



Time at risk: Individual spatial behaviour drives effectiveness of marine protected areas and fitness



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ARTICLE INFO

Keywords:

Marine protected areas
Conservation ecology
Fish behaviour
Fully protected area
Movement ecology
Individual behaviour
Home range
Repeatability

ABSTRACT

The effectiveness of Marine Protected Areas (MPAs) depends on the mobility of the populations that are the target of protection, with sedentary species likely to spend more time under protection even within small MPAs. However, little is understood about how individual variation in mobility may influence the risk of crossing an MPA border, as well as the fitness costs associated with being exposed to spillover fisheries. Here we investigated the repeatability of spatial behaviour, its role in determining the probability of being at risk (i.e. exposed to the fishery) and the fitness consequences for the individuals. We acoustically tracked the movements and fate of 282 individuals of three fish species during 8 years in a southern Norwegian fjord. We found that for individuals with a home range centroid inside the MPA, the probability of being at risk outside the MPA increased rapidly with reduced distance from the home range centroid to MPA borders, particularly for individuals having larger and more dispersed home ranges. We also detected that the seasonal expansions of the home range are associated with increased time at risk. Last, we show that individuals spending more time at risk were also more likely to be harvested by the fishery operating outside the MPA. Our study provides clear links between individual fish behaviour, fisheries-induced selection, and the effectiveness of protected areas. These links highlight the importance of intraspecific trait variation for understanding the spatial dynamics of populations and emphasize the need to consider individual behaviour when designing and implementing MPAs.

1. Introduction

Marine protected areas (MPAs) are valuable tools for protecting fish from overharvesting and are expected to support fisheries beyond their boundaries through the net export of pelagic eggs and larvae and the spillover of juveniles and mature fish (Abesamis and Russ, 2005; Harrison et al., 2012; Di Lorenzo et al., 2016a). The effectiveness of MPAs depends on a number of factors, from good governance to the physical properties of the MPAs and characteristics of protected populations (Claudet et al., 2008, 2010; Edgar et al., 2014). In particular, given that MPAs are spatially-explicit management tools (Claudet et al., 2006), fish spatial behaviour plays a key role in driving the effectiveness of MPAs

(Lowe et al., 2003; Afonso et al., 2009; Di Lorenzo et al., 2016b) and as such it is often taken into account in all the steps of MPA design, implementation and management (Claudet et al., 2020).

The degree of protection granted by an MPA to juvenile and mature fish will ultimately depend on the amount of time that individuals spend within its borders. Thus, the effectiveness of MPAs is expected to be higher for less mobile species (Pilyugin et al., 2016), although positive effects have also been detected for large pelagic and migratory species (Hays et al., 2014; Mee et al., 2017; Dwyer et al., 2020). The conservation benefits of MPAs typically increase exponentially with MPA size (Claudet et al., 2008; Edgar et al., 2014), but small MPAs may still offer long-term protection to some species. For instance, small MPAs of only

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2.8 km² were successful in protecting the sedentary dusky grouper (Afonso et al., 2011), and MPAs smaller than 10 km wide seem effective in protecting most commercial reef fish species (Krueck et al., 2018). For species moving within a home range, it is anticipated that MPA size can be informed by focal species' home range sizes (Kramer and Chapman, 1999). In consequence, most empirical studies have focused on investigating the relationship between the scale of a species' home range and the size of the MPA (Green et al., 2015; Di Franco et al., 2018; Krueck

et al., 2018). However, simply displaying home range behaviour, even if its size is smaller than the MPA, does not guarantee protection. For instance, location of the home range in relation to the reserve border can also influence the level of protection (Kramer and Chapman, 1999; Thorbjørnsen et al., 2021; Calenge, 2019).

In spite of recent efforts to protect large areas of the ocean (Hays et al., 2014), most MPAs in the world are still relatively small compared to the degree of movements of most fish species (Claudet et al., 2008;

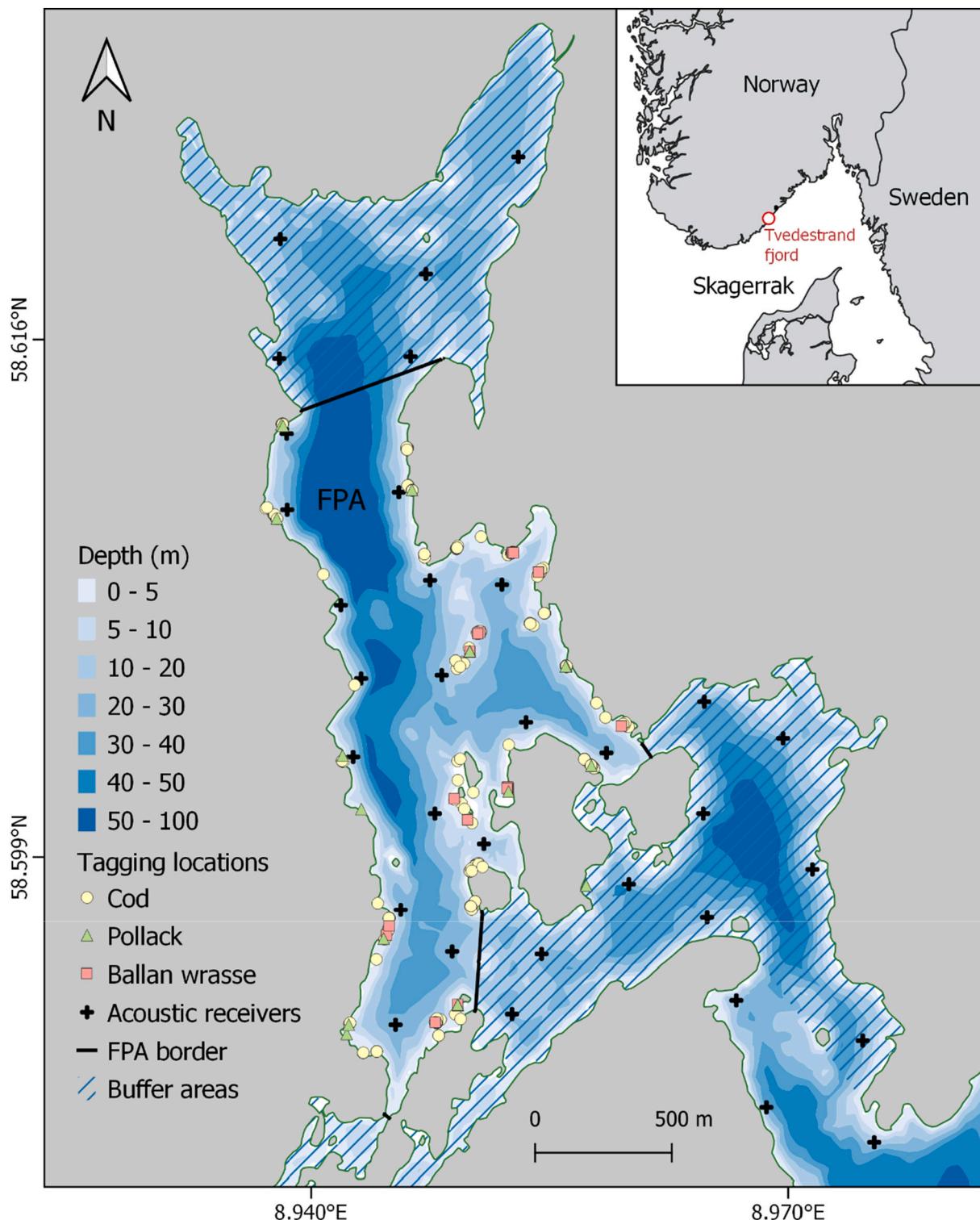


Fig. 1. Map of the study area showing the location of the 33 Innovasea VR2W receivers in Tvedstrand fjord, the tagging location of the different individuals and the borders of the fully protected area (FPA).

McCauley et al., 2015; Di Franco et al., 2018). Therefore, individuals with different mobility phenotypes may experience different degrees of protection (Mee et al., 2017). However, such intraspecific variability in spatial ecology has typically been overlooked in studies of MPA effectiveness (but see Parsons et al., 2010; Mee et al., 2017; Thorbjørnsen et al., 2021; Calenge, 2019). Focusing on average mobility critically fails to acknowledge potential evolutionary consequences of spatial protection (Baskett et al., 2005; Baskett and Barnett, 2015; Arlinghaus et al., 2017; Villegas-Ríos et al., 2017a), resulting from heritable variation in behaviour linked to the tendency to leave the MPA (Mee et al., 2017). Indeed, recent evidence has demonstrated that individuals within populations of species such as cod or lobster differ consistently in aspects of their mobility such as home range size (Villegas-Ríos et al., 2017b; Moland et al., 2019). If individuals with different spatial behaviour differ in their degree of exposure to the fishery and thus mortality risk, this may have fitness consequences eventually driving evolutionary changes towards decreased dispersal and spillover (Parsons et al., 2010; Mee et al., 2017; Villegas-Ríos et al., 2017a). Buffer areas - zones of partial protection surrounding fully protected areas – could function as useful tools for mitigating unnatural selection gradients imposed by spillover fisheries (Januchowski-Hartley et al., 2013; Villegas-Ríos et al., 2017a; but see Zupan et al., 2018 for potential negative impacts of increased fishing pressure in buffer areas).

Here, we explore how the spatial ecology of individuals determine their degree of protection and thus their fitness. We used an extensive, long-term telemetry dataset of movement and fate of three fish species moving inside and outside an MPA in southern Norway. First, we hypothesized that the size, shape and location of the home range will determine the movements across the reserve border and thus *directly* impact the proportion of time under protection vs. time at risk. Second, since life-history and environmental drivers typically impact behaviour resulting in seasonal or ontogenetic changes of home range size or location, we further explored how such variability *indirectly* affect protection and the effectiveness of the MPA. Last, we hypothesized that the probability of being harvested outside the MPA will correlate with the amount of time spent at risk. As a preliminary step in our analysis, we document that home range properties such as size or shape differ consistently among individuals. Our findings reveal the major role of individual-level spatial behaviour in determining the effectiveness of MPAs and individual fitness.

2. Material and methods

2.1. Study area and telemetry array

Our study was carried out in the Tvedstrand fjord on the Norwegian Skagerrak coast (Fig. 1) during eight consecutive years (June 2012–May 2019). The study area includes an MPA implemented in June 2012 and comprises waters down to 90 m depth. The MPA is composed of a fully protected area (FPA) of 150 ha where all types of fishing are forbidden, surrounded by three partially protected buffer zones where angling is allowed but fixed fishing gears such as nets and traps are banned. The whole area was monitored with a presence/absence acoustic system of 33 VR2W omnidirectional receivers (Innovasea, Halifax, Canada) fixed at three-meter depth and pointing downwards (Fig. 1). Fish detection data, consisting of records of tag identity, tag depth, tag detection time and receiver identity, were downloaded twice per year while maintenance of the array was conducted once per year. Range testing conducted in 2011 through the study area suggested that the detection range of the transmitters used in this study and the spacing of receivers provided a very good coverage of the study area (see Villegas-Ríos et al., 2020 for details).

2.2. Study species

Gadus morhua (Atlantic cod) is a demersal generalist predator with

severely depleted populations in Skagerrak (Knutsen et al., 2018; Barth et al., 2019). Coastal cod often, but not always, exhibit limited movement compared to more oceanic populations (Robichaud and Rose, 2004; Rogers et al., 2014; Villegas-Ríos et al., 2017b). *Pollachius pollachius* (pollack) is a benthopelagic piscivore common to Skagerrak coastal areas (Fromentin et al., 1998). *Labrus bergylta* (ballan wrasse) is a long-lived, hermaphrodite rocky reef mesopredator with a complex life history (Muncaster et al., 2010; Villegas-Ríos et al., 2013a). Recent studies have revealed highly resident behaviour of the ballan wrasse (Villegas-Ríos et al., 2013b; Mucientes et al., 2019).

2.3. Capture and tagging

A total of 282, 23 and 22 individuals of cod, pollack and ballan wrasse, respectively, were captured and tagged during May 2012–2018 and in December 2014 (Table 1). Fish were captured using fyke-nets soaked for 1–3 days at 1–10 m depth, anesthetized in clove oil and equipped with Innovasea V9P and V13P transmitters inserted in the abdominal cavity. Transmitters provide information of the current depth along with a unique identity code. Transmitters were set to transmit a signal every 110–250 s, with a random interval in order to reduce code collision, and with an expected battery life between 350 and 1292 days depending on transmitter configuration. Following full recovery from anaesthesia (typically 5–10 min) all fish were released at their capture location. All fish were tagged inside the FPA except one pollack which was tagged in the buffer zone (Fig. 1). Cod, pollack and ballan wrasse were tracked for an average of 280, 336 and 452 days in total, respectively (Table 1). The study was carried out in accordance with permissions number 15,671 (pollack), 15,778 (ballan wrasse) and 15,882 (cod) issued by the Norwegian Food Safety Authority.

