*, 199(3), 330–344. https://doi.org/10.25338/B8W610

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, 68(4), 619–640.

Mangel, M., & Clark, C. W. (1986). Towards a unified foraging theory. *Ecology*, 67(5), 1127–1138.

Mariotti, A. (1983). Atmospheric nitrogen is a reliable standard for natural ^{15}N abundance measurements. *Nature*, 303(5919), 685–687.

McCormack, S. A., Trebilco, R., Melbourne-Thomas, J., Blanchard, J. L., Fulton, E. A., & Constable, A. (2019). Using stable isotope data to advance marine food web modelling. *Reviews in Fish Biology and Fisheries*, 29(2), 277–296. https://doi.org/10.1007/s11160-019-09552-4

McKechnie, A. E. (2004). Stable isotopes: Powerful new tools for animal ecologists. *South African Journal of Science*, 100(3–4), 131–134.

Meager, J. J., Fernö, A., & Skjæraasen, J. E. (2018). The behavioural diversity of Atlantic cod: Insights into variability within and between individuals. *Reviews in Fish Biology and Fisheries*, 28(1), 153–176. https://doi.org/10.1007/s11160-017-9505-y

Mehner, T. (2012). Diel vertical migration of freshwater fishes—Proximate triggers, ultimate causes and research perspectives. *Freshwater Biology*, 57(7), 1342–1359. https://doi.org/10.1111/j.1365-2427.2012.02811.x

Michalsky, J. J. (1988). The astronomical almanac's algorithm for approximate solar position (1950–2050). *Solar Energy*, 40(3), 227–235.

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). Data from: Atlantic cod individual spatial behaviour and stable isotope associations in a no-take marine reserve. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.pk0p2ngv6

Nakayama, S., Rapp, T., & Arlinghaus, R. (2017). Fast–slow life history is correlated with individual differences in movements and prey selection in an aquatic predator in the wild. *Journal of Animal Ecology*, 86(2), 192–201.

Nathan, R., Monk, C. T., Arlinghaus, R., Adam, T., Alós, J., Assaf, M., Baktoft, H., Beardsworth, C. E., Bertram, M. G., & Bijleveld, A. I. (2022). Big-data approaches lead to an increased understanding of the ecology of animal movement. *Science*, 375(6582), eabg1780.

Nielsen, J. M., Clare, E. L., Hayden, B., Brett, M. T., & Kratina, P. (2018). Diet tracing in ecology: Method comparison and selection. *Methods in Ecology and Evolution*, 9(2), 278–291. https://doi.org/10.1111/2041-210X.12869

Nilsson, P. A., & Brönmark, C. (2000). Prey vulnerability to a gape-size limited predator: Behavioural and morphological impacts on northern pike piscivory. *Oikos*, 88(3), 539–546.

O'Brien, J. W., Evans, B. I., & Browman, H. I. (1989). Flexible search tactics and efficient foraging in saltatory searching animals. *Oecologia*, 80(1), 100–110. https://doi.org/10.1007/BF00789938

Olsen, E. M., Heupel, M. R., Simpfendorfer, C. A., & Moland, E. (2012). Harvest selection on Atlantic cod behavioral traits: Implications for spatial management. *Ecology and Evolution*, 2(7), 1549–1562. https://doi.org/10.1002/ece3.244

Peterson, B., & Fry, B. (1987). Stable isotopes in ecosystem studies. *Annual Review of Ecology, Evolution, and Systematics*, 18, 293–320.

Post, D. M. (2002). Using stable isotopes to estimate trophic position: Models, methods and assumptions. *Ecology*, 83(3), 703–718. https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2

Queiroz, N., Humphries, N. E., Noble, L. R., Santos, A. M., & Sims, D. W. (2010). Short-term movements and diving behaviour of satellite-tracked blue sharks *Prionace glauca* in the northeastern Atlantic Ocean. *Marine Ecology Progress Series*, 406, 265–279.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82(2), 291–318.

