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1 **Scaling marine fish movement behaviour from individuals to populations.**

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6
7 **Running Head:** Scaling fish movement behaviour.

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Abstract

1. Understanding how, where and when animals move is a central problem in marine ecology and conservation. Key to improving our knowledge about what drives animal movement is the rising deployment of telemetry devices on a range of free-roaming species. An increasingly popular way of gaining meaningful inference from an animal's recorded movements is the application of hidden Markov models (HMMs), which allow for the identification of latent behavioural states in the movement paths of individuals. However, the use of HMMs to explore the population-level consequences of movement are often limited by model complexity and insufficient sample sizes.
2. Here, we introduce an alternative approach to current practices and provide evidence of how the inclusion of prior information in model structure can simplify the application of HMMs to multiple animal movement paths with two clear benefits: (1) consistent state allocation and (2) increases in effective sample size.
3. To demonstrate the utility of our approach we apply HMMs and adapted HMMs to over 100 multivariate movement paths consisting of conditionally dependent daily horizontal and vertical movements in two species of demersal fish: Atlantic cod (*Gadus morhua*; n=46) and European plaice (*Pleuronectes platessa*; n=61).
4. We identify latent states corresponding to two main underlying behaviours: resident and migrating. As our analysis considers a relatively large sample size and states are allocated consistently, we use collective model output to investigate state-dependent spatio-temporal trends at the individual- and population-level. Specifically, we show how both species shift their movement behaviours on a seasonal basis and demonstrate population space-use patterns that are consistent with previous individual-level studies.

48 5. Tagging studies are increasingly being used to inform stock assessment models, spatial
49 management strategies and monitoring of marine fish populations. Our approach provides
50 a promising way of adding value to tagging studies because inferences about movement
51 behaviour can be gained from a larger proportion of datasets, making tagging studies more
52 relevant to management and more cost effective.

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55 **Keywords:** Atlantic cod, data storage tags, European plaice, hidden Markov modelling,
56 movement behaviour, population-level patterns, priors.

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82 1. **Introduction**

83

84 The spatial management of the marine world requires in-depth information about how animals
85 move, when they move and where they move to. Key to increasing our understanding of species
86 space use, movement patterns, and how individuals interact with the environment they inhabit, is
87 the rising deployment of small and reliable data loggers and transmitters on free-roaming marine
88 animals (Costa, Breed, & Robinson, 2012; Hussey et al., 2015; Hays et al., 2016). Capable of
89 recording a range of movement metrics, including horizontal and vertical movement alongside
90 basic environmental information such as water temperature, salinity and ambient daylight, these
91 devices have revolutionized our understanding of fundamental ecology (Hussey et al., 2015),
92 documented ocean-wide dispersal events (Block et al., 2011), highlighted areas that are essential
93 for species survival (Raymond et al., 2015) and even allowed us to test the effectiveness of current
94 conservation policies (Scott et al., 2012; Pittman et al., 2014).

95

96 One of the main motivations for animal-borne telemetry studies is that by understanding individual
97 movement behaviour, we might infer the population-, species- and community-level consequences
98 of movement (Block et al., 2011; Wakefield et al., 2011; Raymond et al., 2015; Hindell et al.,
99 2016). This is especially true in marine systems, as individual observations provide our only
100 insight into the otherwise unobservable. Achieving this scaling of inference from individual
101 movement patterns to population dynamics requires two important components. The first is an
102 adequate sample size (number of individuals) to address the ecological question of interest
103 (Hebblewhite & Haydon, 2010) and second, a statistical means by which we gain meaningful

104 inference at the individual- and population-level from a finite sample of individuals (e.g. Langrock
105 et al., 2012; McClintock, Russell, Matthiopoulos, & King, 2013; Jonsen, 2016).

106

107 The issue of sample size has been extensively discussed, especially when considering how
108 movement studies can inform marine conservation and spatial management (Hebblewhite &
109 Haydon, 2010; McGowan et al., 2017; Nguyen et al., 2017; Ogburn et al., 2017). Tags can be
110 expensive (McGowan et al., 2017), are liable to occasional failure or loss and often result in
111 individual pathways that are data-poor or have a low number of observations. As a result, meeting
112 the minimum sample size of 20+ individuals when making simple statistical comparisons between
113 populations is uncommon (Hebblewhite & Haydon, 2010), with even greater numbers needed
114 when testing for the effects of age, sex and species identity (Lindberg & Walker, 2007). In the
115 absence of a collaborative effort across multiple institutions (e.g. Block et al., 2011; Hindell et al.,
116 2016), a significant increase in funding or a community wide shift to data sharing (e.g. via online
117 data repositories like Movebank - Kranstauber et al., 2011); it would appear that the most viable
118 route towards robust population-level inferences are approaches that make the most of the tagging
119 data we already have.

120

121 Among the many methodological developments that utilize movement data to answer ecological
122 questions, hidden Markov models and hidden semi-Markov models have taken centre stage (e.g.
123 McKellar et al., 2015; DeRuiter et al., 2016; Michelot et al., 2016; Towner et al., 2016). Favoured
124 because they match our intuitive understanding that movement is governed by switches in an
125 animal's motivation (Patterson et al., 2017), HMMs provide a computationally efficient means of

126 objectively classifying movement into discrete states, with different statistical properties,
127 indicating differences in underlying behaviour (Langrock et al., 2012).

128

129 HMMs have been fitted to multiple individual pathways simultaneously in both the frequentist
130 (e.g. Langrock et al., 2012; McKellar et al., 2015) and Bayesian statistical paradigms (McClintock
131 et al., 2013; Jonsen, 2016). However, these approaches are typically implemented by specialist
132 statisticians and require the coupling of HMM and hierarchical structures, producing a hierarchical
133 Hidden Markov model (HHMM). The alternative is the use of HMMs or other state-space
134 approaches that fit on an individual by individual basis (e.g. Jonsen, Myers, & James, 2007;
135 Michelot et al., 2017). This latter, more frequently used approach has its advantages, the most
136 notable being an ease of use for statisticians and biologists alike. Fitting per individual also has its
137 disadvantages. The first is that it requires individual movement paths that are suitably data-rich to
138 achieve model convergence, imposing even stricter restrictions on sample size. The second is a
139 distinct lack of any formal process by which state one in animal A is ensured consistency with
140 state one in animal B. This lack of consistency means that estimated parameters can readily inform
141 individual-level movement studies but will result in tricky interspecific and intraspecific
142 comparisons, limiting a researcher's ability to ask *post-hoc* population-level questions of their
143 data.

144

145 Our objective is to introduce an alternative framework that uses HMMs to overcome the described
146 limitations of individually fitted HMMs whilst maintaining their heralded ease of use advantages.
147 Our approach combines an N -state HMM and several hierarchical structures but bypasses the need
148 to integrate over the random effects (as in HHMMs; Langrock et al., 2012) by using information

149 we gain from our data-rich pathways as *a priori* approximations of each states movement
150 parameters. Doing so not only allows us to achieve coherent individual- and population-level state
151 classification, but also ensures that we maximise our sample size by gaining meaningful inference
152 from our data-poor and data-rich movement paths.

153

154 To illustrate our approach, we apply it to a real ecological problem – quantifying seasonal space
155 use patterns in Atlantic cod (*Gadus morhua*) and European plaice (*Pleuronectes platessa*) in the
156 North Sea and English Channel. Both Atlantic cod and European plaice have significant
157 commercial and conservation value and as a result have been the subject of several long-term
158 tagging programs (e.g. Righton, Metcalfe, & Connolly, 2001; Hunter, Metcalfe, Arnold, &
159 Reynolds, 2004; Hunter, Metcalfe, O’Brien, Arnold, & Reynolds, 2004; Hobson, Righton,
160 Metcalfe, & Hays, 2007, 2009). Drawing on this, the rest of this paper considers a case study of
161 107 individual bivariate movement paths, many of which (n=73) have limited observations and/or
162 lack clear biological signals. Our findings demonstrate clear spatio-temporal patterns in the
163 movement behaviour of either species that are consist with individual-level studies (Hunter,
164 Metcalfe, Arnold, et al., 2004; Hunter, Metcalfe, O’Brien, et al., 2004; Hobson et al., 2007, 2009;
165 Neat et al., 2014). Furthermore, by analyzing a relatively large dataset, we provide a unique insight
166 into how differing sub-stocks of cod and plaice shift their behaviour on a seasonal basis, with clear
167 consequences for fisheries management and conservation.

168

169 2. Materials & Methods

170

171 2.1. Case study data

172

173 Movement paths were taken directly from the deployment of data storage tags (DSTs) on free-
174 roaming fish in the North Sea or English Channel. The dataset includes 107 individuals from two
175 species of European demersal fish: Atlantic cod (n=46) and European plaice (n=61). All fish were
176 tagged and released between December 1996 and June 2011. Fish were broadly separated into sub-
177 stocks based on release location (see Figure 1) and displayed considerable variation in movement
178 path duration (Table S1).

179

180 Each DST was programmed to record depth (m) at 10-minute intervals for the duration of
181 deployment. The first two weeks and the last day of every time series were excluded to remove
182 any erroneous or irregular measurements associated with release and recapture events as per
183 Hobson et al., (2007). For details of tag type, fish catchment, tag implantation and measurement
184 accuracy see Righton et al. (2010; *Gadus morhua*) or Hunter, Metcalfe, Arnold, et al. (2004;
185 *Pleuronectes platessa*).

186

187 Each movement path is a bivariate time series of horizontal and vertical movement per day. Net
188 vertical movement (m day^{-1}) of each fish was taken directly from the raw DST data by calculating
189 the absolute difference between corresponding 10-minute depth measurements and summing the
190 values for each day at liberty. Horizontal movement (m day^{-1}), in comparison, was inferred
191 indirectly from the depth data in a two-step approach. First, daily geolocation estimates were
192 produced via a Fokker-Planck-based method that combines Metcalfe & Arnold's (1997) tidal
193 location method and a Bayesian state-space model (see Pedersen, Righton, Thygesen, Andersen,
194 & Madsen 2008 for model details). The straight-line distance between daily geographic estimates

195 (commonly referred to as ‘step-length’) was then calculated using the Great Circle equation. Both
196 vertical (v) and horizontal (h) movement metrics were log (natural log) transformed prior to model
197 implementation. Only time series that were longer than 40+ days and had complete depth
198 recordings were used in this study. For descriptions of horizontal and vertical movement in
199 Atlantic cod and European plaice see Hunter, Metcalfe, Arnold, et al. (2004), Hunter, Metcalfe,
200 O’Brien, et al. (2004) and Hobson et al. (2007; 2009).

201

202 *2.2. The model*

203

204 Previous individual-level studies demonstrate that Atlantic cod and European plaice display
205 periods of high activity while in the water column punctuated by periods of relatively low activity
206 while on the seabed (Metcalfe, Hunter, & Buckley, 2006; Righton et al., 2010). Thus, we consider
207 a discrete 2-state HMM. We label state one as ‘resident’ (R), representing periods of time with low
208 movement rates. We label state two as ‘migrating’ (M), representing a much more active phase
209 where movement rates in the horizontal and vertical dimension are greatly increased. As in all
210 attempts to infer behaviour from movement observations, state labels must be interpreted with care
211 as they provide simplified proxies of unobserved behavioural modes, not direct equivalents
212 (Patterson et al., 2017).

213

214 For a movement path of length T , it is assumed that an underlying, non-observed state sequence
215 S_1, \dots, S_T , taking values in $\{R, M\}$ describes the persistence within and stochastic switching
216 between states. The time varying evolution of this state process takes the form of a (first-order)
217 Markov chain, with transition probability matrix Γ

218

$$219 \quad \Gamma = \begin{pmatrix} \gamma_{R \rightarrow R} & \gamma_{R \rightarrow M} \\ \gamma_{M \rightarrow R} & \gamma_{M \rightarrow M} \end{pmatrix} \quad [1]$$

220 and

$$221 \quad \gamma_{j \rightarrow k} = \Pr(S_{t+1} = k | S_t = j) \quad [2]$$

222

223 for any j, k in $\{R, M\}$. Given a state j at time t the observation x_t is assumed to be drawn from a
224 multivariate normal distribution (MVN):

$$225 \quad x_t \sim MVN(\mu_j, \Sigma_j) \quad [3]$$

226 with

$$227 \quad \mu_j = \begin{pmatrix} \mu_{jH} \\ \mu_{jV} \end{pmatrix} \quad [4]$$

228 and

$$229 \quad \Sigma_j = \begin{pmatrix} \sigma_{jH}^2 & \rho_j \sigma_{jH} \sigma_{jV} \\ \rho_j \sigma_{jH} \sigma_{jV} & \sigma_{jV}^2 \end{pmatrix} \quad [5]$$

230

231 and H and V represent movements made in the horizontal and vertical dimension, respectively.

232 Thus, the complete-data likelihood given a state sequence S_1, \dots, S_T is

233

$$234 \quad \omega_{S_1} \phi_{S_1}(x_1) \gamma_{S_1 \rightarrow S_2} \phi_{S_2}(x_2) \dots \gamma_{S_{T-1} \rightarrow S_T} \phi_{S_T}(x_T) \quad [6]$$

235

236 where the row vector ω is the Markov chain initial state probability (which we assume to be

237 uniform at $t=1$) and ϕ_j refers to the multivariate normal density stated in equation 3. We allow

238 distinct parameters for each fish, indexed by $i = 1, \dots, 107$, and write these as Γ^i , μ_j^i and Σ_j^i .

239

240 In practice, standard HMM algorithms allow us to calculate the actual likelihood, when the states
241 are unobserved, very efficiently by integrating over all possible state sequences using the forward
242 algorithm (Zucchini, MacDonald, & Langrock, 2016). Framing the model in this way enables us
243 to conduct parameter estimation using a Bayesian approach, by numerically maximising the
244 posterior density. The classification probability of each state at t is then determined using the
245 backward smoothing algorithm (Zucchini et al., 2016). More details for how the efficient HMM
246 machinery can be used to conduct statistical inference are given in Zucchini et al. (2016), for the
247 particular case of animal movement modelling see Patterson et al. (2017). For our case study, we
248 used the R optimisation routine *optim* to numerically maximize the log posterior density. State
249 allocation is carried out by selecting the most likely state at each time point separately.

250

251 Periods of relative inactivity (low h and v movement rates) can persist for 3-5 months in either
252 species (Metcalf et al., 2006; Righton et al., 2010). To accommodate this persistence within state,
253 we have imposed a prior penalty term on the transition probabilities, such that

254

$$255 \quad \gamma_{11} \sim \text{beta}(\alpha, \beta) \quad [7]$$

256 and

$$257 \quad \gamma_{22} \sim \text{beta}(\alpha, \beta) \quad [8]$$

258

259 where $\alpha = 99$ and $\beta = 1$. This prior, termed here after as the transition probability prior, is designed
260 to ensure that states R and M correspond to strong seasonal shifts in movement behaviour and not
261 day-to-day fluctuations.

262

263 2.3. *Classifying fish movements*

264

265 We apply the model described in section 2.2. to all 107 individual movement paths, such that each
266 fish gets its own parameter set. Each parameter set consists of 12 estimated parameters, two
267 transition probabilities and 2 sets of 5 parameters describing the mean (μ_j) and covariance (Σ_j) of
268 each state. A total number of 24,624 days (Atlantic cod = 9290 days; European plaice = 15,334
269 days) were considered. As expected, the resulting state sequences are predominately made up of
270 two clearly defined behavioural modes – one more active and one less active (see Figure S1 and
271 S2 for example output). However, the parameters describing the numerical structure of these
272 modes showed great variation among fish, with no clear consistency. Moreover, a handful of
273 movement paths failed to achieve model convergence, as an upper threshold of observations is
274 needed for robust parameter estimation (Patterson, Basson, Bravington, & Gunn, 2009).

275

276 To avoid the wasteful removal of valuable data or a tedious *post-hoc* description of the individual
277 variation that exists in the HMMs output, we adopted an alternative approach. Based on the
278 selection criteria outlined in Figure S3, we select model output from 34 fish (Atlantic cod, n=11;
279 European plaice, n=23) spread evenly across the five sub-stocks (Table S2). We then calculate
280 summary statistics (means m and variances δ) that describe the numerical structure of the two
281 states (Figure S4). These summary statistics are used to construct Gaussian distributions (Figure
282 2), $N(m, \delta)$ where m and δ are dimension (h or v) d , state j and species specific given the selected
283 sample. These informative distributions (4 per species), termed here after as priors on the model's

284 movement parameters, are then introduced directly into the HMMs likelihood function, such that
285 equation 6 is multiplied by

286

$$287 \quad \prod_j \prod_d \phi(\mu_{jd} \mid m_{jd}, \delta_{jd}) \quad [9]$$

288

289 where $\phi(\cdot \mid m, \delta)$ is the Gaussian density with mean m and variance δ . Thus, our informative priors
290 act to constrain the mean parameters of each state during the classification process.

291

292 This adapted approach is applied to the classification of the remaining 73 individual pathways
293 (Atlantic cod, n=35; European plaice, n=38), outputting state sequences that comprise comparable
294 states across all fish. This enables *post-hoc* comparisons to be made at the individual- and
295 population-level with relative ease. For an example of how prior inclusion influences the
296 classification process see Figure S5. Furthermore, demonstrations of how comparable states are
297 across multiple fish (Figure S6) and differences between model fit for one of the data-poor
298 movement paths are provided (Figure S7).

299

300 All HMMs were coded and implemented in R (R Core Team, 2016; see Supplementary
301 Information document 2 for example code). All plots were generated using the *ggplot2* (Wickham,
302 2009) and *ggmap* (Kahle & Wickham, 2013) packages in R (R Core Team, 2016). Bathymetric
303 data was sampled from the General Bathymetric Chart of the Oceans online repository (GEBCO,
304 www.gebco.net), which is a global topographic dataset with a one-minute spatial (1') spatial
305 resolution.

306

307 *2.4. Prior sensitivity analysis*

308

309 When imposing prior distributions in statistical models it is always important to test what influence
310 those priors have on the models' predictions, in our case the model's estimated state sequences.
311 To test the sensitivity of our model to changes in the transition probability prior we varied the α
312 and β values that characterise the priors' beta distribution and re-ran the HMM for all 34 'selected'
313 fish. In test 1 ($\alpha = 49.5$, $\beta = 0.5$) we still expect a behavioural switch to occur at an order of every
314 100 days. However, we approximately double our prior's variance. In test 2 ($\alpha = 49$, $\beta = 1$) the
315 expected rate of switching is halved.

316

317 To test the model's sensitivity to changes in the movement parameter priors, we varied the
318 variances (δs) that describe the spread of each state and re-ran the adapted HMM for 10 randomly
319 selected fish from each species. In test A, we increased all δ values by 10%, reflecting a prior
320 expectation of greater variability between the parameters of individual fish, and in test B we
321 decreased all δ values by 10%, reflecting an expectation of reduced variability. During all re-runs
322 of the adapted HMM (Test A and Test B) the state transition prior is kept constant, therefore
323 ensuring that any change in state is a direct consequence of the changes to the model's movement
324 parameter prior.

325

326 *2.5. Univariate modelling*

327

328 To assess the advantages of using bivariate responses, we also carried out an analysis using a
329 univariate observation model, considering only movements made in the horizontal dimension. The

330 same model for transition probabilities is used as described above. We apply this approach to the
331 34 fish (Atlantic cod, n=11; European plaice, n=23) previously characterized as data-rich
332 movement paths. Reported comparisons reflect the percentage change, if any, in the resultant state
333 sequences for each individual fish.

334

335 *2.6. Inferring population patterns*

336

337 Since population dynamics emerge as the sum of the individuals that comprise the population we
338 used individual movement behaviours to explore spatiotemporal patterns. Annual temporal
339 patterns of movement behaviour were calculated for each species in two ways. First, the daily
340 individual probabilities of each fish being in each state were averaged across all individuals and
341 over each week of the year. Secondly, the proportion of fish classified to each state was calculated
342 by averaging the daily number of fish in each state and smoothing it, again to the weekly time step.
343 Week refers to weeks of the year, starting on the 1st January and ending on the 31st December and
344 is independent of year.

345

346 Patterns of space use while in either state were quantified using utilization distributions (Worton,
347 1989; Kie et al., 2010; Womble & Gende, 2013). For each species and sub-stock, utilization
348 distributions were calculated by pooling all daily horizontal geolocations for specified time periods
349 and spatially binning them into 5km² grid cells (Maxwell et al., 2011; Womble & Gende, 2013).
350 Specified time periods were state dependent and based on a weekly averaged probability of
351 observing a given state across all individuals exceeding 0.5. Successive weeks classified to the
352 same behavioural state were then grouped. In Atlantic cod this meant locations that were classified

353 to a resident state between June – October and locations classified to a migrating state between
354 November – May were used. In European plaice locations classified to a resident state between
355 April – September and locations classified to a migrating state between October – March were
356 used.

357

358 3. Results

359

360 3.1. Individual fish movement

361

362 Mapping the posterior probability of being in a particular state indicated that individual fish from
363 either species switch between periods of highly directed movement when in a migratory state and
364 periods of random and highly localized movements when in the less active resident state (Figure
365 3). Time spent in either state and the transitions between states were shown to vary in space and
366 time and can be linked to certain habitats. For example, cod 1186 spent 197 days (June -
367 November) consecutively in the resident state within the deeper waters of the Celtic Sea and only
368 shifted into a migratory state when transiting through the English Channel. In comparison, plaice
369 1084 undertook long-distance directed movements after its release in the German Bight, spending
370 54 days consecutively in the migrating state before switching to the resident state in the shallow
371 waters of the Central North Sea.

372

373 The majority of individual time series had observations that shifted between resident and migratory
374 states (n=41 Atlantic cod, n=60 European plaice). However, a small number of individuals (n=6)
375 persisted in a single state for the duration of their time series: one European plaice and four Atlantic

376 cod remained in a resident state throughout, whereas the movements of one Atlantic cod were
377 consistently classified to the migratory state. All 6 single state movement paths had short duration
378 times (average movement path duration = 56 ± 21 days) and were released throughout the year
379 (November – May).

380

381 *3.2. Population patterns*

382

383 The mean probability of observing a resident state and the proportion of observations classified to
384 a resident state varied throughout the year (Figure 4). In both species, migratory behaviour
385 dominated throughout the winter and into spring, with the onset of summer signifying a shift in
386 movement behaviour to the resident state. This shift in state occurred earlier in European plaice
387 than in Atlantic cod, with movements of plaice having a higher probability of classification to the
388 slower, less active resident state between late April and September, compared to June through to
389 November in cod.

390

391 The model predicted large variation in average movement rates within each state (Table 1).
392 Horizontal movement rates of plaice tagged and released in the Southern North Sea and German
393 Bight were significantly lower than those tagged in the Central North Sea (resident, Student's *t*-
394 test, $p < 0.001$; migrating, Student's *t*-test, $p < 0.001$). In the resident state, plaice from the Southern
395 North Sea and German Bight moved on average 6.5 km day^{-1} horizontally and between 20.0 - 26.1
396 m day^{-1} vertically compared to 13.9 km day^{-1} horizontally and between 15.6 - 125.8 m day^{-1}
397 vertically in the migratory state. In comparison, plaice tagged in the Central North Sea exhibited

398 much higher horizontal movement rates, moving on average 12.9 km day^{-1} and 19.5 km day^{-1} in
399 the resident and migratory states, respectively.

400

401 Predicted spatial utilization distributions showed that migration occurred throughout the spatial
402 domain, with no clear concentration of migratory activity in either species (Figure 5; Figure S8).

403 In comparison, periods of time spent in a resident state produced clear geographical patches of
404 space use while in certain habitats. These habitats varied with species (Figure 5) and sub-stock

405 (Figure S8), however Southern North Sea cod and plaice both aggregated in the coastal waters off

406 the English mainland. Cod in the English Channel shift to a resident state when in the western

407 mouth of the Channel. In the German Bight, 90% of plaice spent most of their time at liberty within

408 the area, displaying little or no dispersal. Of those plaice tagged in the Central North Sea, 48%

409 were estimated to be in the resident state within the Northern North Sea whilst a further 11 fish

410 undertook southern migrations before shifting to a resident mode in the shallow waters of the

411 Central North Sea.

412

413 *3.3. Prior sensitivity analysis*

414

415 Minimal change in the classification of states was found during prior sensitivity analysis (Table

416 S3). Re-running the HMM with changes to the transition probability prior revealed an average

417 percentage change in state across all individuals of 1.5% in cod and 1.8% in plaice. In comparison,

418 re-running the adapted HMM with changes to the movement parameters priors resulted in a

419 percentage change in state that was on average $<1\%$ in cod and 2.3% in plaice. Such findings

420 demonstrate that the precise details of these priors are not crucial, with state classifications and
421 biologically-important results being robust to fairly large changes in prior parameters.

422

423 *3.4. Distribution of state dwell times*

424

425 In an HMM, the length of time that an individual spends in one state before switching to the other
426 necessarily follows a geometric distribution. Pooling across individuals, we find that these
427 distributions are indeed geometric (see Figure S9 and Figure S10), and so the dynamics of the
428 fitted changes in state are consistent with the Markov nature of the model. Further model
429 assessment is provided by residual plots in Figure S11 and Figure S12.

430

431 *3.5. Comparison to univariate modelling*

432

433 State allocation was found to be different across the two tested observation models. The bivariate
434 model resulted in state sequences that differed from the univariate model in 8.0% and 23.3% of
435 cases in Atlantic cod and European plaice, respectively. This result confirms the need for the
436 bivariate analysis.

437

438 **4. Discussion**

439

440 One of the main objectives of animal movement studies is the scaling of inference about movement
441 behaviours from individuals to populations (Block et al., 2011; Wakefield et al., 2011; Raymond
442 et al., 2015; Hays et al., 2016; Hindell et al., 2016). HMMs (Patterson et al., 2009; McKellar et al.,

443 2015; Michelot et al., 2016) or their Bayesian equivalents (Jonsen et al., 2013; McClintock et al.,
444 2013) provide a powerful way of achieving this objective but only when movement behaviours are
445 identified consistently across multiple individuals. Here we have achieved this consistency by
446 ‘borrowing’ information from a finite sample of individuals and using it to provide our model with
447 data-driven approximations of each state. Using this novel extension to HMM methodology, we
448 investigated spatial and temporal shifts in movement behaviour from a large sample size of
449 bivariate movement pathways. We demonstrated where and when shifts between two ecologically
450 meaningful states are most likely to occur and add further confidence to observations of seasonal-
451 dependence in the movements of commercially important demersal fish. Our biological findings
452 complement and advance current understanding and highlight how our approach has significant
453 utility in the fields of movement ecology and conservation.

454

455 Our approach to behaviour classification has two major advantages. First, it enabled us to gain
456 meaningful inference from 73 (68% of the dataset) additional movement pathways, many of which
457 are data-poor and would otherwise be subject to *post-hoc* removal. This retention of all individual-
458 level information is favorable because it maximised our sample size and lends more information
459 to our analysis. Second, our approach ensures that state labels are allocated consistently across
460 multiple individuals, without resorting to large increases in model complexity. As a direct
461 consequence of these two advantages, we were able to ask population-level *post-hoc* questions of
462 our movement data and provide answers that are meaningful for conservation and spatial
463 management.

464

465 Studies that classify behaviour based on horizontal and vertical movements are rare (but see Breed,
466 Bowen, & Leonard, 2013; Bestley, Jonsen, Hindell, Harcourt, & Gales, 2015; DeRuiter et al.,
467 2016). Here, we have assumed that h_t and v_t are conditionally dependent given latent states, which
468 is a novel addition to the movement ecology literature. Our reasons for doing so are linked to *a*
469 *priori* information about how the species of interest alter their activity levels within an annual
470 cycle (e.g. Hobson et al., 2009). However, we intuitively expect other species occupying three-
471 dimensional environments to exhibit similar degrees of coupling. For example, Bestley et al.
472 (2015) reveal that the directed horizontal movements in multiple Antarctic pinniped species are
473 associated with longer dive durations, whereas an inverted relationship is noted in blue whales
474 (*Balaenoptera musculus*) with perceived shallow foraging behaviours being characterised by
475 shallow dives and short horizontal movements (DeRuiter et al., 2016). Future studies may find
476 similar observation models a powerful tool for investigating the dependences of horizontal and
477 vertical movement rates (Carter, Bennett, Embling, Hosegood, & Russell, 2016).

478

479 Our estimates of average movement rates are consistent with previous work. In cod, horizontal
480 movements rates whilst in the migratory state are shown to be approximately 13.5km day⁻¹ which
481 is comparable to past observations (Hobson et al., 2009) and laboratory studies (Bainbridge, 1957;
482 Videler & Wardle, 1991). In plaice, previous research reports that seven tagged individuals swam
483 on average 255 ± 60.2km during pre-spawning migrations (Hunter, Metcalfe, & Reynolds, 2003).
484 Assuming an average migrating of 2-4 weeks (as noted in Hunter et al., 2003), our estimates of
485 horizontal movement rates between 13-20km day⁻¹ seem reasonable. Therefore, we are confident
486 that our choice of state labels is biologically meaningful for the species in question.

487

488 Much work has considered the horizontal and vertical movements of Atlantic cod (Hobson et al.,
489 2007, 2009) and European plaice (Hunter, Metcalfe, Arnold, et al., 2004; Hunter, Metcalfe,
490 O'Brien, et al., 2004), noting strong seasonal dependence in the movement patterns of individual
491 fish. Here we add confidence to these findings by providing a mechanistic view of how fish switch
492 between two movements modes during their annual cycle. Specifically, we show that cod and
493 plaice are more likely to occupy a resident state during the summer months (April – September in
494 plaice; June – November in cod). These periods are dominated by low horizontal and vertical
495 movement rates, therefore our findings support the hypothesis that both species spend their
496 summer in a sedentary state with minimal activity levels (Metcalfe et al., 2006; Righton et al.,
497 2010). Movement rates then ramp up during the winter and early spring (October – March in
498 plaice; December – May in cod), resulting in a collective shift in state. As in previous studies
499 (Hunter, Metcalfe, O'Brien, et al., 2004; Hobson et al., 2007), we interpret this shift to be reflective
500 of pre-spawning migrations, the onset of spawning and subsequent post-spawning migrations. One
501 limitation of the two-state model considered here is that we cannot directly infer foraging or
502 spawning behaviour. Foraging and spawning events are likely to represent an immediate activity
503 level, with both behaviours involving notable vertical displacement to and from the water column
504 (Hobson et al., 2009). The inclusion of a third immediate state would be a relatively
505 straightforward extension to model structure (see Vermard, Rivot, Mahévas, Marchal, & Gascuel,
506 2010; Peel & Good, 2011; Michelot et al., 2017 for examples of HMMs that consider >2 states).
507 However, it is unlikely that the scale of these vertical excursions is large enough to allow
508 classification at the daily time step. Therefore, we suggest that future studies either deploy more
509 sophisticated tags which are capable of recording more refined information about the underlying
510 movement process (e.g. accelerometers; Leos-Barajas, Photopoulou, et al., 2017) or consider a

511 nested hierarchical HMMs in which vertical and horizontal movements are recorded and classified
512 at differing time scales (e.g. Leos-Barajas, Gangloff, et al., 2017).

513

514 Over the last 70 years, landings data for the North Sea and English Channel demonstrate that catch
515 per unit effort (CPUE) for demersal species is higher during the summer months (Righton,
516 Townhill, & Van Der Kooij, 2009). Such increases in CPUE are undoubtedly linked to changes in
517 the populations' underlying movement behaviour, as time spent on the seabed results in an
518 increased vulnerability to commercial exploitation (Righton et al., 2009). By assuming that time
519 spent in a resident state is linked to sea-bottom dwelling, we show that cod and plaice aggregate
520 in certain habitat types. For example, cod in the English Channel have greatest density in the deeper
521 waters at the western mouth of the English Channel. In contrast, cod and plaice in the Southern
522 North Sea aggregate in coastal waters off the English mainland. We also demonstrate that plaice
523 in the German Bight remain exclusive within this region, suggesting the presence of a sedentary
524 resident population in which fish spawn and forage in the same locality (previously noted in plaice
525 by Hunter, Metcalfe, O'Brien, et al., 2004 and in cod by Neat et al., 2006). Such spatial information
526 is essential for defining multi-species management measures, as strategies typically involve gear
527 restrictions (Moustakas, Silvert, & Dimitromanolakis, 2006) aimed at limiting the exploitation of
528 certain species/life stages and spatial fisheries closures aimed at protecting areas of particular
529 importance for species survival e.g. foraging and spawning grounds (Hunter, