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# Conservation benefits of marine reserves depend on knowledge integration of genotypic and phenotypic diversity

Barbara Koeck [a,d,*], Esben Moland Olsen [b,c], Libor Závorka [a,d], Amélie Crespel [a,e], Carla Freitas [b,g], Katja Enberg [f], Even Moland [b,c], Marte Sodeland [c], Henrik Høiberg Jessen [f], Héloïse Marte [d], Shaun S. Killen [a]

[a] *School for One Health and Veterinary Medicine, University of Glasgow, Scotland, United Kingdom*
[b] *Institute of Marine Research, His, Norway*
[c] *Department of Natural Sciences, Centre for Coastal Research (CCR), University of Agder, Kristiansand, Norway*
[d] *WasserCluster Lunz-am-See, Inter-University Centre for Aquatic Research, Austria*
[e] *Department of biology, University of Turku, Finland*
[f] *Department of Biological Sciences, University of Bergen, Norway*
[g] *MARE - Marine and Environmental Sciences Centre, 9020-105 Funchal, Madeira, Portugal*

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ABSTRACT

Conserving intraspecific trait variation is vital for maintaining the viability of species. It ensures a species to adapt to warming and increasingly stochastic environments, and to recover following extreme events. Here we investigate the selective effects of spatial management on intraspecific genetic and phenotypic variation of two sympatric but genetically distinct Atlantic cod ecotypes in a Norwegian fjord. We found that phenotypic differences between sympatric cod genotypes were mainly driven by morphological and metabolic traits. Offshore cod had higher metabolic maintenance costs at cool temperatures but lower aerobic capacity at warm acclimation than coastal ecotypes, indicative of thermal constraint of aerobic physiological processes beyond metabolic maintenance. Offshore cod also had larger and thicker peduncles and better body condition. We found that protection benefits from the no-take zone (NTZ) of the Tvedestrand marine protected area were independent of individual space-use size, but instead resulted from ecotype-specific differences in habitat occupation. Results specifically show that the current delimitations of the NTZ do not cover habitats occupied by the coastal and highly resident cod ecotype which shows greater metabolic thermal tolerance but is considered to already be in a depleted state. Our study exemplifies why protecting intraspecific diversity is directly relevant for management implementations aimed at reducing the impact of further selection pressures such as ongoing environmental change. Careful investigation of intraspecific diversity and integration of such knowledge to fisheries management and design of protected areas may prevent unwanted additional selective pressures and contribute to offer broad protection to genotypes and phenotypes.

## 1. Introduction

Intraspecific genetic diversity provides the raw material for evolutionary adaptations. Preserving this diversity increases the likelihood that at least a subset of the population will be able to adapt to novel selective pressures that could challenge population persistence and facilitate evolutionary rescue (Moran et al., 2016). In that context, harvest by fishing is recognized to be one of the strongest human-induced selection pressures (Fugère and Hendry, 2018) causing rapid changes in phenotypic distribution (Handford et al., 1977; Law, 2000) including life history traits of target populations induced by selection differentials of natural and fishing selection (Darimont et al., 2009), *i.e.*, fisheries-induced evolution FIE. To counter the demographic and evolutionary effects of fishing and thereby dampen the effects of FIE, a number of studies have highlighted the potential of marine protected areas MPAs, *i.e.*, spatially defined areas where human activities and especially extractive practices such as fishing are regulated (Baskett et al., 2005; D'Aloia et al., 2017). Within MPAs, particularly zones

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* Corresponding author.
*E-mail address:* koeckbarbara@hotmail.com (B. Koeck).

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where fishing is entirely prohibited, such as marine reserves or no-take zones NTZs, are known to serve as spatial refuges to a fraction of large and old individuals which otherwise are selectively targeted by fisheries (Dunlop et al., 2015; Fernández-Chacón et al., 2020; Twardek et al., 2017). Because fecundity increases with maternal age and size, protecting this fraction contributes to increased overall reproductive output (Baskett and Barnett, 2015; Lubchenco et al., 2003) and ensures the necessary supply of recruits to maintain healthy population sizes and genetic diversity (Chen et al., 2023). A recent study has also shown that in Atlantic cod large females are connecting spawning sites (Olsen et al., 2023), contributing disproportionately to gene flow. This example further highlights the potential of MPAs, by providing shelter from fishing to large individuals which contribute to maintain the natural genetic structure of harvested populations.

On the flipside, little is known about the selective protection of MPAs from extractive harvest and its evolutionary effects (Baskett and Barnett, 2015; Chen et al., 2023; Olsen et al., 2012). In fact, although conservation benefits of MPAs are numerous in terms of population demographics (Lester et al., 2009; Lubchenco et al., 2003), MPAs may also act as additional selective force differing from natural selection, causing unknown evolutionary effects. By definition, MPAs are spatially defined management tools and are often limited in their size (Wood et al., 2008). For them to function as evolutionary rescue areas, protecting genetically and phenotypically diverse populations, this implies some level of knowledge on spatial structuring of populations as well as phenotypic drivers affecting space use patterns and habitat selection (D'Aloia et al., 2017; Grüss et al., 2011). Density-dependent effects and abiotic parameters, such as thermal or salinity gradients, can for instance constraint and structure habitat occupation by fish (Guzzo and Blanchfield, 2017; Swain and Wade, 1993) and cause trade-offs with foraging and mating opportunities defining important life-history traits such as growth and offspring production (Robinson, 2000; Rosenzweig, 1991). Resulting habitat selection may also vary among individuals within and between populations (Koeck et al., 2013) depending on their behavioural and physiological phenotypes (Parker and Sutherland, 1986). Beyond habitat selection, differences in movement such as space used to cover regular behavioural expression (*e.g.,* utilisation distributions that estimate the size of a spatio-temporally defined area of intensive use or home-ranges; Worton, 1989) can further affect the protection benefits provided by an MPA (Di Franco et al., 2018) and define their selective risk of fishing mortality (Villegas-Ríos et al., 2021). Variation in space use was formalized as a function of resource consumption and resource availability (Harestad and Bunnel, 1979; Rosten et al., 2016), so that fish with varying metabolic requirements may be more or less protected by an MPA due to intraspecific differences in space use. Few studies have also established positive links between individual movement patterns in the wild (*e.g.,* space use and dispersal) and behavioural traits assessed in controlled laboratory assays (Harrison et al., 2015; Villegas-Ríos et al., 2017; Závorka et al., 2016). In that context, investigating intraspecific variation in habitat use and movement patterns, and their genetic and phenotypic determinants can not only contribute to enlighten our knowledge on mechanisms driving fishing selection but also inform us on how to optimize the use of spatially explicit management tools to preserve intraspecific diversity.