Rindorf, A., Cadigan, N., Howell, D., Eero, M., & Gislason, H. (2020). Periodic fluctuations in recruitment success of Atlantic cod. *Canadian Journal of Fisheries and Aquatic Sciences*, 77(2), 236–246.

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 of the United States of America*, 108(5), 1961–1966. https://doi.org/10.1073/pnas.1010314108

Ryan, M. R., Killen, S. S., Gregory, R. S., & Snelgrove, P. V. R. (2012). Predators and distance between habitat patches modify gap crossing behaviour of juvenile Atlantic cod (*Gadus morhua*, L. 1758). *Journal of Experimental Marine Biology and Ecology*, 422–423, 81–87. https://doi.org/10.1016/j.jembe.2012.04.017

Scharf, F., Juanes, F., & Rountree, R. (2000). Predator size-prey size relationships of marine fish predators: Interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Marine Ecology Progress Series*, 208, 229–248. https://doi.org/10.3354/meps208229

Schröder, A., Kalinkat, G., & Arlinghaus, R. (2016). Individual variation in functional response parameters is explained by body size but not by behavioural types in a poeciliid fish. *Oecologia*, 182(4), 1129–1140. https://doi.org/10.1007/s00442-016-3701-7

Segura, A. M., Franco-Trecu, V., Franco-Fraguas, P., & Arim, M. (2014). Gape and energy limitation determine a humped relationship between trophic position and body size. *Canadian Journal of Fisheries and Aquatic Sciences*, 72(2), 198–205. https://doi.org/10.1139/cjfas-2014-0093

Sims, D. W., Wearmouth, V. J., Southall, E. J., Hill, J. M., Moore, P., Rawlinson, K., Hutchinson, N., Budd, G. C., Righton, D., & Metcalfe, J. D. (2006). Hunt warm, rest cool: Bioenergetic strategy underlying diel vertical migration of a benthic shark. *Journal of Animal Ecology*, 75(1), 176–190.

Sommer, N. R., & Schmitz, O. J. (2020). Differences in prey personality mediate trophic cascades. *Ecology and Evolution*, 10(17), 9538–9551. https://doi.org/10.1002/ece3.6648

Spiegel, O., Leu, S. T., Bull, C. M., & Sih, A. (2017). What's your move? Movement as a link between personality and spatial dynamics in animal populations. *Ecology Letters*, 20(1), 3–18. https://doi.org/10.1111/ele.12708

Theódórsson, B. K., & Ólafsdóttir, G. Á. (2022). Laboratory measures of boldness correlate with ecological niche in threespine stickleback. *Ecology and Evolution*, 12, e9235. https://doi.org/10.1002/ece3.9235

Therneau, T. M., & Lumley, T. (2015). Package 'survival'. *R Top Doc*, 128(10), 28–33.

Thomson, C. E., Bayer, F., Crouch, N., Farrell, S., Heap, E., Mittell, E., Zurita-Cassinello, M., & Hadfield, J. D. (2017). Selection on parental performance opposes selection for larger body mass in a wild population of blue tits. *Evolution*, 71(3), 716–732.

Toscano, B. J., Gownaris, N. J., Heerhartz, S. M., & Monaco, C. J. (2016). Personality, foraging behavior and specialization: Integrating behavioral and food web ecology at the individual level. *Oecologia*, 182(1), 55–69. https://doi.org/10.1007/s00442-016-3648-8

Tupper, M., & Boutilier, R. G. (1995). Size and priority at settlement determine growth and competitive success of newly settled Atlantic cod. *Marine Ecology Progress Series*, 118(1/3), 295–300.

Vander Zanden, M. J., Clayton, M. K., Moody, E. K., Solomon, C. T., & Weidel, B. C. (2015). Stable isotope turnover and half-life in animal tissues: A literature synthesis. *PLoS One*, 10(1), e0116182.

Videler, J. J., & Wardle, C. S. (1991). Fish swimming stride by stride: Speed limits and endurance. *Reviews in Fish Biology and Fisheries*, 1(1), 23–40.

