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David Villegas-Ríos, Joachim Claudet, Carla Freitas, Even Moland, Susanna Huneide Thorbjørnsen, Alexandre Alonso-Fernández, Esben M Olsen, Susanna Thorbjørnsen

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1 **Time at risk: individual spatial behaviour drives fitness and marine**
2 **protected area effectiveness**

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4 David Villegas-Ríos^{1,2,*}, Joachim Claudet³, Carla Freitas^{4,5}, Even Moland^{4,6}, Susanna
5 Thorbjørnsen^{4,6}, Alexandre Alonso-Fernández², Esben M. Olsen^{4,6}

6
7 ¹Instituto Mediterráneo de Estudios Avanzados (CSIC-UIB), Department of Ecology and Marine
8 Resources, C/Miquel Marquès 21, 07190 Esporles, Balearic Islands, Spain.

9 ²Instituto de Investigaciones Marinas (IIM-CSIC), Department of Ecology and Marine Resources.
10 Eduardo Cabello 6, 36208 Vigo, Pontevedra, Spain.

11 ³ National Center for Scientific Research, PSL Université Paris, CRIOBE, USR 3278 CNRS-
12 EPHE-UPVD, Maison des Océans, Paris, France

13 ⁴ Institute of Marine Research, Flødevigen, 4817 His, Norway

14 ⁵ MARE, Marine and Environmental Sciences Center, Madeira Tecnopolo, 9020-105 Funchal,
15 Madeira, Portugal

16 ⁶ Centre for Coastal Research (CCR), Department of Natural Sciences, University of Agder,
17 P.O. Box 422, 4604 Kristiansand, Norway

18 * Correspondence: dvillegas@iim.csic.es (D. Villegas-Ríos)

19
20 **Abstract**

21 The effectiveness of marine protected areas (MPAs) depends on the mobility of the
22 populations that are the target of protection, with sedentary species likely to spend more time
23 under protection even within small MPAs. However, little is understood about how individual
24 variation in mobility may influence the risk of crossing an MPA border, as well as the fitness
25 costs associated with being exposed to spillover fisheries. Here we investigated the
26 repeatability and the role of individual fish spatial behavior in determining the probability of
27 being at risk (i.e. exposed to the fishery) and the fitness consequences. We acoustically tracked
28 the movements and fate of 282 individuals of three fish species during 8 years in a southern
29 Norwegian fjord. We found that for individuals with a home range centroid inside the fully

30 protected MPA, the probability of being at risk outside the MPA increased rapidly with reduced
31 distance from the home range centroid to MPA borders, particularly for individuals having larger
32 and more dispersed home ranges. We also detected that the seasonal expansions of the home
33 range are associated with increased time at risk. Last, we show that individuals spending more
34 time at risk were also more likely to be harvested by the fishery operating outside the MPA. Our
35 study provides clear links between individual fish behavior, fisheries-induced selection, and the
36 effectiveness of protected areas. These links highlight the importance of intraspecific trait
37 variation for understanding the spatial dynamics of populations and emphasize the need to
38 consider individual behavior when designing and implementing MPAs.

39

40

41 **Introduction**

42 Marine protected areas (MPAs) are valuable tools for protecting fish from overharvesting
43 and are expected to support fisheries beyond their boundaries through the net export of pelagic
44 eggs and larvae and the spillover of juveniles and mature fish (Abesamis & Russ 2005; Harrison
45 *et al.* 2012; Di Lorenzo *et al.* 2016a). The effectiveness of MPAs depend on a number of factors,
46 from good governance to the physical properties of the MPAs and characteristics of protected
47 populations (Claudet *et al.* 2008, 2010; Edgar *et al.* 2014). In particular, given that MPAs are
48 spatially-explicit management tools (Claudet *et al.* 2006), fish spatial behavior plays a key role in
49 driving MPA effectiveness (Lowe *et al.* 2003; Afonso *et al.* 2009; Di Lorenzo *et al.* 2016b) and as
50 such it is often taken into account in all the steps of MPA design, implementation and
51 management (Claudet *et al.* 2020).

52 The degree of protection granted by an MPA on juvenile and mature fish will ultimately
53 depend on the amount of time that individuals spend within its borders. Thus, MPA effectiveness
54 is expected to be higher for less mobile species (Pilyugin *et al.* 2016), although positive effects
55 have also been detected for large pelagic and migratory species (Hays *et al.* 2014; Mee *et al.*
56 2017; Dwyer *et al.* 2020). The conservation benefits of MPAs typically increase exponentially with
57 MPA size (Claudet *et al.* 2008; Edgar *et al.* 2014), but small MPAs may still offer long-term
58 protection to some species. For instance, small MPAs of only 2.8 km² were successful in
59 protecting the sedentary dusky grouper (Afonso *et al.* 2011), and MPAs smaller than 10 km wide
60 seem effective in protecting most commercial reef fish species (Krueck *et al.* 2018). For species
61 moving within a home range, it is anticipated that MPA size can be informed by focal species'
62 home range sizes (Kramer & Chapman 1999). In consequence, most empirical studies have
63 focused on investigating the relationship between the scale of a species' home range and the
64 size of the MPA (Green *et al.* 2015; Di Franco *et al.* 2018; Krueck *et al.* 2018). However, simply
65 possessing a home range behaviour, even when smaller than the MPA, does not guarantee
66 protection. For instance, location of the home range in relation to the reserve border can also
67 influence the level of protection (Kramer & Chapman 1999; Thorbjørnsen *et al.* 2019).