In Atlantic cod, *Gadus morhua*, population and genetic structuring has been extensively investigated (Olsen et al., 2004, 2009), in the attempt to improve the management of exploited stocks (Dahle et al., 2018). For western Skagerrak Atlantic cod populations for instance, molecular studies have identified two sympatric but genetically distinct ecotypes: an offshore and a coastal ecotype (Knutsen et al., 2018). The continued coexistence of these ecotypes suggests restricted introgression, although interbreeding is observed in captivity and putative admixed individuals are occasionally identified in the wild (Jorde et al., 2018). As often observed between seemingly incipient subspecies, natural selection together with intrinsic genetic mechanisms is likely to shape divergence and effectiveness of introgression (Schumer et al., 2018). In fact, while long term monitoring along the Norwegian Skagerrak has revealed that both cod ecotypes coexist in similar proportions in coastal habitats, at a local scale coastal cod become predominant the further inside a fjord and away from open-sea (Knutsen et al., 2018). This further supports the hypothesis that genetic differentiation between cod ecotypes could stem from local adaptative processes (Barth et al., 2017, 2019). In the present study we investigated the Atlantic cod population from the Tvedestrand fjord (southern Norway), known as predominantly resident (Villegas-Ríos et al., 2021) and composed of sympatric but genetically distinct coastal and offshore ecotypes (Knutsen et al., 2018). This fjord harbours an MPA where fishing is entirely prohibited in its central part (*i.e.* a no-take zone NTZ) and restricted to recreational angling in its inner and outer parts (*i.e.*, buffer zones), offering a suitable study system for investigating the effects and mechanisms of fishing selection *via* habitat use and movement patterns on the genetic and phenotypic diversity of Atlantic cod populations. At time of establishment of this MPA, knowledge on cod ecotypes was however absent and became only recently available. Further, beyond genetic differences, knowledge on phenotypic differences of cod ecotypes upon which selection (natural, fishing and management) could operate affecting eco-evolutionary processes, is currently limited to differences in size at age (Knutsen et al., 2018) and trophic niche (Kristensen et al., 2021).

The aim of this study is therefore to provide a phenotypic characterization (based on morphometric, behavioural and metabolic traits) of sympatric but genetically distinct ecotypes of Atlantic cod, and to estimate the conservation benefit provided to each ecotype by the local fishing ban within a marine reserve. To do so, we investigated differences in space use size (*i.e.,* core Kernel Utilisation Distribution KUD) and in proportion of time fish spend inside *versus* outside the no-take zone (NTZ) of a marine protected area (MPA) in coastal and offshore cod ecotypes of known sex. We aim to answer the following specific questions:

(1) Do sympatric cod ecotypes diverge phenotypically?
(2) Is space use linked to (phenotypic differences of) cod ecotypes?
(3) Do ecotypes differ in conservation benefits provided by the MPA?

Based on reported faster growth in offshore ecotypes relative to coastal ones (Knutsen et al., 2018), we hypothesize that offshore cod have a higher energetic demand causing them to be more active and exploratory, leading to the expression of larger utilisation distributions in the wild in response to higher requirements of foraging opportunities (Jetz et al., 2004; Rosten et al., 2016). As a consequence, we further hypothesize that time at risk of fishing (estimated by time spend outside the NTZ) in the Tvedestrand MPA will be greater for offshore than coastal ecotypes. Based on existing knowledge on local scale variation in habitat occupation of both ecotypes (Knutsen et al., 2018 but see Kristensen et al., 2021), we also hypothesize that habitat occupation of offshore and coastal ecotypes varies across the fjord, with a dominance of coastal ecotypes in the inner fjord. Consequently, we expect that ecotype difference in space use and habitat occupation together will affect their spatio-temporal overlap with the central NTZ of the Tvedestrand fjord and therefore the relative protection benefits provided by the MPA.

## 2. Material and method

### 2.1. Study area and acoustic telemetry array

The study was carried out in the Tvedestrand fjord which contains a 5 km long acoustic telemetry array throughout the fjord (Fig. 1), deployed and maintained since 2011 to evaluate the performance of Norway's first no-take marine reserve, established in june 2012. The Tvedestrand MPA comprises a no-take zone (NTZ) in the central part of the fjord, where fishing is entirely prohibited, and three surrounding

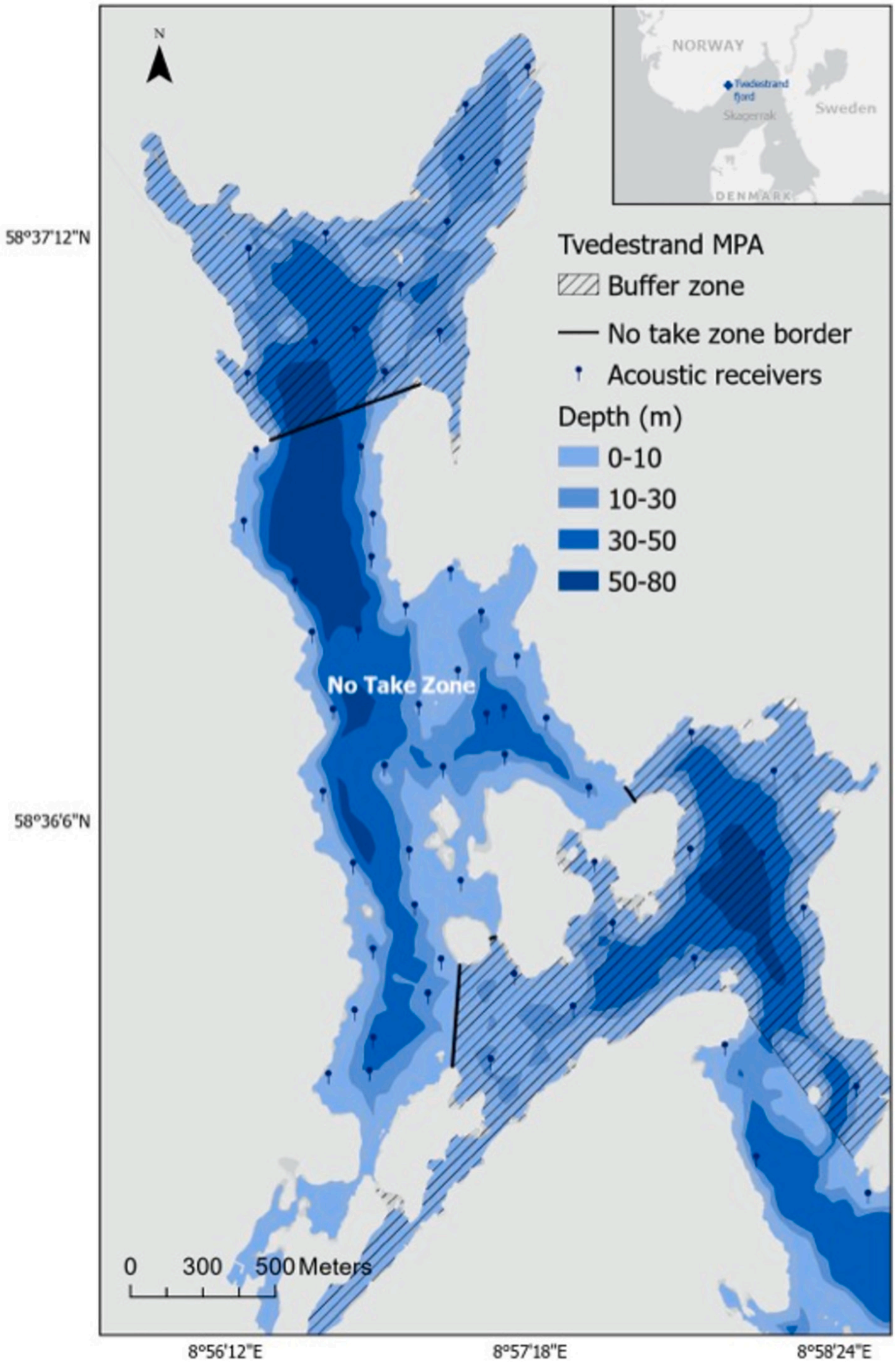

**Fig. 1.** Study area of the Tvedestrand fjord on the Skagerrak coast, southern Norway, with its' central no-take zone and surrounding buffer zones where only recreational angling is permitted. The fjord is equipped with a telemetry array deployed since 2011 consisting of 56 acoustic receiver stations.

buffer zones, where only recreational angling is permitted. The fjord was initially equipped with a presence/absence acoustic system comprised of 32 Vemco VR2W receivers deployed at 3 m depth and later extended to a Vemco Positioning System (VPS array) providing more precise fish positioning. The current VPS array is composed of (a) 55 acoustic receivers (VR2W, 69 kHz), used to record data transmitted by the tagged fish; (b) 55 sync tags (V16-4L), moored along with each receiver to correct for clock drift between receivers; and (c) seven reference tags (4 V13P-1L and 3 V13T-1L) placed within the receiver grid to measure system performance during location estimation. Earlier performance tests indicated that the median location error of the VPS array within the NTZ was 1.8–4.4 m (Freitas et al., 2016).