2.4. Estimation of behavioural metrics, time at risk and fate

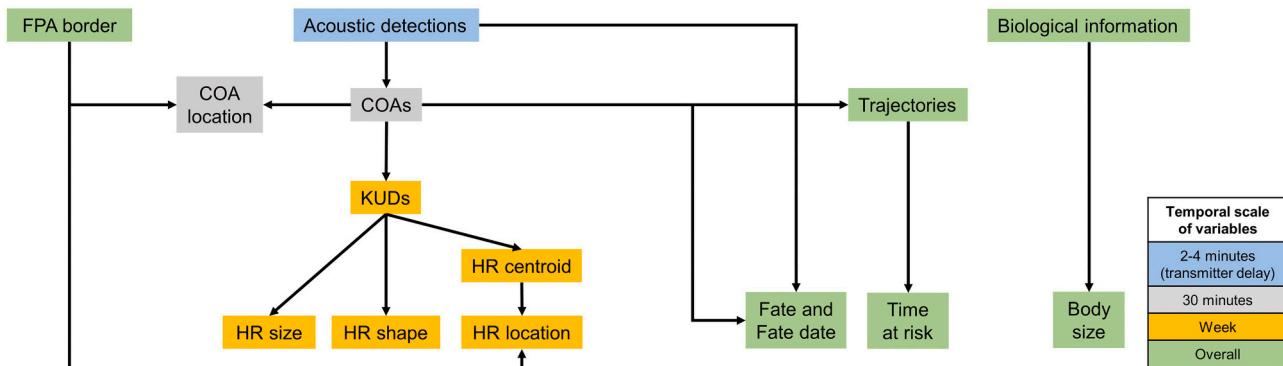
An overview of the different variables estimated is available in Fig. 2. For each tagged individual, centres of activity (COA) were calculated for every 30 min time-bin following Simpfendorfer et al. (2002). Code collisions and false detections were eliminated by the use of a minimum of 2 detections per 24-h period filter (Villegas-Ríos et al., 2013b). Each COA was classified as being located either inside or outside the FPA. A small percent of COAs ($n = 13,384$; 0.3%) that fell inland were removed from analyses. Then the weekly kernel utilization distribution (*kud*) for each fish was estimated using the ATT package (Udyawer et al., 2018) using all the COAs from each particular week and fish. For smoother *kud* estimation, only weeks with at least five distinct COAs and with data on at least five days in that week (not necessarily consecutive) were used to compute home ranges ($n = 3,385,590$; 91.5%). We then used *kuds* to obtain three descriptors of the spatial ecology of each individual. First, *home range size* was computed as the area of the polygon of the 95%*kud*. Second, *home range shape* was estimated as the ratio between the area of the home range and the area of bounding box of the home range (i.e. the box with the smallest area within which all the polygons that define the home range of an individual lie). Values closer to one indicate compact home ranges whereas values closer to zero indicate dispersed home ranges. Last, *home range location* was estimated as the distance from the centroid of each weekly home range to the closest border of the FPA following a straight line. Positive values indicated centroids located inside the FPA, whereas negative values indicated centroids outside the FPA. Instances in which centroids for a particular week fell on land were removed from analyses ($n = 173$; 1.2%). Weekly estimates of all the variables were used as replicates in our study as they are less affected by temporal autocorrelation than monthly estimates (Villegas-Ríos et al., 2017b).

We estimated a new variable, “time at risk”, as the percent of time that each individual spent outside the FPA during any particular week. For that, we interpolated the time series of COAs for each individual and created a trajectory connecting all the COAs using the *adehabitatLT*

Table 1

Summary of the characteristics of the individuals tracked in this study. Information includes total number of individuals tagged per year (n), mean (minimum, maximum) body size (TL) and mean (minimum, maximum) tracking time (TT).

	Cod			Pollack			Ballan wrasse		
	n	TL (cm)	TT (days)	n	TL (cm)	TT (days)	n	TL (cm)	TT (days)
2012	70	47 (30–65)	311 (0–619)						
2013	25	45 (30–64)	300 (0–520)				3	31 (28–35)	306 (300–312)
2014	65	44 (30–50)	273 (0–805)						
2015	30	51 (35–68)	280 (8–886)	14	39 (35–52)	357 (52–701)	8	34 (26–42)	463 (57–703)
2016	25	50 (34–74)	298 (0–933)	3	44 (40–51)	218 (114–402)	5	34 (28–39)	455 (271–701)
2017	25	45 (35–61)	359 (7–835)	3	45 (42–47)	368 (1–922)	4	39 (35–40)	541 (161–923)
2018	42	49 (37–60)	191 (0–562)	3	48 (44–51)	324 (188–562)	2	39 (37–41)	442 (319–565)



Model	Objective	Response	Explanatory	Type	Random effect	Notes
1	Investigate sources of variation of home range properties	HR size HR shape HR location	Week Body size Latitude of HR centroid Longitude of HR centroid	GAMM	Fish ID	One model per species and per home range trait
2	Investigate the effect of home range properties on the probability of being at risk	COA location	HR location HR shape	GLMM	Fish ID	One model per species and per home range size class.
3	Investigate the effect of season and body size on the probability of being at risk	COA location	Week Body size Zone	GAMM	Fish ID	One model per species
4	Investigate the effect of time at risk on the probability of being harvested outside the FPA	Fate and fate date	Time at risk	Cox regression		Only for cod

Fig. 2. On top, workflow showing the steps performed to obtain the different variables considered in this study, showing the temporal scale at which each variable was computed (colour scale). On the bottom, summary table of the four models used indicating the objective and variables used on each of them. COA = centre of activity; KUD = kernel utilization distribution; FPA = fully protected area; HR = home range. For details on how each variable was computed, please see Material and Methods section.

package in R (Calenge, 2019). Assuming constant speed between consecutive COAs, we then estimated how much time each fish spent inside vs. outside of the FPA using the *recurve* library in R (Bracis et al., 2018). Note that periods of time when the fish temporarily left the array were not excluded to estimate “time at risk” because although we didn’t know the exact fish locations during those periods of time, we knew that they were moving outside the FPA.

Fish fate was classified following Villegas-Ríos et al. (2020). In brief, time series of depth, COA latitude and COA longitude were plotted and used to classify the fish as either: 1) survived within the study area (i.e. multiple detections indicated horizontal and vertical movements until the end of the battery life), 2) dispersed from the study area (i.e. detections indicated directional movement towards the outermost receivers followed by an absence of detections for the rest of the battery life), 3) natural mortality when the fish stopped showing horizontal and vertical activity (usually with continued signals from a fixed depth within the study area) or 4) harvested within the study area when the fish disappeared from the receiver array before the end of the battery life and the last detections were recorded at receivers not in the edge of the array. Despite interdicted, some fish were captured inside the FPA. Fished individuals were therefore classified as either fished inside or outside the FPA based on the location of the last COA.

2.5. Data analysis

A total of four different models were run (Fig. 2).

2.5.1. Investigating sources of variation of home range properties

As a preliminary step, we investigated the sources of variation of home range size, shape and location for the three species (cod, pollack and ballan wrasse) using generalized additive mixed-effects models (GAMMs). We focused on three of the main sources of variation of home range properties according to the literature: seasonal effects, body size effects and consistent variation among individuals. Seasonal effects are expected to result from both environmental (e.g. temperature) and life-history (e.g. reproductive cycle) drivers. One GAMM was fitted for each home range trait and for each species as:

$$HR\ trait_{i,w} = \alpha + \beta_1 Body\ size_i + f_1(Week) + f_2(Latitude_{i,w} \cdot Longitude_{i,w}) + f_3(ID) + \varepsilon_{i,w}$$

where $HR\ trait_{i,w}$ represents home range size (log transformed to meet model assumptions), shape (exponential transformation) or location of individual i on week w . Body size was entered as a linear term. f_n are non-parametric smoothing functions using thin plate splines, fitted with

five knots in order to avoid overfitting describing the effect of Week (the week of the year; from 0 to 52) and the interaction between the latitude and the longitude of each weekly centroid (only for the home range shape and size models) to remove potential effects of where individuals were moving in the fjord. A random effect for individual identity (ID) was included to account for repeated measures within individuals using a random effect smoothing basis. To account for potential temporal autocorrelation in the residuals a correlation structure was added to the model following an auto-regressive model of order 1. Models were fitted using the *bam* function in library *mgcv* in R (Wood et al., 2020), and model selection was performed based on AIC. Effects were interpreted based on *p*-values, confidence bands and effect sizes (Lin et al., 2013). A Gaussian family distribution was used in the models of home range size and location. The model of home range shape was initially run using a beta distribution. Results were compared with the same model run using a Gaussian distribution. Given no major differences in the model results using both family distributions, the final model was run using a Gaussian distribution to facilitate the computation of repeatability estimates. Support for the existence of individual variation in home range properties among individuals was evaluated by comparing the AIC of the models above with that of the same model with no random effects included (Dingemanse and Dochtermann, 2012). When support for the inclusion of the random effect for individual identity was found, repeatability in home range traits was computed from the models above using the package *rptGam* as:

$$\text{Repeatability} = \frac{V_{\text{ind}}}{V_{\text{ind}} + V_{\text{res}}}$$

where V_{ind} represents variation among individuals, and V_{res} represents residual variation (i.e. variation within-individuals). Note that repeatability in this case is estimated after controlling or other effects (e.g. season, body size) so it is considered adjusted repeatability.

2.5.2. Effect of spatial ecology on risk

The impact of the spatial ecology of the individuals on the probability of being at risk at any point in time was modelled using generalized linear mixed-effects models (GLMMs) with COA location relative to the FPA as response variable ("1" = outside; "0" = inside; Bernoulli family distribution). The distribution of home range sizes and shapes was not balanced over the whole range of home range locations (Fig. S1) due to the fact that all but one fish were tagged inside the FPA (Fig. 1). Therefore, instead of using a triple interaction with the three home range traits as explanatory variables in the model, we discretized home range size into several classes and split the dataset accordingly. A different number of home range size classes were defined for each species based on the available data (Fig. S1). Seven classes were defined for cod (<10 ha, 10–15 ha, 15–20 ha, 20–25 ha, 25–50 ha, 50–75 ha and > 75 ha), four for pollack (<10 ha, 10–15 ha, 15–20 ha and > 20 ha) and three for the ballan wrasse (10 ha, 10–15 ha and > 15 ha). We then investigated the effect of home range location on the probability of being at risk within each home range class for each species. In the case of cod, we further included home range shape and the interaction between home range size and shape (except in the model for home range > 75 ha):

$$P_{i,t} = \alpha + \beta_1 \text{HR location}_{i,w(t)} + \beta_2 \text{HR shape}_{i,w(t)} + \beta_3 \text{HR location}_{i,w(t)} \cdot \text{HR shape}_{i,w(t)} + f_1(\text{ID}) + \varepsilon_{i,t}$$

where $P_{i,t}$ is the probability of being at risk, based on each COA location, for an individual i at time t , where t is defined as 30-min time bins; and *HR location* and *HR shape* for each individual are entered as the weekly

measure of the week on which each COA fell within ($w(t)$). A random effect for individual identity, ID, was included to account for repeated measures within individuals using a non-parametric smoothing function, f_1 , with a random effect smoothing basis. As in the previous model a correlation structure was added to the model following an auto-regressive model of order 1. Models were fitted using library *bam* in library *mgcv* in R (Wood, 2001). Model diagnosis were conducted by inspecting the residual plots. Model selection was not performed as we were interested in testing the effect of all the explanatory variables according to our hypothesis and we wanted to compare the effects for the different models (Sarmento and Berger, 2017).

2.5.3. Life-history and environmental drivers of risk

To investigate the effect of season and body size on the probability of being at risk, we fit GAMMs, one per species, with the following structure:

$$P_{i,t} = \alpha + \beta_1 \text{Body size}_i + \beta_2 \text{Zone}_{i,t} + f_1(\text{Week}_i) + f_2(\text{ID}) + \varepsilon_{i,t}$$

where $P_{i,t}$ is the probability of being at risk, based on each COA location as explained in the previous model, for an individual i at time t , where t is defined as 30-min time bins. Body size was entered as a linear term, f_1 is a non-parametric smoothing function using thin plate splines and fitted by five knots in order to avoid overfitting, describing the effect of Week (the week of the year, from 0 to 52). A random effect for individual identity, ID, was included to account for repeated measures within individuals using a non-parametric smoothing function, f_2 , with a random effect smoothing basis. As we hypothesized that the seasonal variation of the probability of being at risk would be impacted by where in the FPA the individuals were moving (i.e. how close to the FPA border), we also took into account where, on average, each individual moved in the study area over the whole tracking period. For that we included in the model a new categorical variable called "zone" that reflected the distance from the home range centroid (over the whole period) to the FPA closest border. This variable had four levels: 0–150 m, 150–300 m, 300–600 m and > 600 m. For this analysis, we excluded fish that had a home range centroid outside the FPA due to poor data availability and individuals that never left the FPA. The effects of week and body size were then assessed based on *p*-values, size effects and confidence bands (Lin et al., 2013).

2.5.4. Fitness consequences of time at risk

To explore the effect of time at risk on fishing mortality of cod, we fitted the following cox proportional hazard model:

$$h(t) = h_0(t) \cdot e^{(\beta_1 \cdot \text{Time at Risk})}$$

where $h(t)$ is the hazard function, i.e. the probability of being harvested at time t and is based on information of fate (harvested = 1, survived = 0) and fate date for each individual cod, and $h_0(t)$ represents the baseline hazard. The only explanatory variable in the model was time at risk. Survivors included fish that survived during the whole duration of the battery life ($n = 39$), dispersers ($n = 24$), fish dead of natural causes ($n = 55$) and cod fished inside the FPA ($n = 59$). These latter three groups were considered to be alive until fate date. Our final model included 192 individuals and 14 cases of fishing mortality outside the FPA. Ballan

wrasse and pollack were not included in this analysis due to insufficient available data. The model was fitted using the *coxph* function in library *survival* in R (Therneau and Lumley, 2013) after checking model assumptions.

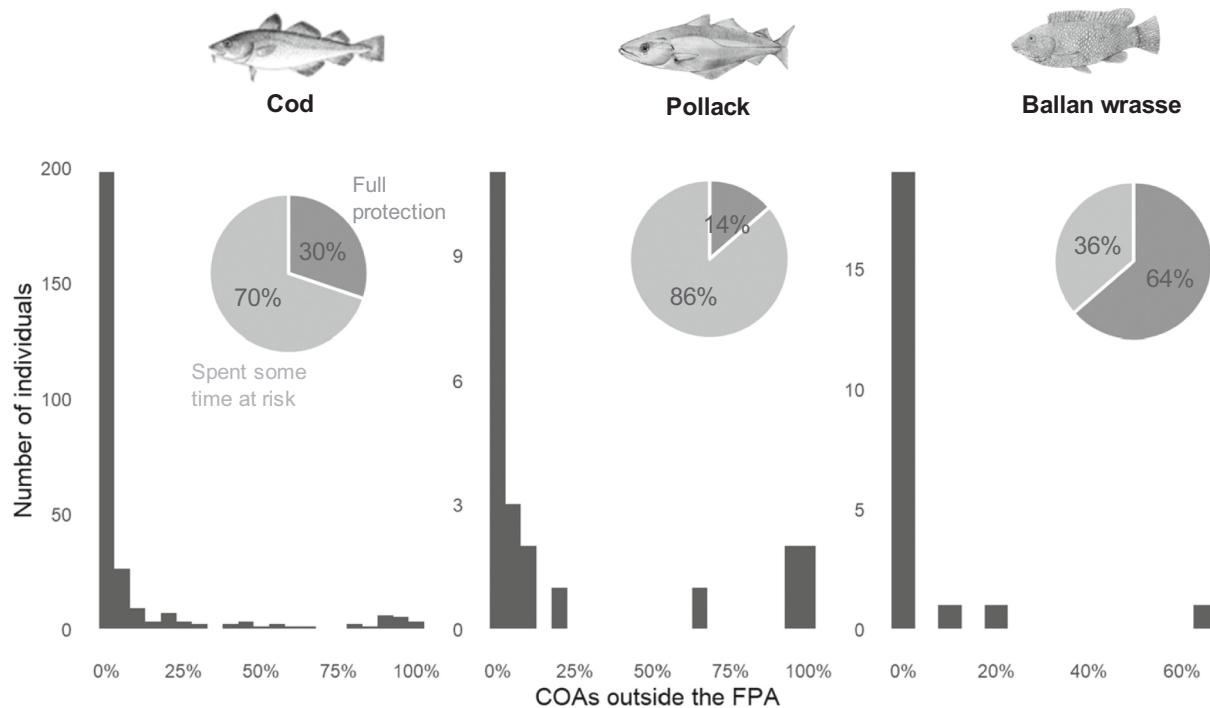


Fig. 3. Frequency distribution of the time at risk, estimated as the percent of centres of activity (COAs) that fell outside the fully protected area for cod, pollack and ballan wrasse over the whole tracking period. The pie-charts show the percent of individuals that never left the fully protected area (dark grey) vs. those that spent some time at risk (light grey).

3. Results

All three study species remained inside the FPA for some proportion of the study duration (Fig. 3). Home range properties greatly varied among individuals (Fig. S2). Home range size and shape were repeatable, i.e. consistent, among individuals in the three species. Conversely, the inclusion of a random effect was not supported in the models for home range location. Repeatability estimates for home range size and shape were 0.55 and 0.50 for cod, 0.81 and 0.76 for pollack and 0.57 and 0.45 for ballan wrasse.

3.1. Sources of variation of home range properties

We observed a seasonal variation of the home range size for cod and ballan wrasse, with a contrasting pattern of variation between these two species (Fig. S3, Table S1). Cod increased the home range size by 35.5% in the winter weeks with a maximum home range size around week 7. Ballan wrasse increased home range size by 47.1% in summer weeks with a peak around week 34. Neither the home range size of pollack nor the home range shape and location of any of the three species varied in a relevant way over the year (Fig. S3, Table S1), with either the confidence intervals suggesting no effect, or the effect being non relevant. Body size was not a significant explanatory variable in any of the models ($p > 0.05$ in all cases).

3.2. Effect of spatial ecology on risk

For all three species, we observed a significant effect of home range location on the probability of being at risk. For individuals with the centroid of the home range inside the FPA, the probability of being at risk increased with decreasing distance to the border of the FPA, whereas the opposite pattern was observed when the centroid was outside the FPA (Fig. 4, Table S2).

The probability of being at risk, however, was also mediated by home range size (Fig. 4; Table S2). Taking into account the whole study period,

the mean home range size was 29 ha, 35 ha and 23 ha for cod, pollack and ballan wrasse respectively, which is $\sim 1/5$ th of the FPA size (150 ha). For any given home range location, increasing home range size increased the probability of being at risk for individuals with the centroid of the home range inside the FPA, and decreased it for individuals with the centroid of the home range outside the FPA. Indeed, model predictions showed that fish with larger home range sizes need to stay further inside the FPA to obtain the same level of protection (Fig. 4; Table S2). For instance, individuals from any of the three species with a home range < 10 ha can obtain almost 95% protection even when they live very close to the FPA border (92 m on average). However, individuals with a home range size of 15–20 ha would need to stay at ~ 167 m from the border to obtain 95% of protection. In the case of cod with home range sizes between 50 and 75 ha, the same level of protection would be achieved only with home ranges centred ~ 553 m inside the FPA (Fig. 4; Table S2). According to model predictions, cod with home ranges > 75 ha will still experience 12% of risk even at 930 m inside the FPA border. Note that the maximum recorded distance to the FPA border for any weekly centroid was 970 m (Fig. 1), meaning that distances larger than that value may not be possible given the geomorphology of the Tvedstrand FPA.

We also observed a significant effect of the home range shape of cod on the probability of being at risk (Fig. 4; Table S2). Compact home ranges had a positive effect on protection (i.e. decreased the probability of being at risk) for individuals with a home range centred inside the FPA, whereas they had a negative effect for individuals with a home range centred outside the FPA. Such effects were more pronounced at larger home range sizes (Fig. 4; Table S2). An individual with a compacted small home range (< 10 ha) with a centroid at 200 m inside the FPA would spend no time at risk, whereas an individual with a large (50–75 ha) at the same location would increase its risk up to 10% with a compacted home range, and up to 23% with a dispersed home range. Indeed, having a compact home range would grant 100% protection (no matter the size of the home range) when located 500 m or more inside the FPA border. In comparison, fish with large and dispersed home