68 In spite of recent efforts to protect large areas of the ocean (Hays *et al.* 2014), most MPAs
69 in the world are still relatively small compared to how fish move (Claudet *et al.* 2008; McCauley

70 *et al.* 2015; Di Franco *et al.* 2018). Therefore, individuals with different mobility phenotypes may
71 experience different degrees of protection (Mee *et al.* 2017). However, such intraspecific
72 variability in spatial ecology has typically been overlooked in studies of MPA effectiveness (but
73 see Parsons *et al.* 2010; Mee *et al.* 2017; Thorbjørnsen *et al.* 2019). Focusing on average mobility
74 critically fails to acknowledge potential evolutionary consequences of spatial protection (Baskett
75 *et al.* 2005; Baskett & Barnett 2015; Arlinghaus *et al.* 2017; Villegas-Ríos *et al.* 2017), resulting
76 from heritable variation in behavior linked to the tendency to leave the MPA (Mee *et al.* 2017).
77 Indeed, recent evidence have demonstrated that individuals within populations of species such
78 as cod or lobster differ consistently in aspects of their mobility such as home range size (Villegas-
79 Ríos *et al.* 2017b; Moland *et al.* 2019). If individuals with different spatial behaviour differ in their
80 degree of exposure to the fishery and thus mortality risk, this may have fitness consequences
81 eventually driving evolutionary changes toward decreased dispersal and spillover (Parsons *et al.*
82 2010; Mee *et al.* 2017; Villegas-Ríos *et al.* 2017). Buffer areas - zones of partial protection
83 surrounding fully protected areas – could function as useful tools for mitigating unnatural selection
84 gradients imposed by spillover fisheries (Januchowski-Hartley *et al.* 2013; Villegas-Ríos *et al.*
85 2017a; but see Zupan *et al.* 2018 for potential negative impacts of increased fishing pressure in
86 buffer areas).

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

99

100 **Material and methods**

101 Study area and telemetry array

102 Our study was carried out in the Tvedestrand fjord on the Norwegian Skagerrak coast
103 (Fig. 1) during eight consecutive years (June 2012-May 2019). The study area is located in an
104 MPA implemented in June 2012 and comprises waters down to 90 m depth. The MPA is
105 composed of a fully protected area (FPA) of 150 ha where all types of fishing are forbidden,
106 surrounded by three partially protected buffer zones where angling is allowed but fixed fishing
107 gears such as nets and traps are banned. The whole area was monitored with a
108 presence/absence acoustic system of 33 VR2-W omnidirectional receivers (Innovasea, Halifax,
109 Canada) fixed at three-meter depth and pointing downwards (Fig. 1). Fish detection data,
110 consisting of records of tag identity, tag depth, tag detection time and receiver identity, were
111 downloaded twice per year while maintenance of the array was conducted once per year.
112 Range testing conducted in 2011 through the study area suggested that detection range of the
113 transmitters used in this study and the spacing of receivers provided a very good coverage of
114 the study area (see Villegas-Ríos *et al.* 2020 for details).

115 Study Species

116 *Gadus morhua* (Atlantic cod) is a demersal generalist predator with severely depleted
117 populations in Skagerrak (Knutsen *et al.* 2018; Barth *et al.* 2019). Coastal cod often, but not
118 always, exhibit limited movement compared to more oceanic populations (Robichaud & Rose
119 2004; Rogers *et al.* 2014; Villegas-Ríos *et al.* 2017b). *Pollachius pollachius* (pollack) is a
120 benthopelagic piscivore common to Skagerrak coastal areas (Fromentin *et al.* 1998). *Labrus*
121 *bergylta* (ballan wrasse) is a long-lived, hermaphrodite rocky reef mesopredator with a complex
122 life history (Muncaster *et al.* 2010; Villegas-Ríos *et al.* 2013a). Recent studies have revealed
123 highly resident behaviour of the ballan wrasse (Villegas-Ríos *et al.* 2013c; Mucientes *et al.*
124 2019).

125 Capture and tagging

126 A total of 282, 23 and 22 individuals of cod, pollack and ballan wrasse, respectively, were
127 captured and tagged during May 2012-2018 and in December 2014 (Table 1). Fish were

128 captured using fyke-nets soaked for 1–3 days at 1–10 m depth, anesthetized in clove oil and
129 equipped with Innovasea V9P and V13P transmitters inserted in the abdominal cavity.
130 Transmitters provide information of the current depth along with a unique identity code.
131 Transmitters were set to transmit a signal every 110–250 s, with a random interval in order to
132 reduce code collision, and with an expected battery life between 350 and 1,292 days depending
133 on transmitter configuration. Following full recovery from anaesthesia (typically 5-10 min) all fish
134 were released at their exact capture location. All fish were tagged inside the FPA except one
135 pollack which was tagged in the buffer zone (Fig. 1). Cod, pollack and ballan wrasse were
136 tracked for an average of 280, 336 and 452 days in total, respectively (Table 1). The study was
137 carried out in accordance with permissions number 15,671 (pollack), 15,778 (ballan wrasse)
138 and 15,882 (cod) issued by the Norwegian Food Safety Authority.

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

140 An overview of the different variables estimated is available in Fig. 2. For each tagged
141 individual, centres of activity (COA) were calculated for every 30 min time-bin following
142 Simpfendorfer et al. (2002). Code collisions and false detections were eliminated by the use of a
143 minimum of 2 detections per 24-h period filter (Villegas-Ríos *et al.* 2013b). Each COA position
144 was classified as being located either inside or outside the FPA. A small percent of COAs
145 ($n=13,384$; 0.3%) that fell inland were removed from analyses. Then the weekly kernel
146 utilization distribution (*kud*) for each fish was estimated using the *ATT* package (Udyawer *et al.*
147 2018) using all the COAs from each particular week and fish. For smoother *kud* estimation, only
148 weeks with at least five distinct COAs and with data on at least five days in that week (not
149 necessarily consecutive) were used to compute home ranges ($n=3,385,590$; 91.5%). We then
150 used *kuds* to obtain three descriptors of the spatial ecology of each individual. First, *home range*
151 *size* was computed as the area of the polygon of the 95%*kud*. Second, *home range shape* was
152 estimated as the ratio between the home range area and the area of bounding box of the home
153 range (i.e. the box with the smallest area within which all the polygons that define the home
154 range of an individual lie). Values closer to 1 indicate compact home ranges whereas values
155 closer to zero indicate dispersed home ranges. Last, *home range location* was estimated as the
156 distance from each weekly home range centroid to the closest exit of the FPA following a
157 straight line. Positive values indicated centroid located inside the FPA, whereas negative values

158 indicated centroids outside the FPA. Instances in which centroids for a particular week fell on
159 land were removed from analyses (n=173; 1.2%). Weekly estimates of all the variables were
160 used as replicates in our study as they are less affected by temporal autocorrelation than
161 monthly estimates (Villegas-Ríos *et al.* 2017b).

162 We estimated a new variable, “time at risk”, as the percent of time that each individual spent
163 outside the FPA during any particular week. For that, we interpolated the time series of COAs
164 for each individual and created a trajectory connecting all the COAs using the *adehabitatLT*
165 package in R (Calenge 2019). Assuming constant speed between consecutive COAs, we then
166 estimated how much time each fish spent inside vs. outside of the FPA using the *recurse* library
167 in R (Bracis *et al.* 2018). Note that periods of time when the fish temporarily left the array were
168 not excluded to estimate “time at risk” because although we didn’t know the exact fish locations
169 during those periods of time, we knew that they were moving outside the FPA.