## 2.2. *Fish sampling and holding*

Atlantic cod (*Gadus morhua* L.) were collected between 23 April and 31 May 2019 using fyke-nets, repeatedly and randomly deployed across the fjord (at 1 to 10 m depth, soak time of 1 to 3 days), tagged on deck of the boat with a passive integrated transponder for individual identification, then transported to the Institute of Marine Research at Flødevigen. In total, 37 cod were captured (total length TL 300 to 500 mm, 412 ± 55 mm, mean ± sd) and held in groups of 6 to 7 fish in 6 flow-through circular tanks of 1100 L (130 × 100 cm) for 35 to 53 days until completion of behavioural and metabolic measurements. Two fish had to be euthanized during the experimentation period due to fatal capture injuries. Fish were fed daily with unfrozen shrimps (*Pandalus borealis*), a naturally occurring prey. Additional information on fish holding conditions and handling is provided in Appendix A.

### 2.3. Metabolic measurements

Experimental assays commenced after a period of 8 to 14 days of acclimatization (11 ± 2 days). Standard and maximum metabolic rates (SMR, MMR) were estimated for individual fish by measuring rates of oxygen uptake ($MO_2$ in mg $O_2$ $h^{-1}$) using intermittent flow-through respirometry (see Appendix B for details on system set-up). Prior measurements, fish were not fed for 72 h in order to ensure post-absorptive metabolic rate measurement (Fry and Hart, 1948). Fish were placed to the chambers between 12:00 and 14:00 and removed the following day between 08:00 and 09:00. After that, fish were subjected to a chasing protocol for 5 min (tank dimensions: 150 × 150 × 40 cm, filled to 20 cm high) used to exercise fish until exhaustion *i.e.,* no response to pinching of the tail peduncle (Killen et al., 2021) and returned for 1h30min to respirometry chambers for estimating maximum aerobic metabolic rate. For estimation of mass-specific metabolic rates, fish were then measured for their body mass in a wet cloth and returned to their holding tanks. To quantify across thermal context repeatability of metabolic traits, measurements of metabolism were repeated for each fish at 3 incremental temperatures: once at 7.5 °C (*i.e.* ambient temperature when fish were captured), at 11 °C and 14 °C. The selected temperatures encompassed temperatures naturally experienced by cod in the study area (Freitas et al., 2016). Between each temperature treatment, fish were gradually warm acclimated following an increment of 1 °C per day and kept at temperature for another 12 to 14 days before measuring their metabolism again.

### 2.4. Behavioural assays

After refeeding fish following first metabolic measurements and a 24 h period of fasting in their holding tanks, behavioural traits of cod were scored individually using an 'emergence test' assessing the propensity to take risks and explore a novel environment in a compartmentalized experimental tank (overall dimensions: 150 cm × 150 cm × 50 cm deep but filled only to 30 cm) and an 'open-field test' assessing overall activity of fish based on distance moved and proportion time spend moving for a set-time. For the behavioural assays, fish were released individually from an emergence compartment (*i.e.*, a shelter) to an experimental tank. After 15 min settling, a panel was hoisted remotely allowing the fish to leave the shelter and enter the open tank. A video camera placed above the experimental tank was recording the time until fish exit the shelter, with a trial duration of 30 min. After that, the divider was removed from the tank and activity of fish in the barren tank was recorded for 10 min after a settling time of 15 min. Open-field and emergence tests inform on behavioural types and discriminate individuals based on their exploratory propensity, activity, and boldness (Sih et al., 2004).

### 2.5. Fish tagging and tracking

At completion of experimental trials, cod were implanted with an acoustic transmitter equipped with a pressure and a temperature sensor (Innovasea VEMCO; see Appendix A for protocol details). For that, individual fish were anaesthetized in a solution of 150 mg l–1 MS-222 buffered with sodium bicarbonate NaHCO3 to saturation. An acoustic transmitter (V9TP-2 L: 69 kHz) was inserted to the coelomic cavity *via* a 15 mm midventral incision. The incision was closed with non-absorbable prolene sutures (Ethicon Ltd., UK). Fish were released back to their capture location of the study fjord within the same or the following day. Acoustic signals emitted from tagged cod allowed us to track their locations across time (x, y, z, t) and occupied thermal habitat throughout the Tvedestrand fjord equipped with receiver stations. Tracking data encompasses summer and autumn (2019), when differences in fishing pressure between the buffer and NTZ were the strongest.

### 2.6. Body metrics and genetic determination of sex and ecotype

A photograph for morphometric analysis was taken on cod that were anaesthetized before transmitter implantation. A fin clip was sampled from the pectoral fin and preserved in ethanol at −20 °C until genetic determination of sex (Star et al., 2016) and ecotype (Jorde et al., 2018; Knutsen et al., 2018) using 7 and 26 single-nucleotide polymorphisms respectively (see Appendix C for detailed protocol). Pelvic fin length, a secondary sexual attribute, used as indicator of mating success in males (Skjæraasen et al., 2006) and peduncle width and height as an easy to measure onboard proxy for condition (E.M. Olsen, personal communication) were also measured to the nearest mm. Measures of wet body mass and total length were used to calculate nutritional condition at onset of experimentations using Fultons' K (Ricker, 1975), with wet body mass in g and total length TL in cm:

$$K = \left(\frac{Mass}{TL^3}\right) \times 100$$

and specific growth rate over the course of the experimental period expressed in mm per day (Brett and Groves, 1979):

$$SGR = \left(\frac{ln(TL_{t2}) - ln(TL_{t1})}{t2 - t1}\right)$$

### 2.7. Data analysis

#### 2.7.1. Calculation of metabolic rates

Estimates of metabolic rates were obtained after correcting each $MO_2$ (mg $O_2$ $h^{-1}$) estimate of fish by background bacterial respiration based on linear regression between blank oxygen consumption measurements taken prior fish were inserted to respirometry chambers and after fish were removed. Individual estimates of standard metabolic rates SMR (mg $O_2$ $h^{-1}$), *i.e.,* the minimum oxygen uptake to sustain life, were determined as the lowest 20th percentile of $MO_2$ throughout the measurement period excluding the first 3 measurement hours, generating a minimum of 87 $MO_2$ recordings per fish for each acclimation temperature. Individual estimates of maximum metabolic rate MMR (mg $O_2$ $h^{-1}$), *i.e.*, the maximum aerobic oxygen uptake, were determined using a rolling regression slope every 2 s over 90 s after a wait period of 30 s obtained up to 1 h following the exhaustive exercise protocol. Aerobic scope AS (mg $O_2$ $h^{-1}$), *i.e.,* the capacity to deliver oxygen to support aerobic physiological processes above maintenance including activity, digestion, growth and reproduction, was calculated as the difference between MMR and SMR. The R-package RespR was used to extract $MO_2$ values and calculate SMR estimates (Harianto et al., 2019).