Villegas-Ríos, D., Claudet, J., Freitas, C., Moland, E., Thorbjørnsen, S. H., Alonso-Fernández, A., & Olsen, E. M. (2021). Time at risk: Individual spatial behaviour drives effectiveness of marine protected areas and fitness. *Biological Conservation*, 263, 109333. https://doi.org/10.1016/j.biocon.2021.109333

Villegas-Ríos, D., Freitas, C., Moland, E., Huneide Thorbjørnsen, S., & Olsen, E. M. (2020). Inferring individual fate from aquatic acoustic telemetry data. *Methods in Ecology and Evolution*, 11(10), 1186–1198. https://doi.org/10.1111/2041-210X.13446

Villegas-Ríos, D., Réale, D., Freitas, C., Moland, E., & Olsen, E. M. (2017). Individual level consistency and correlations of fish spatial behaviour assessed from aquatic animal telemetry. *Animal Behaviour*, 124, 83–94. https://doi.org/10.1016/j.anbehav.2016.12.002

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. https://doi.org/10.1111/1365-2656.12872

Ward, A. J., Webster, M. M., & Hart, P. J. (2006). Intraspecific food competition in fishes. *Fish and Fisheries*, 7(4), 231–261.

Werner, E. E., & Gilliam, J. F. (1984). The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics*, 15(1), 393–425. https://doi.org/10.1146/annurev.es.15.110184.002141

Winter, E. R., & Britton, J. R. (2021). Individual variability in stable isotope turnover rates of epidermal mucus according to body size in an omnivorous fish. *Hydrobiologia*, 848, 363–370.

Wolf, M., & Weissing, F. J. (2012). Animal personalities: Consequences for ecology and evolution. *Trends in Ecology & Evolution*, 27(8), 452–461.

Woo, K. J., Elliott, K. H., Davidson, M., Gaston, A. J., & Davoren, G. K. (2008). Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour. *Journal of Animal Ecology*, 77(6), 1082–1091. https://doi.org/10.1111/j.1365-2656.2008.01429.x

Wootton, J. T., & Emmerson, M. (2005). Measurement of interaction strength in nature. *Annual Review of Ecology, Evolution, and Systematics*, 36, 419–444.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table A1. Posterior mean estimates and their 95% credible intervals for effects estimated in multivariate generalized mixed effects models. DVM represents diel vertical migration distance.

Figure A1. The sampling periods and tracking duration for all individual cod. Each black rectangle indicates the duration an individual cod was tracked with acoustic telemetry during this study, starting from the date of transmitter implantation, and ending when either the fish left the study area, died (from predation, natural mortality or fishing mortality) or the battery life of the transmitter ended. Red vertical lines indicate dates of sampling. Sampling was grouped in five events (spring 2018, spring 2019, fall 2019, spring 2020 and fall 2020).

Figure A2. An overview of the spatial distribution (Panel a) of lower trophic $\delta^{15}N$ values indicative of the baseline $\delta^{15}N$ values in the fjord (Panel a), from samples of filamentous green algae, *Ascophylum nodosum*, *Littorina* spp. *Mytilus edulis* and *Cerastoderma edule*. Panels

(b, c) show the same measurements along longitude and latitude respectively.

Figure A3. An overview of all cod sampling locations in Tvedestrand Fjord (Panel a). Panel b shows the longitude and latitude of $\delta^{13}C$ values and $\delta^{15}N$ values used to assess spatial biases in isotope values.

Figure A4. Cod isotope values ($\delta^{13}C$ and $\delta^{15}N$) and fork lengths across sampling periods.

Figure A5. The relationship between diel vertical migration distance and $\delta^{15}N$ scaled relative to cod body size. Red points represent individual median values.

Figure A6. The relationship between activity, activity space size, depth and diel vertical migration distance, and $\delta^{13}C$. Black points represent daily measurements, and red points represent individual median values.

Figure A7. The relationship between activity, activity space size, depth and diel vertical migration distance, and $\delta^{15}N$. Black points represent daily measurements, and red points represent individual median values.