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

181 Data analysis

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

183 Investigating sources of variation of home range properties. As a preliminary step, we
184 investigated the sources of variation of home range size, shape and location for the three
185 species (cod, pollack and ballan wrasse) using additive mixed-effects models (GAMMs). We
186 focused on three of the main sources of variation of home range properties according to the

187 literature: seasonal effects, body size effects and consistent variation among individuals.
188 Seasonal effects are expected to result from both environmental (e.g. temperature) and life-
189 history (e.g. reproductive cycle) drivers. One GAMM was fitted for each home range trait and for
190 each species as:

$$191 \quad HR\ trait_{i,w} = \alpha + \beta_1 Body\ size_i + f_1(Week) + f_2(Latitude_{i,w} \cdot Longitude_{i,w}) + f_3(ID) + \varepsilon_{i,w}$$

192 Where $HR\ trait_{i,w}$ represents home range size (log transformed to meet normality
193 assumptions), shape (exponential transformation) or location of individual i on week w . Body
194 size was entered as a linear term. f_n are non-parametric smoothing functions using thin plate
195 splines, fitted with five knots in order to avoid overfitting describing the effect of Week (the week
196 of the year; from 0 to 52) and the interaction between the latitude and the longitude of each
197 weekly centroid (only for the home range shape and size models) to remove potential effects of
198 where individuals were moving in the fjord. A random effect for individual identity (ID) was
199 included to account for repeated measures within individuals using a random effect smoothing
200 basis. To account for potential temporal autocorrelation in the residuals a correlation structure
201 was added to the model following an auto-regressive model of order 1. Models were fitted using
202 the *bam* function in library *mgcv* in R (Wood *et al.* 2020), and model selection was performed
203 based on AIC. Effects were interpreted based on p-values, confidence bands and effect sizes
204 (Lin *et al.* 2013). Support for the existence of individual variation in home range properties
205 among individuals was evaluated by comparing the AIC of the models above with that of the
206 same model with no random effects included (Dingemanse & Dochtermann 2013). A Gaussian
207 family distribution was used in the models of home range size and location. The model of home
208 range shape was initially run using a beta distribution. Results was compared with the same
209 model run using a Gaussian distribution. Given no major differences in the model results using
210 both family distributions, the final model was run using a Gaussian distribution to facilitate the
211 computation of repeatability estimates. When support for the inclusion of the random effect for
212 individual identity was found, repeatability in home range traits was computed from the models
213 above using the package *rptGam* as:

$$214 \quad Repeatability = \frac{V_{ind}}{V_{ind} + V_{res}}$$

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

218 Effect of spatial ecology on risk. The impact of the individual spatial ecology on probability
219 of being at risk at any point in time was modelled using generalized linear mixed-effects models
220 (GLMMs) with COA location relative to the FPA as response variable (“1”=outside; “0”=inside;
221 Bernoulli family distribution). The distribution of home range sizes and shapes was not balanced
222 over the whole range of home range locations (Fig. S1) due to the fact that all but one fish were
223 tagged inside the FPA (Fig. 1). Therefore, instead of using a triple interaction with the three home
224 range traits as explanatory variables in the model, we discretized home range size into several
225 classes and split the dataset accordingly. A different number of home range size classes were
226 defined for each species based on the data available (Fig. S1). Seven classes were defined for
227 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
228 ha, 10-15 ha, 15-20 ha and > 20 ha) and three for the ballan wrasse (10 ha, 10-15 ha and >15
229 ha). We then investigated the effect of home range location on the probability of being at risk
230 within each home range class for each species. In the case of cod, we further included home
231 range shape and the interaction between home range size and shape (except in the model for
232 home range >75 ha):

$$233 \quad P_{i,t} = \alpha + HR\ location_{i,w(t)} \cdot HR\ shape_{i,w(t)} + f_1(ID) + \varepsilon_{i,t}$$

234 where $P_{i,t}$ is the probability of being at risk, based on each COA location, for an individual
235 i at time t , where t is defined as 30-minute time bins; and $HR\ location$ and $HR\ shape$ for each
236 individual are entered as the weekly measure of the week on which each COA fell within ($w(t)$). A
237 random effect for individual identity, ID, was included to account for repeated measures within
238 individuals using a non-parametric smoothing function, f_1 , with a random effect smoothing basis.
239 As in the previous model a correlation structure was added to the model following an auto-
240 regressive model of order 1. Models were fitted using library *bam* in library *mgcv* in R (Wood
241 2001). Model diagnosis were conducted by inspecting the residual plots. Model selection was not
242 performed as we were interested in testing the effect of all the explanatory variables according to

243 our hypothesis and we wanted to compare the effects for the different models (Sarmiento & Berger
244 2017).

245 Life-history and environmental drivers of risk. To investigate the effect of season and body
246 size on the probability of being at risk, we fit generalized additive mixed-effects models (GAMMs),
247 one per species, with the following structure:

$$248 \quad P_{i,t} = \alpha + \beta_1 \text{Body size}_i + \beta_2 \text{Zone}_{i,t} + f_1(\text{Week}_t) + f_2(\text{ID}) + \varepsilon_{i,t}$$

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

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

$$266 \quad h(t) = h_0(t) \cdot e^{(\beta_1 \cdot \text{Time at Risk})}$$

267 where $h(t)$ is the hazard function, i.e. the probability of being harvested at time t and is
268 based on information of fate (harvested=1, survived=0) and fate date for each individual cod, and
269 $h_0(t)$ represents the baseline hazard. The only explanatory variable in the model was time at risk.
270 Survivors included fish that survived during the whole duration of the battery life (n=39),

271 dispersers (n=24), fish dead of natural causes (n=55) and cod fished inside the FPA (n=59).
272 These latter three groups were considered to be alive until fate date. Our final model included 192
273 individuals and 14 cases of fishing mortality outside the FPA. Ballan wrasse and pollack were not
274 included in this analysis due to insufficient available data. The model was fitted using the *coxph*
275 function in library *survival* in R (Therneau & Lumley 2013) after checking model assumptions.