#### 2.7.2. Across-context repeatability of phenotypic traits

Repeatability is a measure of the upper limit of heritability of a given phenotype, *i.e.,* the proportion of genetic variance in relation to the total trait variance and can inform on the potential of a trait to evolve in response to selection (Dochtermann et al., 2015). Repeatability of behavioural traits related to exploration propensity and boldness on cod of similar size range from the same study area has been demonstrated in an earlier study (Villegas-Ríos et al., 2018). Because of this, and in order to minimize stress due to repeated manipulation while maximizing biological information, trait repeatability across thermal context was only assessed for metabolic rates. As metabolic traits were calculated across thermal context, repeatability estimates here represent the combined influence of genetic variation and thermal plasticity on metabolic phenotype (Niemelä and Dingemanse, 2017). Repeatability of metabolic traits (SMR, AS) adjusted for acclimation temperature (fixed factor) and grouped by ecotype and sex (4 level fixed factor) was calculated with fish ID as random effect using generalized linear mixed models (rptR package in R: Stoffel et al., 2017). Confidence intervals of repeatability scores were calculated using 1000 parametric bootstrap iterations.

### *2.7.3. Morphometric image analysis*

Differences in overall body shape of cod ecotypes and sexes were analysed using MorphoJ (Klingenberg, 2011) based on 21 landmarks, which were digitized on lateral photographs (Appendix D1) for each fish using tpsDig (version 2.31; Rohlf, 2017). As body shape would vary over the size range of experimental fish (30 to 50 cm TL), residuals from allometric regression between the procrustes-coordinates and the centroid size were extracted and then used in a canonical analysis grouping fish by sex and ecotype to identify morphological differences.

### *2.7.4. Pre-processing of telemetric data & calculation of space use metrics*

Fish detection data downloaded from the VR2W receivers were processed by Vemco/Innovasea, in order to estimate fish locations. The fish location dataset was composed of fish ID, detection time, latitude, longitude, depth, and horizontal position error (HPE), a unitless estimate of how sensitive a calculated position is to errors in its inputs. Visual inspection of mapped individual fish trajectories and associated HPE allowed to filter unlikely positions that could cause erroneous interpretations (upper threshold of HPE was set to 58.6, above which positioning error was considered to be excessive leading for example to positions far inland). One coastal female cod was detected in the study area for less than a day and therefore removed from analysis. Individual core Kernel Utilisation Distribution (50%KUD) were calculated (grid size = 1000 pixels, smoothing parameters h = 60, extent =0.5) using fish positions available between the 28th of June and 24th of November 2019, using the adehabitatHR package (Calenge, 2006) following the method described (Worton, 1989). Individual protection provided by the MPA was estimated by the proportion of time cod would spend inside the NTZ, *i.e.* representing the inverse of time at risk, and calculated by summing time intervals between successive estimated positions overlapping with the NTZ divided by overall time interval of detection. Surface temperature during the considered period of tracking was ranging between 6.23 and 22.8 °C and averaging 14.88 ± 4.44 °C (mean ± sd).

### *2.7.5. Data exploration and statistical model analysis*

All data management and analysis were done under R statistical environment (R Development Core Team, 2022). To correct for allometric scaling, mass corrected residuals of metabolic traits (*i.e.*, residuals issued from linear regression between SMR, MMR, AS and body mass measurements taken after individual respirometry measurements) were calculated and used for statistical analyses. Allometric effects were also visible on pelvic fin length, peduncle height and width, activity, time to emerge and 50 % KUD area. Variables were therefore corrected for initial total length TL and residuals considered for further data analysis. Data exploration using pairwise correlogram plots and regression coefficients were used to identify collinearity among variables and reduce covariables under consideration for statistical hypothesis testing (Dormann et al., 2013). Peduncle height and pelvic fin length were highly correlated and collinear ($R^2 = 0.683$), so that we only preserved peduncle height as covariable. AS was highly correlated to MMR ($R^2 > 0.798$) but only weakly to SMR ($0.398 < R^2 < 0.473$) at any acclimation temperature. MMR was therefor dropped for statistical testing. Based on our initial working hypothesis and results from corelogram analysis, phenotypic traits retained for statistical hypothesis testing were TL total length, peduncle width, peduncle height, Fulton's condition factor K, activity, time to emerge, AS aerobic scope and SMR standard metabolic rate taken at 7, 11 and 14 °C.

Phenotypic characterization of cod ecotypes was done using a multinomial regression analysis (R package nnet; Venables and Ripley, 2002) using the data of all 35 cod. It models the log odds of individuals belonging to the offshore ecotype as a linear combination of residual values of phenotypic traits. The coastal ecotype serves as baseline against which comparisons are made. The model took the following form:

$$log\frac{P(Ecotypes = Offshore|\mathrm{X})}{P(Ecotypes = Coastal|\mathrm{X})} = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots \beta_n X_n$$

$\beta 1$ to $\beta n$ are the coefficients for variables $X1$ to $Xn$ to be estimated for predicting the offshore ecotype and $\beta_0$ is the intercept. Model performance was compared: i) based on lowest Akaike Information Criterion AIC, which is an information-theoretic method that in addition to the later also considers model complexity and not only goodness of fit (Akaike, 1981; Burnham et al., 2011), and ii) on how well the model would assign individuals to known ecotypes based on molecular analysis.

Differences in space use and time at risk between ecotypes and sex were modelled using generalized linear models using the data from $N = 33$ fish (data from one female cod had to be discarded due to missing data for KUD computation, for another fish sex could not be determined genetically and had to be discarded). Space use was modelled using 50 % KUD as response variable, ecotype and sex as covariables with their two-way interaction. The full model took the following form:

$$50\%\mathrm{KUD} = \beta_0 + \beta_1 \mathrm{X}_{\mathrm{ecotype}} + \beta_2 \mathrm{X}_{\mathrm{sex}} + \beta_3 \left(\mathrm{X}_{\mathrm{ecotype}} \mathrm{X}_{\mathrm{sex}}\right) + \epsilon$$

In another model, explanatory variables were swapped to phenotypic traits, without any interaction term, to investigate the drivers of space use. As KUD was positively related to TL of cod, a similar model was build using size corrected residues of KUD50% as response variable instead. To model the protection benefit provided by the NTZ of the Tvedestrand MPA, proportion of time spend inside the NTZ was used as response variable with TL and 50 % KUD as covariables and interaction terms with factors ecotype and sex:

$$\begin{aligned}\mathrm{P}\ (\mathrm{Y} = 1|\mathrm{X}) = \phi \Bigg( & \beta_0 + \beta_1 X_{ecotype} + \beta_2 X_{sex} + \beta_3 X_{TL} + \beta_4 X_{KUD} \\ & + \beta_5 \left(X_{ecotype} X_{sex}\right) + + \beta_6 \left(X_{ecotype} X_{TL}\right) + \beta_7 \left(X_{ecotype} X_{KUD}\right) \\ & + \beta_8 (X_{sex} X_{KUD}) + \beta_9 \left(X_{ecotype} X_{sex}\ X_{KUD}\right) \Bigg) + \epsilon\end{aligned}$$

$\beta_0$ is the intercept. $\beta_1$ to $\beta_9$ are the coefficients respectively associated with modelled predictors and their interactions. $\epsilon$ is the error term capturing the deviation of observed values from the line of best fit. $\phi$ denotes the cumulative distribution function of the standard normal distribution, reflecting the probit link. P (Y = 1 | X) represents the probability that the response variable (proportion of time spent inside the NTZ) is equal to 1 given the predictors. For each model, stepwise backward and forward selection of the best model was implemented using the AIC. Stepwise selection was done using the MASS package (Venables and Ripley, 2002). Fit of selected models was investigated by visual inspection of residuals distribution and quantile-quantile plots against fitted values. Cook's distance was used to identify influential observations and spot eventual outliers.