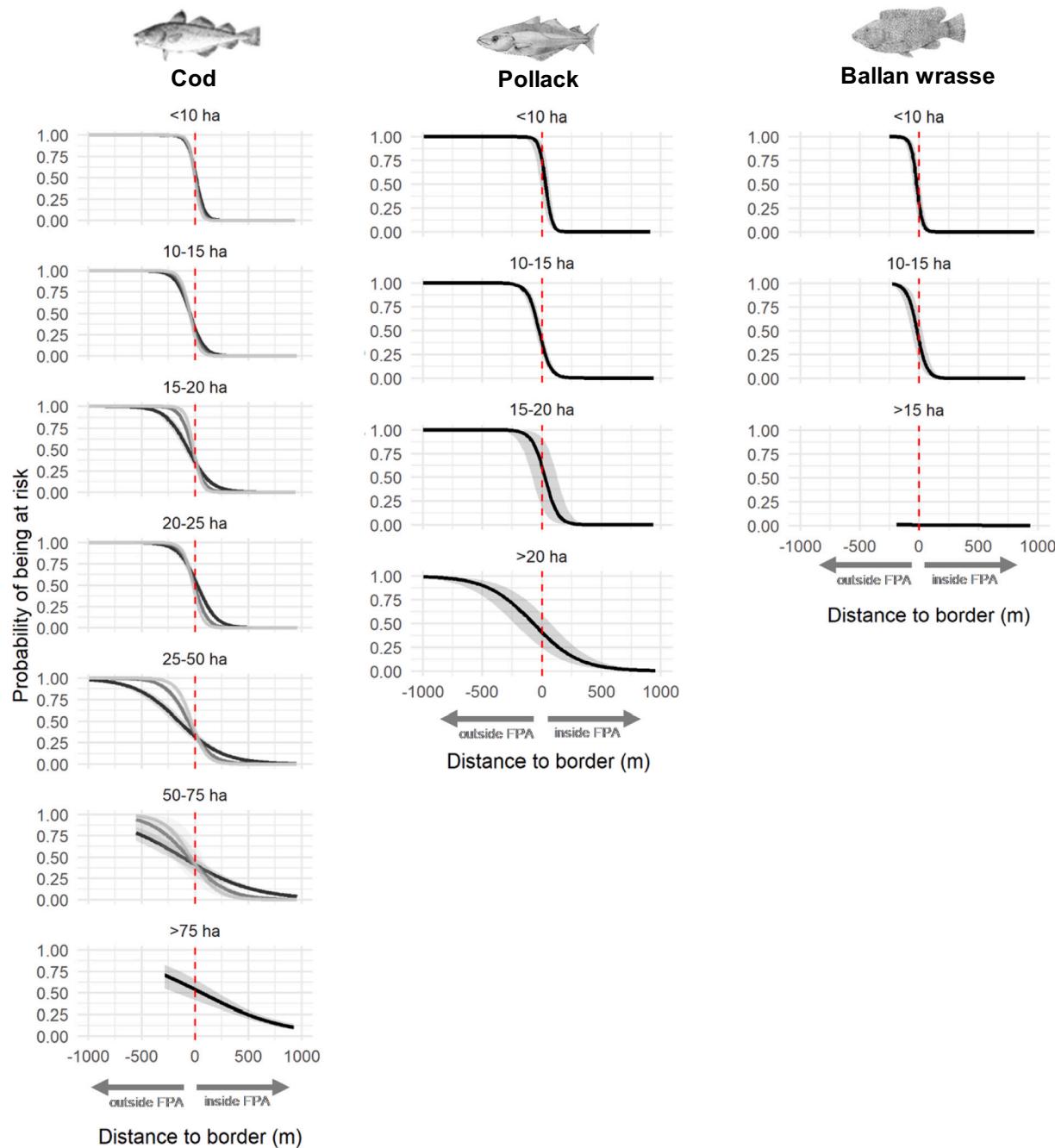


Fig. 4. Predicted effect of home range size, location and shape on the probability of being at risk. The plots show the predicted logistic relationship between the location of the centroid of the home range in relation to the border of the fully protected area (FPA; x-axis) and the probability of being at risk (y-axis). The relationship is provided separately for the different home range size classes as defined in the main text. Besides, in the case of cod, the different coloured lines represent three different shapes of the home range (light grey = compacted, grey = intermediate, dark grey = dispersed), except in the last panel (50–75 ha) where home range shape was not included in the model. The vertical red dashed lines represent the border of the FPA. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

ranges would still spend a small amount of time at risk even when their home ranges are centred more than 900 m inside the FPA (Fig. 4).

3.3. Life-history and environmental drivers of risk

For cod, the probability of being at risk varied over the year, but only for fish moving close to the FPA border (0–150 m) (Fig. 5; Table S3). For those fish, the probability of being at risk was maximum in winter, on week 12 ($p = 0.39$), and minimum in autumn, on week 46 ($p = 0.05$). The opposite pattern was suggested for ballan wrasse (Fig. 5; Table S3),

with the maximum probability of being at risk in late summer around week 34 ($p = 0.71$), and the minimum in spring, on week 18 ($p = 0.13$). No relevant seasonal patterns were observed for cod and ballan wrasse moving beyond 150 m from the FPA border (Fig. 5; Table S3). Body size was not a significant predictor of the probability of being at risk in any of the models ($p > 0.776$ in all cases).

3.4. Fitness consequences of time at risk

We found a significant positive effect of time at risk on the

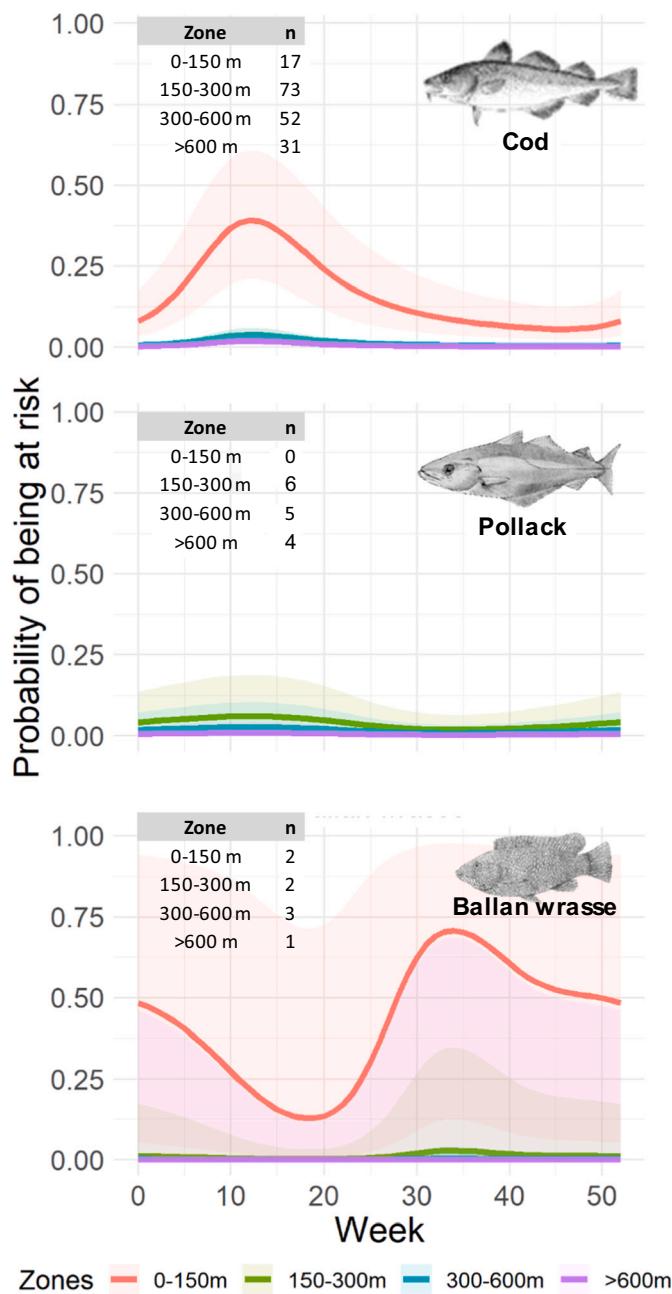


Fig. 5. Seasonal variation of time at risk. Predicted variation over the year in the probability of being at risk for ballan wrasse, cod and pollack moving on different zones within the fully protected area (0–150 m, 150–300 m, 300–600 m, >600 m). The number of fish within each zone is provided in the tables.

probability of being fished outside the FPA (Regression coefficient: 3.160; Hazard ratio: 23.56; Hazard ratio CI: 6.45–86.07; Hazard ratio SE: 0.66; Z-value: 4.78; *p*-value<0.001). Predictions from the model showed a reduction in survival probability of 10.2%, 21.2% and 40.78% after 500 days for cod spending 25%, 50% and 75% of time outside the FPA, respectively (Fig. 6).