276 **Results**

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

283 Sources of variation of home range properties.

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

292 Effect of spatial ecology on risk.

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

297 The probability of being at risk, however, was also mediated by home range size (Fig. 4;
298 Table S2). Taking into account the whole study period, the mean home range size was 29 ha, 35

299 ha and 23 ha for cod, pollack and ballan wrasse respectively, which is $\sim 1/5^{\text{th}}$ of the FPA size (150
300 ha). For any given home range location, increasing home range size increased the probability of
301 being at risk for individuals with a home range centroid inside the FPA, and decreased it for
302 individuals with a home range centroid outside the FPA. Indeed, model predictions showed that
303 fish with larger home range sizes need to stay further inside the FPA to obtain the same level of
304 protection (Fig. 4; Table S2). For instance, individuals from any of the three species with a home
305 range <10 ha can obtain almost 95% protection even when they live very close to the FPA
306 boundary (92 m on average). However, individuals with a home range size of 15-20 ha would
307 need to stay at ~ 167 m from the border to obtain 95% of protection. In the case of cod with home
308 range sizes between 50 and 75 ha, the same level of protection would be achieved only with
309 home ranges centered ~ 553 m inside the FPA (Fig. 4; Table S2). According to model predictions,
310 cod with home ranges >75 ha will still experience 12% of risk even at 930 m inside the FPA
311 border. Note that the maximum recorded distance to the FPA border for any weekly centroid was
312 970 m (Fig. 1), meaning that distances larger than that value may not be possible given the
313 geomorphology of the Tvedestrand FPA.

314 We also observed a significant effect of the home range shape of cod on the probability
315 of being at risk (Fig. 4; Table S2). Compact home ranges had a positive effect on protection (i.e.,
316 decreased the probability of being at risk) for individuals with a home range centered inside the
317 FPA, whereas they had a negative effect for individuals with a home range centered outside the
318 FPA. Such effects were more pronounced at larger home range sizes (Fig. 4; Table S2). An
319 individual with a compacted small home range (<10 ha) with a centroid at 200 m inside the FPA
320 would spend no time at risk, whereas an individual with a large (50-75 ha) at the same location
321 would increase its risk up to 10% with a compacted home range, and up to 23% with a dispersed
322 home range. Indeed, having a compact home range would grant 100% protection (no matter the
323 size of the home range) when located 500 m or more inside the FPA border. In comparison, fish
324 with large and dispersed home ranges would still spend a small amount of time at risk even when
325 their home ranges are centered more than 900 m inside the FPA (Fig. 4).

326 Life-history and environmental drivers of risk.

327 For cod, the probability of being at risk varied over the year, but only for fish moving close
328 to the FPA border (0-150 m) (Fig. 5; Table S3). For those fish, the probability of being at risk was
329 maximum in winter, on week 12 ($p=0.39$) and minimum in autumn, on week 46 ($p=0.05$). The
330 opposite pattern was suggested for ballan wrasse (Fig. 5; Table S3), with maximum probability of
331 being at risk in late summer around week 34 ($p=0.71$) and minimum in spring, on week 18
332 ($p=0.13$). No relevant seasonal patterns were observed for cod and ballan wrasse moving beyond
333 150 m from the FPA border (Fig. 5; Table S3). Body size was not a significant predictor of the
334 probability of being at risk in any of the models ($p>0.776$).

335 Fitness consequences of time at risk.

336 We found a significant positive effect of time at risk on the probability of being fished
337 outside the FPA (Regression coefficient: 3.160; Hazard ratio: 23.56; Hazard ratio CI: 6.45-86.07;
338 Hazard ratio SE: 0.66; Z-value: 4.78; $p\text{-value}<0.001$). Predictions from the model showed a
339 reduction in survival probability of 10.2%, 21.2% and 40.78% after 500 days since tagging for cod
340 spending 25%, 50% and 75% of time outside the FPA, respectively (Fig. 6).

341 **Discussion**

342 This study revealed that the level of protection granted by a fully protected area (FPA) to
343 a fish community is strongly dependent on how individuals use the available space. Interestingly,
344 we show that the use of space varies consistently among individuals. For individuals moving
345 inside the FPA, having larger, more dispersed home ranges closer to the border increased the
346 chances of being at risk outside the reserve. For individuals moving outside the FPA the opposite
347 pattern was seen. We also showed that the protection afforded by an FPA can vary over the year
348 in response to seasonal variation in home range properties. Last, we show that time at risk is
349 associated with reduced fitness, seen as an increased probability of being fished outside the FPA.
350 Here, we discuss the potential implications of these findings from an ecological, evolutionary and
351 conservation perspective.

352 In spite of all but one individual being tagged inside the FPA and having home ranges
353 sizes much smaller ($\sim 1/5^{\text{th}}$) than the FPA, only 25% on average of the tagged population spent
354 the whole time under protection. This suggests that home range size explains only a small part
355 of the probability of being at risk, and it is thus important to understand other factors that make

356 individuals move across FPA borders. This finding somewhat challenges the general assumption
357 that MPA size should be informed by the home range size of the species or populations that are
358 the target of protection (Kramer & Chapman 1999; Krueck *et al.* 2018). Typically, the minimum
359 recommended MPA size for each species has been calculated as twice the average home range
360 size of the protected populations (in all directions) to ensure that the reserve includes the entire
361 home range of at least one individual, and likely many more where individuals have overlapping
362 home ranges (Kramer & Chapman 1999; Green *et al.* 2015; Di Franco *et al.* 2018). Our study
363 found that cod with home ranges larger than 75 ha, corresponding to approximately half the size
364 of the Tvedestrand FPA, will be exposed to certain extent to the fishery no matter where the home
365 range is located. This suggests that the Tvedestrand FPA cannot fully protect home ranges larger
366 than ~75 ha, supporting the perception that for any MPA, there is a maximum home range size
367 than can be fully protected (as Moffitt *et al.* 2009 suggest).

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

378 Given the pivotal role of home range location for MPA effectiveness, it is important to
379 understand what are the factors that determine where individuals establish their home ranges.
380 The distribution of habitats is likely important, which highlights the need for considering habitat
381 use and habitat selection by the different species, and how habitats are distributed inside MPAs
382 (Freitas *et al.* 2016). Importantly, habitat distribution may also explain the shape of the home
383 ranges, especially when the home range size is large relative to the dimension of the patches of
384 suitable habitat. This is the case of the Tvedestrand fjord where patches of suitable habitats for
385 the three species are rather small and distributed around islets and along the shoreline (Freitas

386 *et al.* 2016, 2021), which may facilitate movements across the FPA border. Individuals in our
387 study greatly varied in their home range shape, with many of them possessing a very dispersed
388 home range. Typically, such variation in home range shape has not been considered in models
389 assessing the effectiveness of MPAs (Moffitt *et al.* 2009; Krueck *et al.* 2018). Our results suggest
390 that relaxing this simplification may have important consequences for our understanding of MPA
391 effectiveness.