## 3. Results

### *3.1. Sympatric cod ecotypes differ mainly in morphological and metabolic phenotype but also behaviour*

The multinomial regression model allowed to correctly assigning observations to known ecotypes (*i.e.,* 14 offshore cod were predicted to belong to the offshore group and 21 coastal cod to belong to the coastal group; model accuracy: 1, 95 % CI: 0.9–1), based on the phenotypic traits selected during model fitting. Individual assignment probabilities of observations to ecotypes can be found in Appendix E1. Particularly morphological traits, *i.e.* peduncle height and width, contributed to explain the variance observed between groups, with offshore ecotypes characterized by thicker and higher peduncles than coastal ecotypes (Table 1; Fig. 2). Contribution of total length and behavioural traits to distinguish ecotypes was however comparatively minimal, although offshore ecotypes were larger but also less bold (*i.e.*, took longer time to emerge from shelter in behavioural assay; Table 1; Appendix B1) than coastal cod. Size distribution indicates that offshore ecotypes had less variation in body size and were at the higher end of coastal cod size distribution (Fig. 2). Fulton's condition factor was greater for offshore ecotypes (Table 1; Fig. 2). Furthermore, morphometric analysis revealed that coastal cod morphs show little variation in overall body shape between male and females. Comparatively, offshore ecotypes show larger morphological differences between sexes, with offshore females having overall the most distinct body shape (canonical analysis axis 1 explains 85 % of morphological variation; Appendix D2, D3).

Metabolic traits also significantly contributed to distinguish ecotypes, with offshore cod having higher SMR at 7 °C acclimation temperature and lower AS at 14 °C than coastal cod. (Table 1; Fig. 2). SMR at 11 °C and 14 °C and AS at 7 °C and 11 °C were not selected by the best model (Appendix B2). AS was moderately repeatable across thermal acclimation context when fish were grouped by ecotype and sex ($R = 0.38$, SE = 0.115, CI = [0.138, 0.578], *p*-value = 0.0002). SMR was also moderately repeatable ($R = 0.399$, SE = 0.116, CI = [0.143, 0.593], p-value = 0.0001).

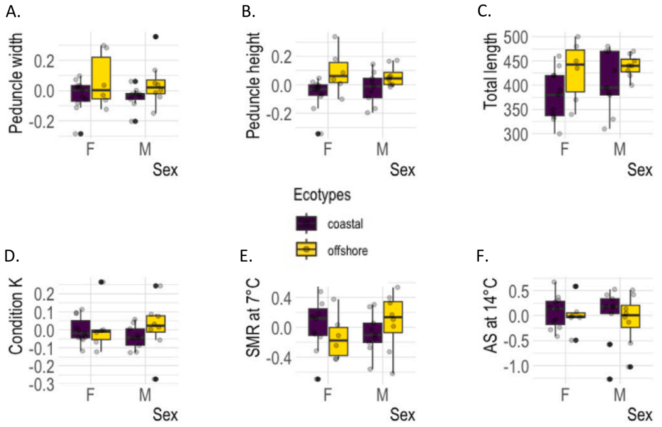

**Fig. 2.** Boxplot of the phenotypic traits characterising offshore and coastal Atlantic cod ecotypes ($N = 35$). Peduncle width (A) and height (B; in cm) and Fulton's condition factor K (D; g cm$^3$), standard metabolic rate SMR measured at 7 °C acclimation (E) and aerobic scope AS at 14 °C (F; mg O2 h$^{-1}$ g$^{-1}$) were expressed as body size corrected residuals. Total length is expressed in mm (C). Boxes show the median and 25th and 75th percentiles. Dots correspond to raw data points. Black dots are values that extend beyond one and half time the interquartile range.

### 3.2. *Cod with higher basal metabolism had larger utilisation distributions*

Atlantic cod ecotypes and sexes did not differ in space use as measured by 50 % KUD (F-statistic = 2.737 on 3 and 29 DF, $R^2 = 0.2206$; Figs. 3 and 4). Individual variation in 50 % KUD (h) was however correlated to differences in peduncle height and in AS at 14 °C of cod (Table 2), indicating that cod with higher peduncles and those with lower AS at 14 °C also had larger areas of space use. Results were comparable when replacing the response variable by body size (total length) corrected 50 % KUD residuals. Fitted models had however low $R^2$ (0.22 and 0.21 respectively) and 5 influential observations were detected without matching to obvious errors in the data. Two of these observations corresponded to very large core KUD of offshore males (Fig. 3). After removal of influential observations, 50 % KUD was mainly explained by SMR at 7 °C and activity (Table 3; $R^2 = 0.5841$). Cod that had higher SMR or were less active during behavioural assays had larger KUD (Fig. 5).

**Table 1**
Multinomial logistic regression model providing phenotypic characterization of cod ecotypes (*i.e.* coastal and offshore). The selected model had the lowest AIC of 20.97 and residual deviance of 2.97, compared to all model combination (*i.e.* dropped covariables were SMR at 11 °C, SMR at 14 °C, AS at 11 °C, AS at 7 °C). All explanatory variables were body size corrected residuals, except metabolic traits (AS aerobic scope and SMR standard metabolic rate) which were body mass corrected residuals. SE denotes standard error.

| | Coefficient | SE | z stat | p value |
|---|---|---|---|---|
| Intercept | 189.406264 | 9.034745 | 20.964206 | <0.00001 |
| Total length (cm) | −0.4196653 | 0.0231527 | −18.125986 | <0.00001 |
| Peduncle height | −226.116496 | 2.154711 | −104.9405 | <0.00001 |
| Peduncle width | −128.26523 | 6.109559 | −20.994187 | <0.00001 |
| Condition factor K | −69.3340317 | 14.3116917 | −4.8445728 | 0.0000013 |
| Time to emerge | −3.2642764 | 0.5340282 | −6.1125542 | <0.00001 |
| Activity | 0.7901729 | 0.6902609 | 1.1447453 | 0.2523 |
| SMR at 7 °C | −71.003909 | 4.508121 | −15.750222 | <0.00001 |
| AS at 14 °C | 53.997251 | 3.099046 | 17.423831 | <0.00001 |

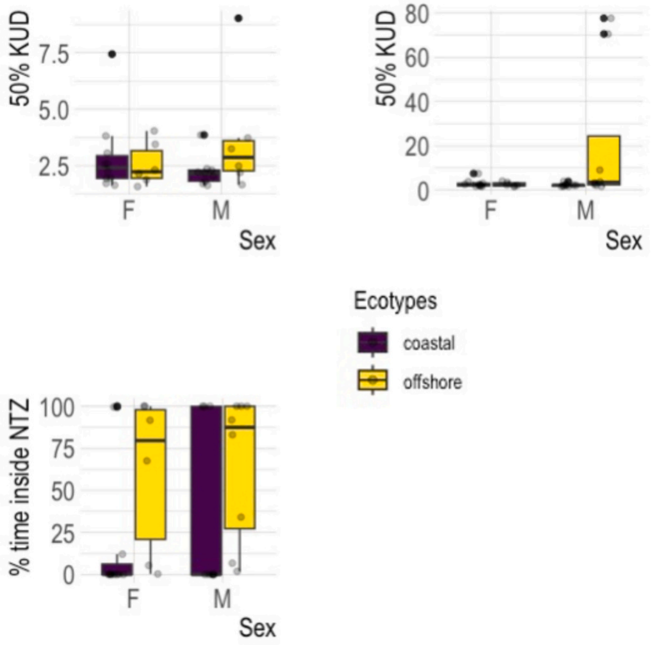

**Fig. 3.** Boxplot representing the core Kernel Utilisation Distribution area (50 % KUD in hectares) without and with outliers (N = 29 and $N = 34$), and the proportion time spent by individuals inside the No-Take Zone (% time inside NTZ). Boxes show the median and 25th and 75th percentiles. Dots correspond to raw data points. Black dots are values that extend beyond one and half time the interquartile range.