4. Discussion

This study revealed that the level of protection granted by a fully protected area (FPA) to a fish community is strongly dependent on how individuals use the available space. Interestingly, we show that the use of space varies consistently among individuals. For individuals moving inside the FPA, having larger, more dispersed home ranges closer to the

border increased the chances of being at risk outside the reserve. For individuals moving outside the FPA the opposite pattern was seen. We also showed that the protection afforded by an FPA can vary over the year in response to seasonal variation in home range properties. Last, we show that time at risk is associated with reduced fitness, seen as an increased probability of being fished outside the FPA. Here, we discuss the potential implications of these findings from an ecological, evolutionary and conservation perspective.

In spite of all but one individual being tagged inside the FPA and having home ranges sizes much smaller (~1/5th) than the FPA, only 25% on average of the tagged population spent the whole time under protection. This suggests that home range size explains only a small part of the probability of being at risk, and it is thus important to understand other factors that make individuals move across FPA borders. This finding somewhat challenges the general assumption that MPA size should be informed by the home range size of the species or populations that are the target of protection (Kramer and Chapman, 1999; Krueck et al., 2018). Typically, the minimum recommended MPA size for each species has been calculated as twice the average home range size of the protected populations (in all directions) to ensure that the reserve includes the entire home range of at least one individual, and likely many more where individuals have overlapping home ranges (Kramer and Chapman, 1999; Green et al., 2015; McCauley et al., 2015; Di Franco et al., 2018). Our study found that cod with home ranges larger than 75 ha, corresponding to approximately half the size of the Tvedstrand FPA, will be exposed to certain extent to the fishery no matter where the home range is located. This suggests that the Tvedstrand FPA cannot fully protect home ranges larger than ~75 ha, supporting the perception that for any MPA, there is a maximum home range size that can be fully protected (as Moffitt et al., 2009 suggest).

In agreement with theoretical predictions (Kramer and Chapman, 1999), we show that home range location largely determines the exposure to the fishery outside the FPA, especially when considered in interaction with home range size. Thorbjørnsen et al. (2019) suggested that protection of *Salmo trutta* (seatrout) tagged inside Tvedstrand FPA decreased with increasing home range size, while the opposite pattern was observed for fish tagged outside the FPA (larger home ranges increased protection). While Thorbjørnsen et al. (2019) assumed a linear relationship between home range size and the degree of protection, we instead modelled the relationship as a logistic curve. Our modelling approach has practical implications, since we were able to detect the maximum home range size that grants full protection depending on where the home range is centred within the FPA.

Given the pivotal role of home range location for the effectiveness of MPAs, it is important to understand what are the factors that determine where individuals establish their home ranges. The distribution of habitats is likely important, which highlights the need for considering habitat use and habitat selection by the different species, and how habitats are distributed inside MPAs (Freitas et al., 2016). Importantly, habitat distribution may also explain the shape of the home ranges, especially when the home range size is large relative to the dimension of the patches of suitable habitat. This is the case of the Tvedstrand fjord where patches of suitable habitats for the three species are rather small and distributed around islets and along the shoreline (Freitas et al., 2016, 2021), which may facilitate movements across the FPA border. Individuals in our study greatly varied in their home range shape, with many of them possessing a very dispersed home range. Typically, such variation in home range shape has not been considered in models assessing the effectiveness of MPAs (Moffitt et al., 2009; Krueck et al., 2018). Our results suggest that relaxing this simplification may have important consequences for our understanding of the effectiveness of MPAs.

We showed that, for cod and ballan wrasse, the seasonal variation in the probability of being at risk mirrored the seasonal variation in home range size. In contrast, no seasonal variation in home range size or time at risk was observed for pollack. This suggests strong links between