392 We showed that, for cod and ballan wrasse, the seasonal variation in the probability of
393 being at risk mirrored the seasonal variation in home range size. In contrast, no seasonal variation
394 in home range size or time at risk was observed for pollack. This suggest strong links between
395 species' life histories and temporal dynamics of protection. In the case of cod, maximum risk was
396 observed in winter (week 12) which coincides with the peak spawning season (Ciannelli *et al.*
397 2010). Larger mobility in winter by fish living close to the FPA border might be related to
398 displacements to spawning grounds outside the FPA. In fact, Ciannelli *et al.* (2010) detected areas
399 of high concentration of cod eggs close to the Tvedestrand FPA border. As sea temperature rises
400 in summer and autumn, cod may be forced to reduce their mobility due to unsuitable thermal
401 conditions in shallow waters that restricts cod to deeper areas (Freitas *et al.* 2015, 2016).
402 Interestingly, this reduction in mobility and time at risk coincides with a seasonal peak in cod
403 recreational fishing in the study area (Kleiven *et al.* 2016), suggesting that the FPA is more
404 effective protecting cod living inside the FPA when more people is trying to fish them. In the case
405 of ballan wrasse, the suggested reduced risk in spring (week 18) may also be associated with
406 spawning, which occurs between April and June in Norway (Muncaster *et al.* 2010). During
407 spawning, ballan wrasse reduce their activity levels (Villegas-Ríos *et al.* 2014) and males display
408 parental care and high site fidelity (Sjölander *et al.* 1972; Mucientes *et al.* 2019). Note that the
409 ballan wrasse may change sex when reaching 34-41 cm (Muncaster *et al.* 2013) so some of the
410 fish in our study were likely males. As the sea warms in late summer, ballan wrasse increase their
411 activity levels (Villegas-Ríos *et al.* 2014), likely explaining more frequent crossings of the FPA
412 border.

413 For cod, we found that increased time at risk translated into increased fishing mortality.
414 This suggests that in populations moving within or around an FPA, fisheries-induced selection
415 could be acting on home range characteristics such as size or shape which vary consistently

416 among individuals. For instance, for any individual with a home range centered inside the FPA,
417 having a larger home range will increase its time at risk and thus reduce its fitness. This might
418 alter selection acting on home range size as compared to a scenario of no protection, where home
419 range size may not always be related to capture probability (Alós *et al.* 2012, 2016). To the extent
420 that home range properties are intrinsic to each individual (i.e. have a genetic basis), spillover
421 fisheries may result in evolutionary changes within the protected populations by eroding the fish
422 that live closer to the FPA border and have larger home ranges (Villegas-Ríos *et al.* 2017a).
423 Although heritability of home range properties have not yet been demonstrated, our repeatability
424 estimates of home range size and shape add to an increasing body of evidence showing that
425 many aspects of the spatial ecology of fishes are repeatable (Harrison *et al.* 2014, 2019; Alós *et*
426 *al.* 2016; Villegas-Ríos *et al.* 2017b). This strongly suggest that there is an underlying heritable
427 component (Dingemanse & Dochtermann 2012). Note that we conducted our study in a semi-
428 enclosed fjord, where the FPA had a small connection to the buffer and the open areas, increasing
429 the probability that individuals remained within FPA borders. While our framework is valid for any
430 type of MPA, we acknowledge that more open MPAs (e.g. coastal or offshore MPAs) may provide
431 less protection to local populations increasing the chances that individuals are exposed to the
432 fishery and therefore amplifying the aforementioned fitness consequences.

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

442 In conclusion, our study provides clear links between individual fish behaviour, fisheries-
443 induced selection and the effectiveness of protected areas. These links highlight the importance
444 of intraspecific trait variation for understanding the spatial dynamics of populations and its
445 applications. It is not our intention to provide basic management considerations. Rather, our study

446 could inspire more specific aspects of MPA monitoring and design. Specifically, we advocate for
447 investigating among-individual variation and consistency in behaviour within the focal populations.
448 Whereas average values can provide a first insight into the degree of movement of a particular
449 species, our study shows that individuals typically vary in their mobility, with major consequences
450 for protection and survival. Considering the individual variation in behaviour and the associated
451 fitness consequences will therefore contribute towards addressing the evolutionary dimension
452 MPAs (Baskett & Barnett 2015; Arlinghaus *et al.* 2017; Villegas-Ríos *et al.* 2017a).