### 3.3. *Offshore cod benefit most from NTZ protection*

Offshore ecotypes spent significantly more time within the NTZ than coastal cod (Table 4; Fig. 3). Except for a few fish which had overlapping

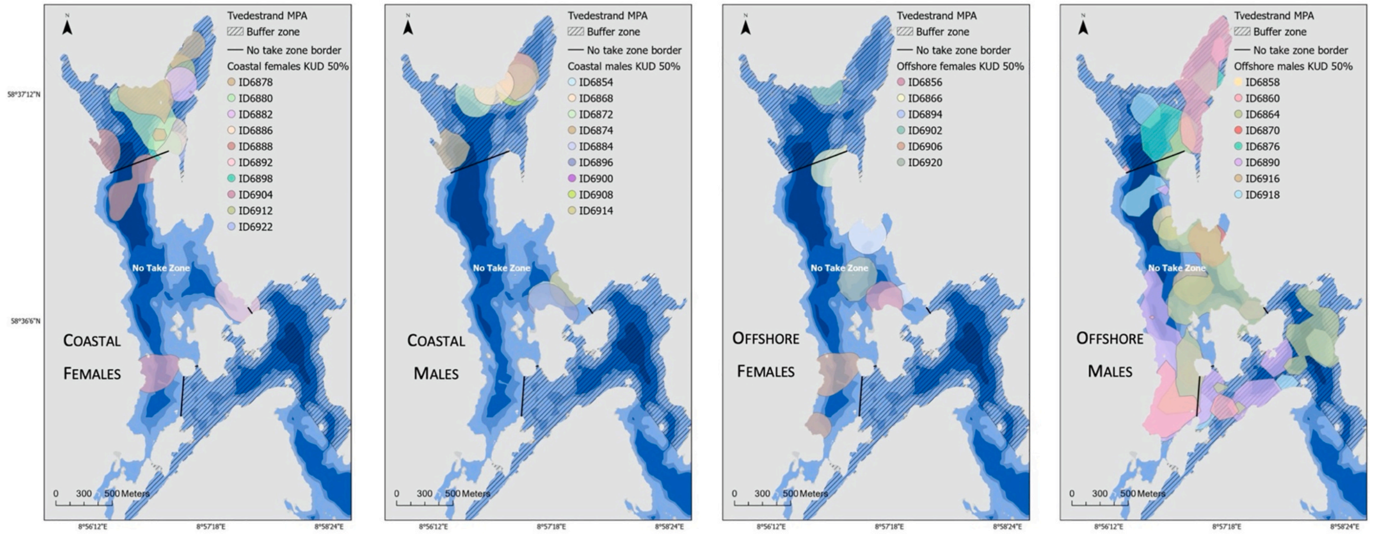

**Fig. 4.** Mapping of individual core kernel utilisation distributions (*i.e.* 50 % KUD) for coastal males ($N = 9$) and coastal females ($N = 10$), for offshore males ($N = 8$) and offshore females ($N = 6$), showcasing differences in overlap of space use (50 % KUD) with the no-take zone inside the Tvedestrand marine protected area (MPA).

**Table 2**
Linear regression modelling the individual variation in space use(*i.e.* 50 % Kernel Utilisation Distribution KUD) as a function of phenotypic characteristics of cod ecotypes. Total length, peduncle width, condition factor K, time to emerge, laboratory scored activity and SMR at 7 °C acclimation temperature were dropped during model selection. The final model was fitted with an F-statistics of 4.405 on 2 and 31 degrees of freedom and an $R^2$ of 0.2213. All explanatory variables were body size corrected residuals, except metabolic traits (AS aerobic scope and SMR standard metabolic rate) which were body mass corrected residuals. SE denotes standard error.

| | Coefficient | SE | t-value | p-value |
|---|---|---|---|---|
| Intercept | 6.522 | 2.683 | 2.431 | 0.021 |
| Peduncle height (res.) | 57.702 | 25.952 | 2.223 | 0.033 |
| AS at 14 °C (res.) | −16.668 | 6.542 | −2.548 | 0.016 |

**Table 3**
Linear regression modelling the individual variation in space use, (*i.e* 50 % Kernel Utilisation Distribution KUD) as a function of phenotypic characteristics of cod ecotypes after removal of influential observations. Significant predictors for explaining variation in 50 % KUD were laboratory scored activity and SMR at cold acclimation of 7 °C. The model was fitted with an F-statistics of 3.511 on 8 and 20 degrees of freedom and an $R^2$ of 0.5841. All explanatory variables were body size corrected residuals, except metabolic traits (AS aerobic scope and SMR standard metabolic rate) which were body mass corrected residuals. SE denotes standard error.

| | Coefficient | SE | t-value | p-value |
|---|---|---|---|---|
| Intercept | 1.854177 | 1.851337 | 1.002 | 0.328533 |
| Total length (cm) | 0.002353 | 0.004481 | 0.525 | 0.605304 |
| Peduncle height | −1.273178 | 3.679716 | −0.346 | 0.732957 |
| Peduncle width | −0.651773 | 2.545293 | −0.256 | 0.800512 |
| Condition factor K | 1.880553 | 2.649603 | 0.71 | 0.486053 |
| Time to emerge | −0.220451 | 0.112497 | −1.96 | 0.064126 |
| Activity | −0.152144 | 0.036985 | −4.114 | 0.000539 |
| SMR at 7 °C | 2.686743 | 1.020465 | 2.633 | 0.01595 |
| AS at 14 °C | −0.156162 | 1.00917 | −0.155 | 0.878575 |

core KUD between the NTZ and surrounding buffer zones, the segregation in space use of the inner and outer fjord (buffer zone) and the NTZ was very clear with most offshore cod residing inside the NTZ and most coastal cod in the inner fjord buffer zone (Fig. 4). A comparative weak interaction effect was visible between ecotypes and TL, with the smallest offshore cod having higher residency inside the NTZ and smallest coastal cod having residency outside the NTZ (Fig. 6; Table 4). The interaction effect between ecotype and sex on proportion time spend inside the NTZ, although not significant, contributed to explain considerable variance and was maintained during the model fitting procedure (Table 4; Fig. 3). 50 % KUD did not contribute to explain much variance in time at risk, although maintained in the final model. Overall results indicate that offshore cod benefit the most from the putative NTZ protection, and coastal cod in particular smaller subadults the least.

## 4. Discussion

In this study we characterized phenotypically two sympatric but genetically distinct Atlantic cod ecotypes and investigated the selective effects of spatial management on intraspecific (genetic and phenotypic) variation. We show that the no-take zone (NTZ) of the Tvedestrand fjord provides selective protection from putative fishing mortality favouring offshore Atlantic cod ecotypes over the coastal ecotype, unrelated to individual space use size. Spatial management as defined by the MPA of the Tvedestrand fjord therefore creates a selective advantage for the offshore genotype but provides only limited protection to the coastal genotype, especially for smaller coastal cod that inhabit the inner fjord only. We further show that coastal ecotypes are characterized by a greater thermal tolerance, *i.e.,* lower metabolic maintenance costs at cooler temperature and higher aerobic capacities under warm conditions, than offshore genotype.

### *4.1. Size-dependent habitat segregation of ecotypes drives differential protection benefits by the MPA*

Protection benefits of the NTZ provided to coastal and offshore cod were also size dependent. Smaller coastal cod (≤ 380 mm TL) were exclusively present in the inner fjord buffer zone, while the largest sampled offshore cod were absent from the NTZ. This pattern could come from differences in size distribution of both ecotypes within the fjord and their adaptations to local conditions. The replenishment of fjord cod populations is indeed known to be highly dependent on local recruitment (Barth et al., 2019). Local recruitment and high residency could explain the presence of smaller coastal cod, comparatively to the offshore ecotype whose presence may be largely driven by dispersal at adult stages towards the fjord. Further, the fact that (smaller) coastal cod are predominantly located in the inner fjord, which compared to the outer fjord is less influenced by currents and water masses from open

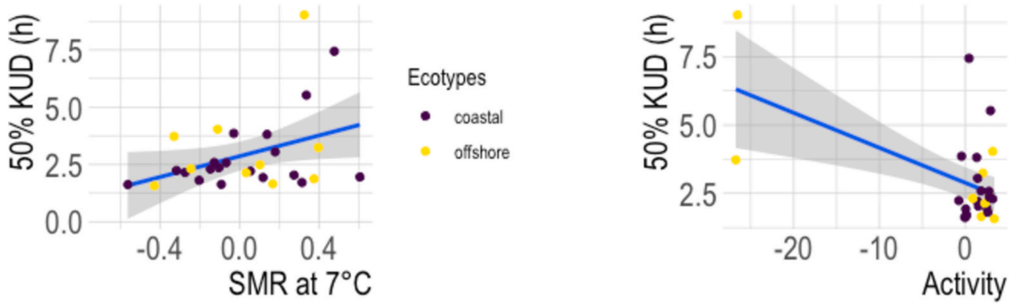

**Fig. 5.** Linear regression (and confidence interval) modelling the relationship between individual core Kernel Utilisation Distribution area (50 % KUD in hectares) without outliers ($N = 29$) and standard metabolic rate (body mass corrected residuals of SMR mg O2 h$^{-1}$ g$^{-1}$), and laboratory scored activity (body size corrected residuals of proportion time spend active) total length of fish (mm) taken at termination of experimental trials.

**Table 4**
Generalized linear regression modelling individual probability of being inside the no-take zone NTZ, (*i.e.* proportion of time spend inside the NTZ was calculated as indicator of putative time at risk), as a function of body size (TL in cm), cod ecotype (coastal and offshore), sex (Male and Female) and size of 50 % Kernel Utilisation Distribution (KUD, in hectares). The model was fitted with a null deviance of 38.324 on 32 degree of freedom and a residual deviance of 17.970 on 23 degree of freedom and an AIC of 41.648. SE denotes standard error.

| | Coefficient | SE | t value | p value |
|---|---|---|---|---|
| Intercept | −17.68465 | 11.37636 | −1.555 | 0.1201 |
| Total length TL (cm) | 0.03966 | 0.02397 | 1.655 | 0.0979 |
| Ecotype (offshore) | 26.22364 | 12.70599 | 2.064 | 0.039 |
| Sex (male) | 14.57795 | 10.60046 | 1.375 | 0.1691 |
| KUD (h) | 0.28534 | 0.61246 | 0.466 | 0.6413 |
| TL:Ecotype | −0.05678 | 0.02657 | −2.137 | 0.0326 |
| Ecotype:Sex | −14.70764 | 10.77052 | −1.366 | 0.1721 |
| Ecotype:KUD | −0.59248 | 0.93091 | −0.636 | 0.5245 |
| Sex:KUD | −7.10428 | 4.986 | −1.425 | 0.1542 |
| Ecotype:Sex:KUD | 7.38887 | 5.03508 | 1.467 | 0.1422 |

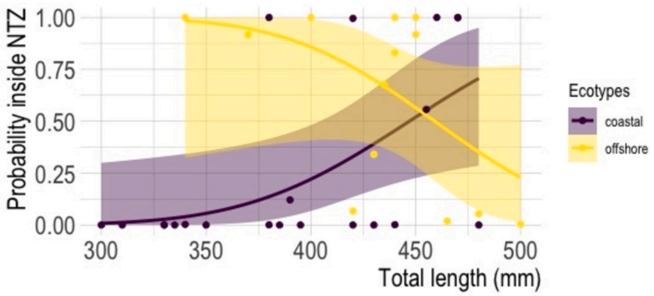

**Fig. 6.** Generalized linear regression (and confidence interval) modelling the probability of ecotypes to be inside the no-take zone (NTZ) of the marine protected area as a function of total length of fish (mm) taken at termination of experimental trials.

coastal waters (Ciannelli et al., 2010), could be the expression of local adaptation to environmental conditions of the fjord but also due to stronger competitive interactions in the central and outer parts of the fjord resulting in niche differentiation at local scales. The absence of larger coastal cod from the inner fjord may also result from recent fishing selection, *i.e.*, selective removal of larger cod from the buffer zones since establishment of the MPA, particularly of coastal ecotypes which are essentially found in the inner fjord.

### 4.2. Space use size does not drive time at risk at the fjord scale

Tying movement and space use patters (*e.g.*, estimates of home range sizes, utilisation distributions or activity space) to MPA design has been of particular interest in the study of spillover effects of MPAs and connectivity among protected areas (D'Aloia et al., 2017; Grüss et al., 2011; Kramer and Chapman, 1999; Moffitt et al., 2009). For instance, in snappers (*Pagrus auratus*) it was shown that compared to fished areas, resident individuals display smaller home ranges in a NTZ, which authors explained by possible density-dependent movement or selection for reduced movement due to protection benefits provided by the MPA (Parsons et al., 2010). In a previous study on cod in the Tvedestrand fjord, it was found that time at risk increased with space use size when centroid was closer to the border of the NTZ (Villegas-Ríos et al., 2018). In contrast, we found that time at risk of fishing was unrelated to size of individual space use of cod, which can be attributed to specificities of sampling design. In fact, in previous acoustic telemetry studies carried out in the Tvedestrand fjord, cod were almost exclusively sampled in the NTZ of the MPA. In the present study, sampling effort was balanced between the NTZ and the surrounding buffer areas, leading to comparable number of fish captured in the NTZ and buffer zones (respectively 16 and 19 cod), most of which were resident to their capture location.

Our results show that during the sampling period, most cod (and all coastal ecotypes) used intensively only a single area which was restricted to less than five hectares and very small compared to the size of the MPA. These restricted areas of use could explain the limited overlap of fish between the NTZ and buffer zone and the absence of link between space use size and time at risk outside the NTZ (*e.g.* Thorbjørnsen et al., 2021 on sea trout). Among offshore cod exclusively, in particular males, some had more dispersed space use and/or visited multiple locations across the fjord. While overall offshore cod had their centres of activity mostly located inside the NTZ, they also have larger variation of movement patterns which could explain the relationship between space use and time at risk observed in Villegas-Ríos et al. (2018). Overall, our study of Atlantic cod movement shows that at the fjord scale it is not intraspecific variation in movement patterns *per se*, *i.e.*, how much cod move and why this differs between individuals, but intraspecific variation in habitat occupation, *i.e.*, where they are and why this differs between individuals, that is selected for in spatially structured management defined by the MPA.

### 4.3. Movement patterns are linked to individual's metabolism

While space use was not directly linked to ecotype or sex, which concurs with results found by Kristensen et al. (2021) for cod from a neighbouring fjord, we found that individual variation in 50 % KUD was correlated to differences in metabolism, morphology, and behaviour. We found that cod with higher peduncles and lower AS under warmer conditions had larger areas of space use. Furthermore, after removal of extreme highly mobile individuals from data analysis, we found that 50 % KUD was negatively related to activity in open field test and positively to metabolic maintenance costs (SMR at 7 °C; Table 3, Fig. 5).

Association and co-variation of phenotypic traits and movement patterns could be indicative of distinct strategies within cod populations, differentiating plastic from rigid phenotypes (see concept of coping styles in (Coppens et al., 2010; Winberg and Thörnqvist, 2016)). Variation in 50 % KUD is largely driven by few offshore cod that show nomadic behaviours investigating distinct intensively used areas and moving opportunistically across the fjord. One could hypothesize that such dispersive individuals adopt an opportunistic (and behaviourally flexible) strategy, to maximize somatic growth by wandering across habitats in search of optimal resource and habitat patches (*e.g.* in terms of foraging and/or thermal habitat), thereby minimizing resource competition and exposure to abiotic conditions outside physiological optimum. On the other hand, variations in movement strategy could also be indicative of intraspecific differences in capacity to physiologically buffer microhabitat variations in temperature; whereby a dispersive strategy may stem from physiological constraint such as a limited thermal tolerance leading to movements associated with behavioural thermoregulation. Moving across habitats allows avoidance of shallow waters where food may be rich, but where during summer months temperatures climb beyond optimum for growth, which may be the case for a subset of offshore cod that display nomadic behaviours investigating distinct intensively used areas during the tracking period of our study. As shown by Freitas et al. (2016), during summer the progressive warming of surface waters in the Tvedestrand fjord forces cod to retreat to deeper areas, a pattern particularly marked for large adult specimens which abandon most profitable vegetated shallows. Growth models based on long-term time series of cod from the Norwegian Skagerrak coast show indeed that summer warming represents a constraint to juvenile and adult growth (Gjøsæter and Danielssen, 2011; Rogers et al., 2011), further illustrating the growth trade-off faced by cod when waters are warming.

After the removal of highly mobile individuals from data analysis, intraspecific variation in utilisation distribution of cod was mainly driven by differences in activity and metabolic maintenance costs of cod. Among fish displaying recurrent movements around a central place (*i.e.,* here movement recursions characterized by single restricted areas of intensive use), the used space necessary may be related to intraspecific variation in basal energy requirements beyond allometric scaling and to behavioural types (Jetz et al., 2004; Rosten et al., 2016; Slavík et al., 2014). Our results seem indeed to indicate that resident cod with higher metabolic maintenance costs have to expand their utilized habitat to increase foraging opportunities, compared to resident cod with lower standard metabolism. Overall, our results therefore suggest that intraspecific variation in movement patterns of cod in the wild depends not only on habitat quality, but also on metabolic phenotype of individuals (Fagan et al., 2013; Jetz et al., 2004; Rosten et al., 2016).

### *4.4. Sympatric cod ecotypes differ in morphological and metabolic phenotype*

Our results show that sympatric cod ecotypes and sexes differ in body condition and overall morphology. A study by Marcil et al. (2006) investigating the drivers of morphological variations across larval cod populations, showed that although body morphology was defined by genetic divergence due to local adaptation, temperature would induce plastic changes in overall morphology. In the current study, differences in local scale habitat use, due to intraspecific environmental niche differentiation associated with temperature or other factors, could explain morphological differences we observed between the sympatric coastal and offshore cod ecotypes. Predominantly coastal cod were found in the inner fjord while offshore cod were more present inside the NTZ and the outer fjord, which could match with local adaptation but also plasticity linked to a gradient in fjord habitat quality.

In comparison to offshore cod, the coastal ecotype has also a lower metabolic maintenance cost at cooler temperature and higher aerobic capacity under warmer conditions implying a greater physiological tolerance to warming. Together, previous genomic analysis (Barth et al., 2017) and the phenotypic characterization provided by the present study converge towards the hypothesis that coastal cod ecotypes might be better adapted to coastal stochastic environments requiring greater physiological tolerance, rendering them less sensitive to environmental variations in salinity and temperature than conspecific offshore genotypes. Fjords are indeed characterized by greater salinity and temperature variation compared to offshore waters (Ciannelli et al., 2010). Spatial segregation of cod ecotypes (as shown by mapping of core space use of individual fish), matching with salinity difference between the inner and the rest of the fjord, also concurs with previously observed differences in genes critical for the survival at low salinities (Barth et al., 2017) and may equip coastal ecotypes with a greater tolerance to fluctuating salinity in link with episodically important freshwater influx. The fact that coastal ecotypes had a lower body condition and predominantly occupied habitats in the inner fjord, may further suggest that they can be outcompeted by the offshore genotype in less physiologically constraining and profitable habitats, including the central no-take zone of the fjord that provides additional shelter from fishing pressure. In depth analysis of habitat utilisation and selection, together with measurements of intraspecific variation in physiological tolerance levels, will be required to verify this hypothesis.

## 5. Conclusion & perspectives

Overall, our results show the potential of marine protected areas to induce novel selective pressures. We show that conservation benefits of marine reserves to cod are driven by ecotype-specific differences in habitat occupation possibly attributable to differences in genetically driven physiological tolerance limits. Coastal cod populations in the Skagerrak are heavily fished and considered to be in a depleted state (Fernández-Chacón et al., 2017; Jorde et al., 2018; Kleiven et al., 2016). Preserving intraspecific trait variation or within-species polymorphism, including genotypes expressing a greater physiological tolerance, may however contribute to species resilience ensuring evolutionary rescue (Norderhaug et al., 2024). As such, MPAs may not protect the ocean from major threats such as those associated to environmental change (Hilborn, 2015) and even cause in some instances a “protection paradox” (Bates et al., 2019) by providing spatial refugia from fishing mortality to phenotypes most sensitive to thermal or salinity stress for instance. To prevent additional selective pressures to already weakened genotypes or sub-populations by strong harvest pressure, more profound knowledge on spatial structuration of populations, and its drivers, is required. In the particular case of the Tvedestrand fjord, assuming socio-political acceptance, increasing the NTZ including the inner fjord buffer zone of the MPA may secure phenotypic and genetic variation of its cod population and specifically contribute to maintain the coastal cod genotype.

Current results are based on putative risk of fishing mortality defined by overlap between fish and spatial management rules. As beyond spatial overlap a number of mechanisms affect fishing selection shaping intraspecific trait variation of target populations (Crespel et al., 2021; Hollins et al., 2018; Killen and Koeck, 2023), empirical data on fishing mortality and survival from mark-recapture data will be required to complement our findings on Atlantic cod. In addition of horizontal overlap, intraspecific differences in depth use of cod may be an important ecological feature driving fishing selection (Olsen et al., 2012) and could be linked, as suggested by our results, to intraspecific variation in thermal physiology of cod. Empirical fishing data in combination with knowledge on fine scale habitat use, metabolic and behavioural phenotype and genotypic background of cod will be necessary to get a full understanding of selective mechanisms (and their interactions) driving eco-evolutionary processes of harvested populations.

## CRediT authorship contribution statement

**Barbara Koeck:** Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Esben Moland Olsen:** Writing – review & editing, Resources, Methodology, Funding acquisition, Data curation, Conceptualization. **Libor Závorka:** Writing – review & editing, Methodology, Investigation, Formal analysis. **Amélie Crespel:** Writing – review & editing, Methodology, Investigation, Formal analysis. **Carla Freitas:** Writing – review & editing, Methodology, Investigation, Data curation. **Katja Enberg:** Writing – review & editing, Funding acquisition, Conceptualization. **Even Moland:** Writing – review & editing, Methodology, Investigation, Data curation. **Marte Sodeland:** Writing – review & editing, Investigation. **Henrik Høiberg Jessen:** Writing – review & editing, Investigation. **Héloïse Marte:** Visualization. **Shaun S. Killen:** Writing – review & editing, Resources, Project administration, Funding acquisition, Conceptualization.

## Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Shaun S. Killen reports financial support was provided by European Research Council. Shaun S. Killen reports financial support was provided by Natural Environment Research Council. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110831.

## Data availability

Data is made available under DOI: 10.6084/m9.figshare.25965205.

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