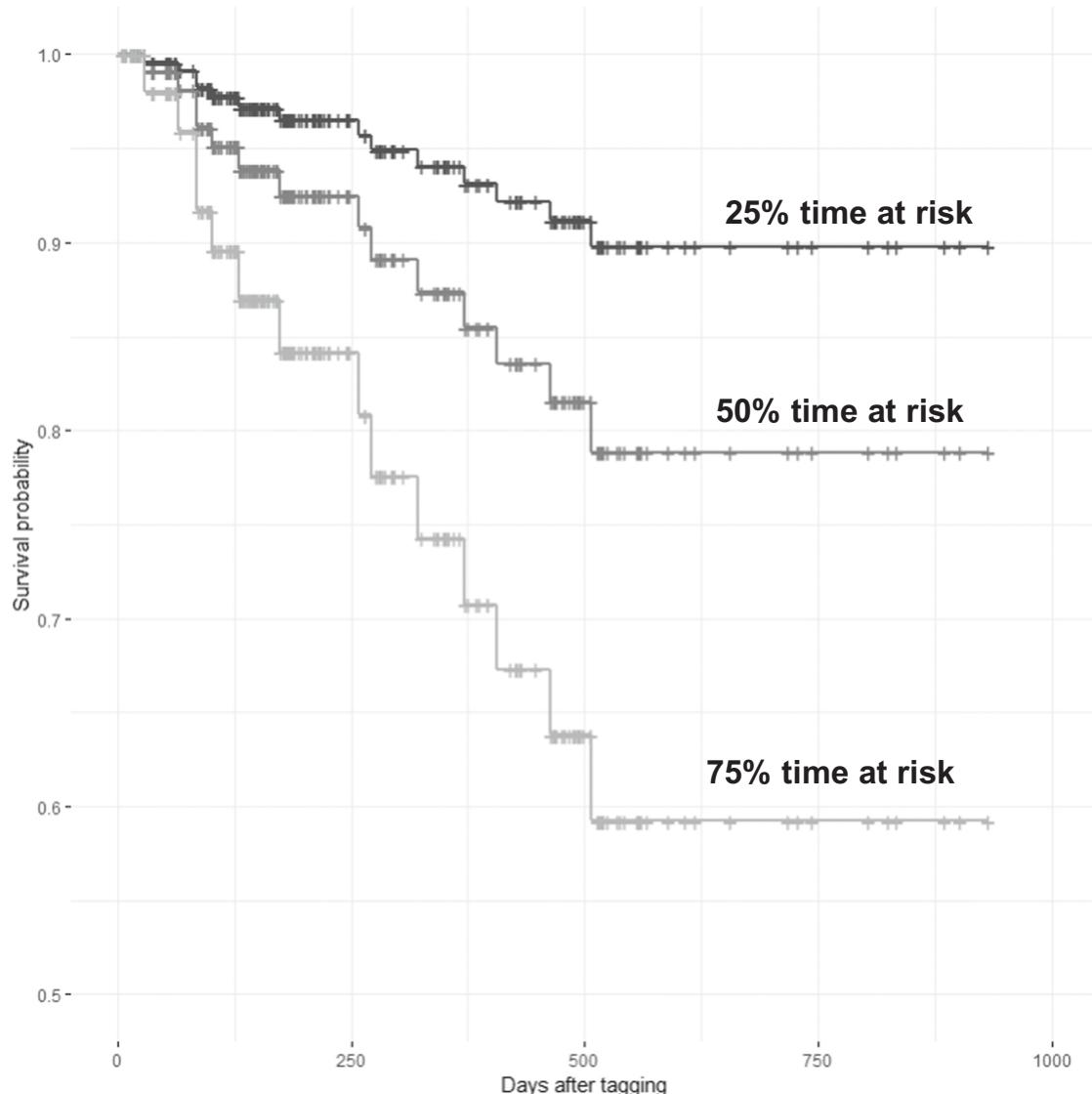


Fig. 6. Fitness consequences of being at risk. Survival probability over time of cod spending 25%, 50% and 75% of the time at risk as predicted from a Cox proportional hazards regression model. Note that the y-axis starts at 0.5.

species' life histories and temporal dynamics of protection. In the case of cod, the maximum risk was observed in winter (week 12) which coincides with the peak spawning season (Ciannelli et al., 2010). Larger mobility in winter by fish living close to the FPA border might be related to displacements to spawning grounds outside the FPA. In fact, Ciannelli et al. (2010) detected areas of high concentration of cod eggs close to the Tvedstrand FPA border. As sea temperature rises in summer and autumn, cod may be forced to reduce their mobility due to unsuitable thermal conditions in shallow waters that restricts cod to deeper areas (Freitas et al., 2015, 2016). Interestingly, this reduction in mobility and time at risk coincides with a seasonal peak in cod recreational fishing in the study area (Kleiven et al., 2016), suggesting that the FPA is more effective protecting cod living inside the FPA when more people are trying to fish them. In the case of ballan wrasse, the suggested reduced risk in spring (week 18) may also be associated with spawning, which occurs between April and June in Norway (Muncaster et al., 2010). During spawning, ballan wrasse reduce their activity levels (Villegas-Ríos et al., 2014) and males display parental care and high site fidelity (Sjölander et al., 1972; Mucientes et al., 2019). Note that the ballan wrasse may change sex when reaching 34–41 cm (Muncaster et al., 2013) so some of the fish in our study were likely males. As the sea warms in late summer,

ballan wrasse increase their activity levels (Villegas-Ríos et al., 2014), likely explaining more frequent crossings of the FPA border.

For cod, we found that increased time at risk translated into increased fishing mortality. This suggests that in populations moving within or around an FPA, fisheries-induced selection could be acting on home range characteristics such as size or shape which vary consistently among individuals. For instance, for any individual with a home range centred inside the FPA, having a larger home range will increase its time at risk and thus reduce its fitness. This might alter selection acting on home range size as compared to a scenario of no protection, where home range size may not always be related to capture probability (Alós et al., 2012, 2016). To the extent that home range properties are intrinsic to each individual (i.e. have a genetic basis), spillover fisheries may result in evolutionary changes within the protected populations by eroding the fish that live closer to the FPA border and have larger home ranges (Villegas-Ríos et al., 2017a). Although heritability of home range properties have not yet been demonstrated, our repeatability estimates of home range size and shape add to an increasing body of evidence showing that many aspects of the spatial ecology of fishes are repeatable (Harrison et al., 2014, 2019; Alós et al., 2016; Villegas-Ríos et al., 2017b). This strongly suggest that there is an underlying heritable

component (Dingemanse and Dochtermann, 2012). Note that we conducted our study in a semi-enclosed fjord, where the FPA had a small connection to the buffer and the open areas, increasing the probability that individuals remained within FPA borders. While our framework is valid for any type of MPA, we acknowledge that more open MPAs (e.g. coastal or offshore MPAs) may provide less protection to local populations increasing the chances that individuals are exposed to the fishery and therefore amplifying the aforementioned fitness consequences.

When the size of the MPAs is small compared to the mobility of the target species, our results support the implementation of partially protected, buffer areas around the FPA to help in mitigating the unnatural selection patterns caused by spillover fisheries, as a way to relax selection on individuals with larger mobility. While allowed fishing activities can clearly benefit from accessing those buffer areas (Di Lorenzo et al., 2020), care should be given that the intensity of such allowed activities does not increase too dramatically (Zupan et al., 2018). Also, how time at risk would be mediated by various degrees of protection levels should be further investigated. Similarly, MPA networks where fish with larger mobility may receive protection from neighbouring MPAs may also help in mitigating potential selection of certain phenotypes.

In conclusion, our study provides clear links between individual fish behaviour, fisheries-induced selection and the effectiveness of protected areas. These links highlight the importance of intraspecific trait variation for understanding the spatial dynamics of populations and its applications. It is not our intention to provide basic management considerations. Rather, our study could inspire more specific aspects of MPA monitoring and design. Specifically, we advocate for investigating among-individual variation and consistency in behaviour within the focal populations. Whereas average values can provide a first insight into the degree of movement of a particular species, our study shows that individuals typically vary in their mobility, with major consequences for protection and survival. Considering the individual variation in behaviour and the associated fitness consequences will therefore contribute towards addressing the evolutionary dimension MPAs (Baskett and Barnett, 2015; Arlinghaus et al., 2017; Villegas-Ríos et al., 2017a).

Authorship statement

Conceived the study: DVR, EMO, JC. Implemented the study: DVR, EMO, EM, CF, ST. Analysed the data: DVR, AAF. Wrote the first draft of the manuscript: DVR. Provided input on further manuscript drafts: JC, CF, EM, ST, AAF, EMO.

Data accessibility

Data used in this study is available at Dryad repository using the following link: <https://doi.org/10.5061/dryad.5hbzkh6m>.

Declaration of competing interest

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

Acknowledgments

The Tvedstrand fjord telemetry array is maintained by the Norwegian Institute of Marine Research (IMR) through the Coastal Zone Ecosystems research programme. We are grateful to colleagues at the IMR Flødevigen Research Station for field assistance. This project has received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No 793627 (BEMAR), from the programme IF_ERC from the Spanish National Research Council (granted to DVR) and from the

Marine Science programme within the Research Council of Norway, grant no. 294926 (CODSIZE). JC received funding from the BiodivERsA program (METRODIVER project). Thanks to Graham Pierce for English revision. The authors declare no conflict of interests.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2021.109333>.

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