453

454

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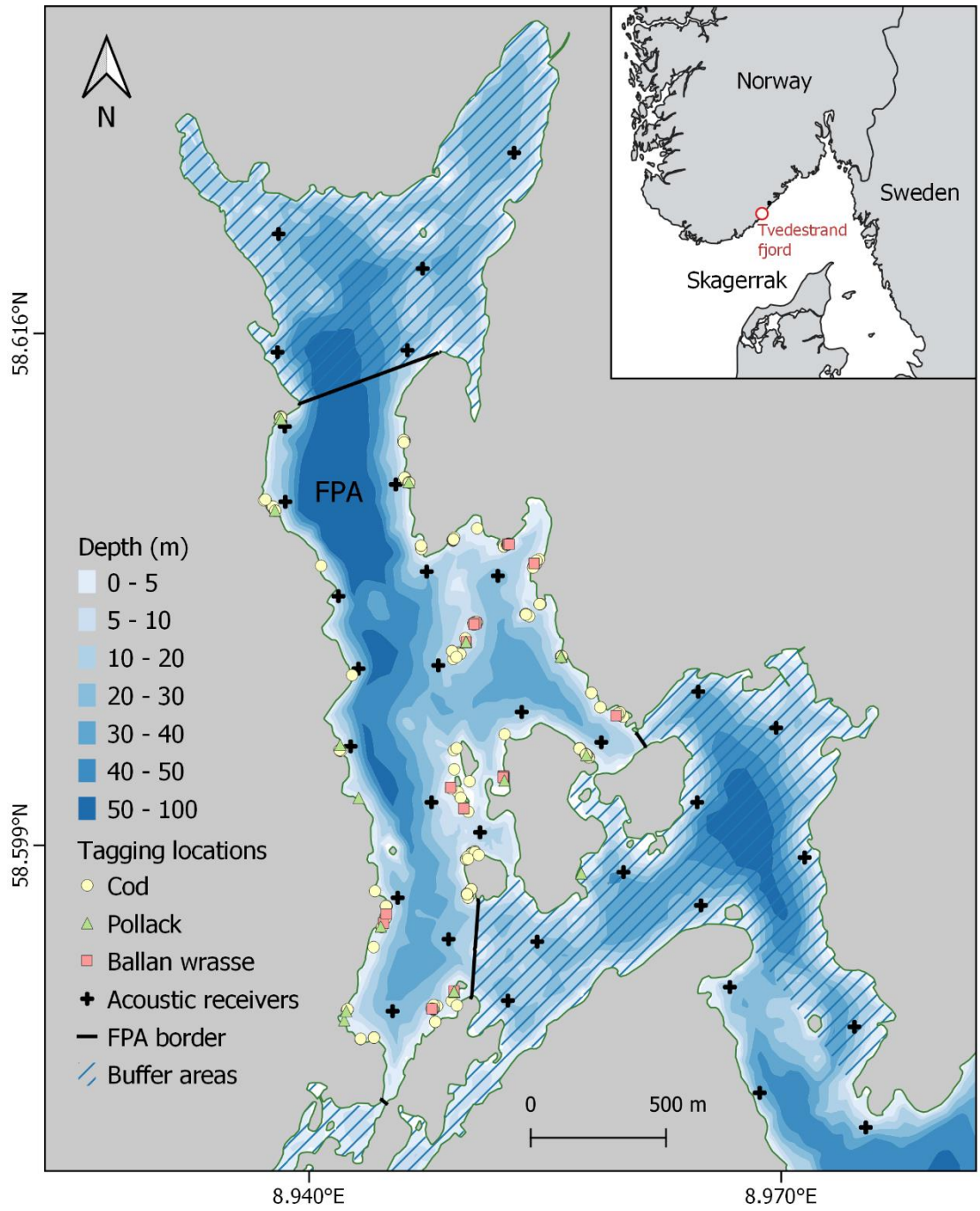
627 **Table 1. Summary of the characteristic of the individuals tracked in this study.** Information
 628 includes total number of individuals tagged per year (n), mean (minimum, maximum) body size
 629 (TL) and mean (minimum, maximum) tracking time (TT).

	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)

630

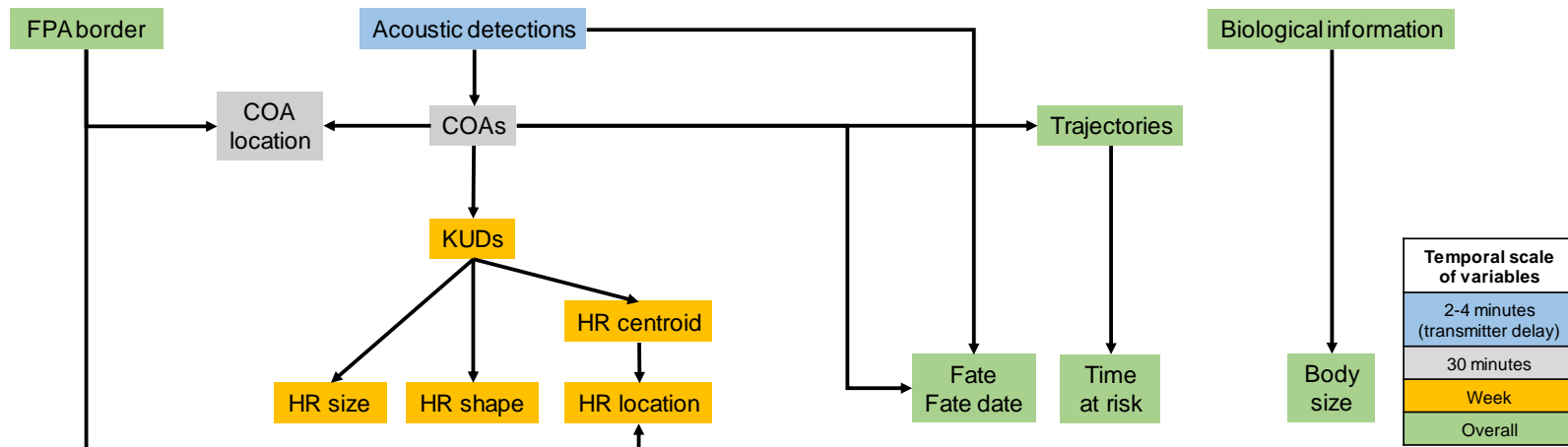
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632 **Figure 1.** Map of the study area showing the location of the 33 Vemco VR2W receivers in
 633 Tvedestrand fjord, the tagging location of the different individuals and the borders of the fully
 634 protected area.
 635



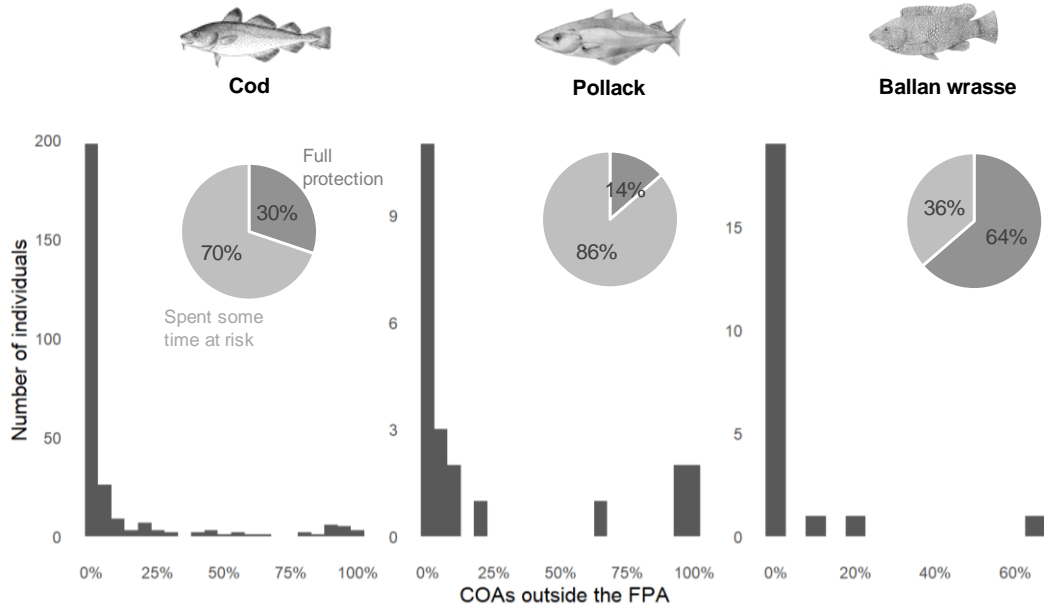
636

637 **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
 638 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.
 639 COA= centre of activity; KUD=kernel utilization distribution; FPA= fully protected area; HR= home range. For details on how each variable was computed,
 640 please see Material and Methods section.



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

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

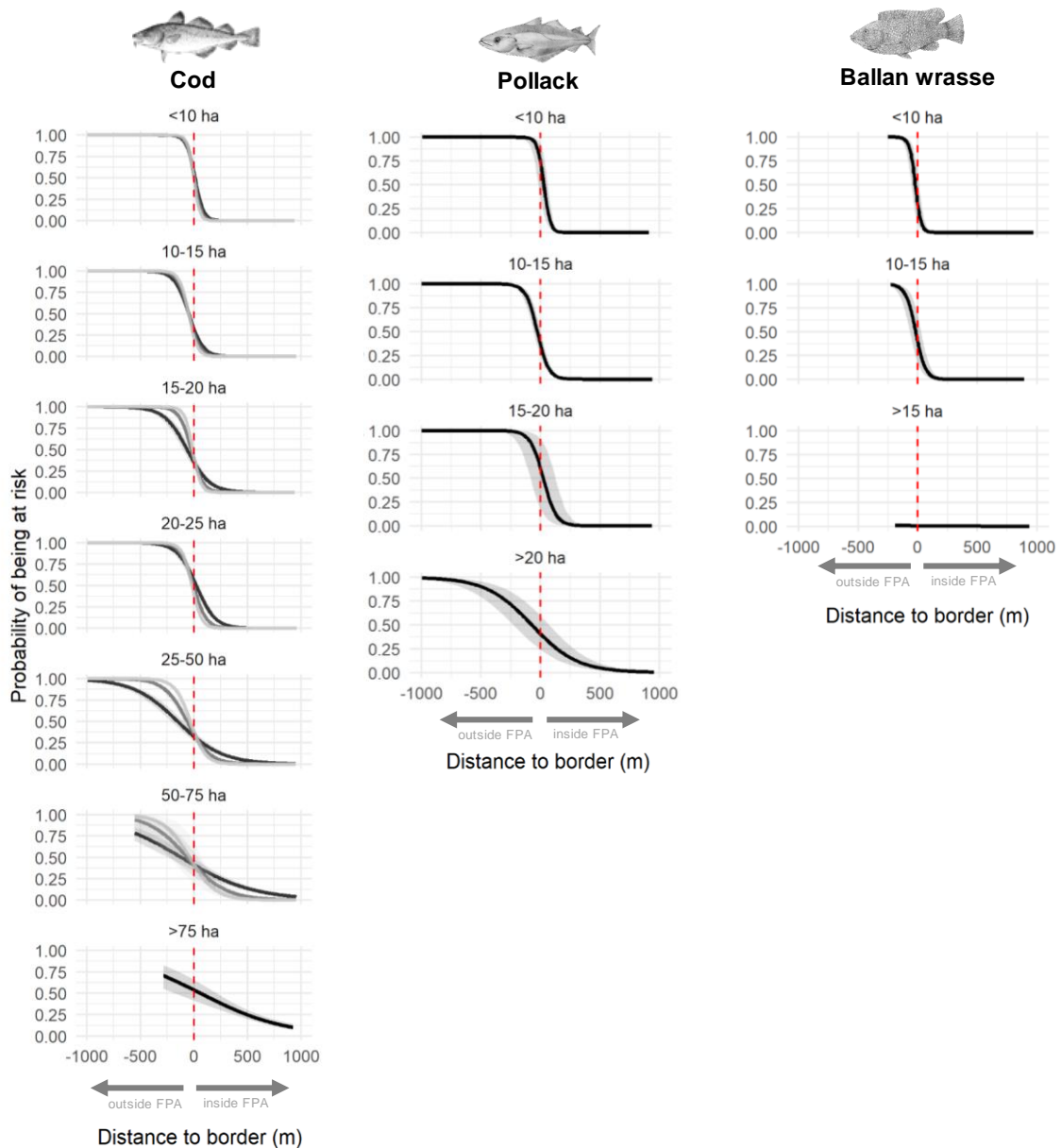


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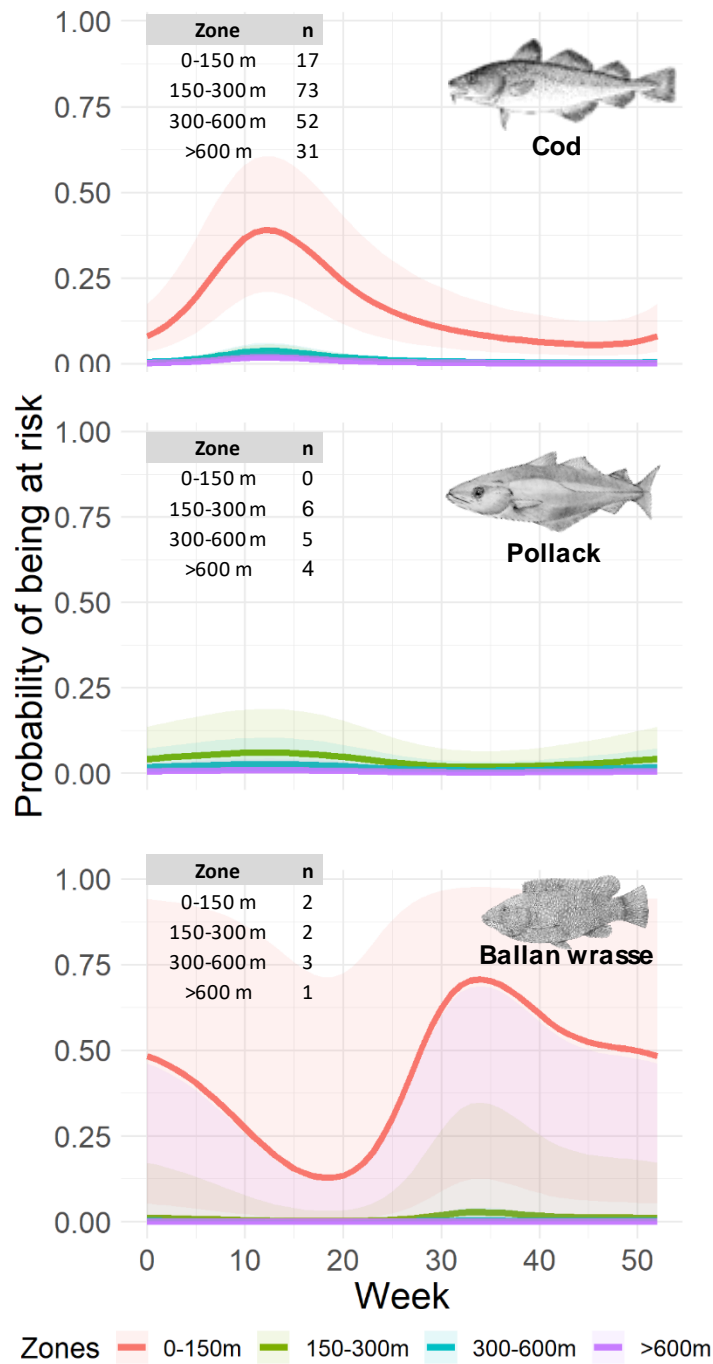
649 **Figure 4. Predicted effect of home range size, location and shape on the probability of**
 650 **being at risk.** The plots show the predicted logistic relationship between the location of the
 651 centroid of the home range in relation to the border of the fully protected area (FPA; x-axis) and
 652 the probability of being at risk (y-axis). The relationship is provided separately for the different
 653 home range size classes as defined in the main text. Besides, in the case of cod, the different
 654 coloured lines represent three different shapes of the home range (light grey= compacted,
 655 grey= intermediate, dark grey=dispersed), except in the last panel (50-75 ha) where home
 656 range shape was not included in the model. The vertical red dashed lines represent the border
 657 of the FPA.



658

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

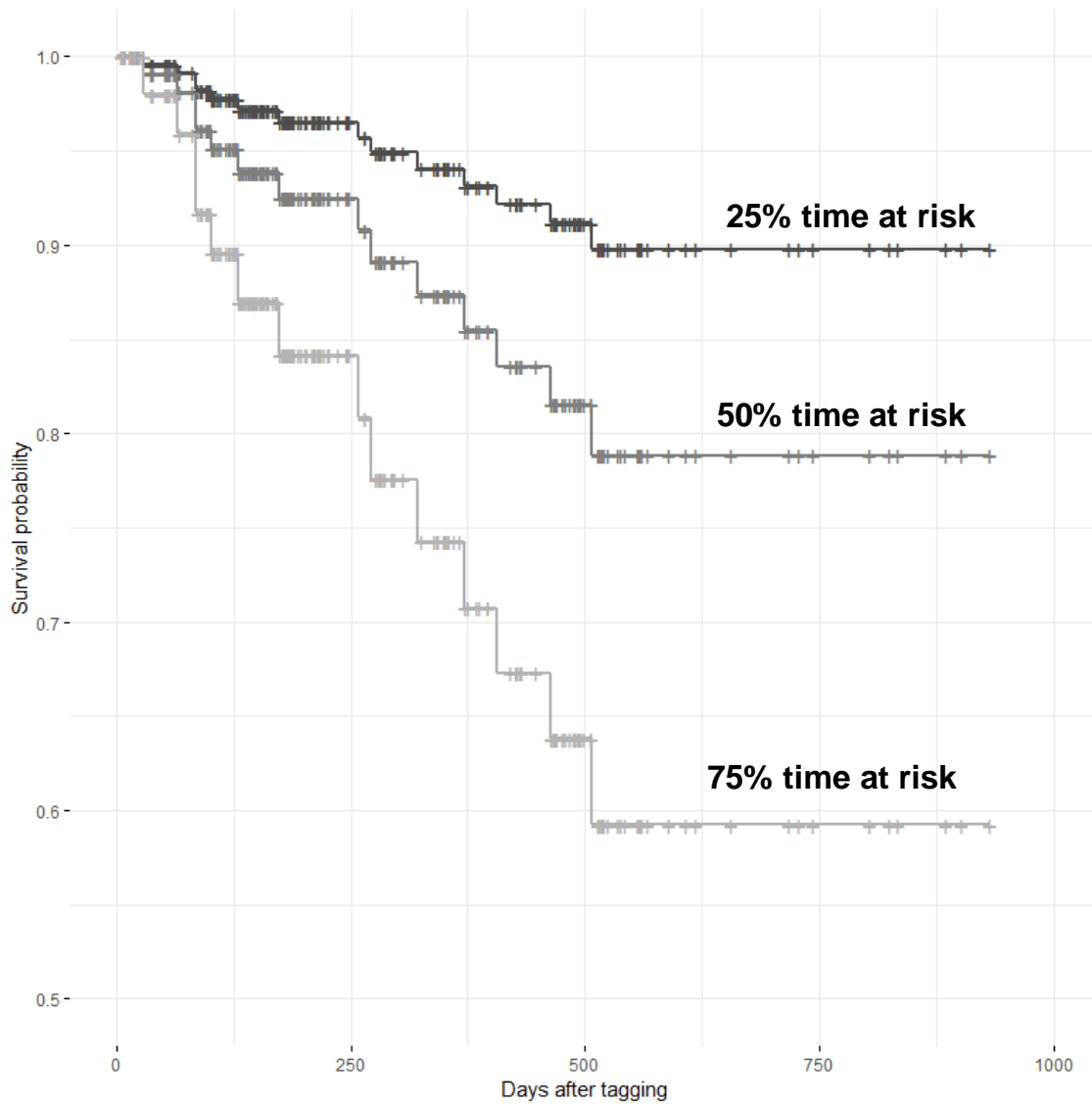
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666 **Fig. 6. Fitness consequences of being at risk.** Survival probability over time of cod spending
667 25%, 50% and 75% of the time at risk as predicted from a Cox proportional hazards regression
668 model. Note that the y-axis starts at 0.5.



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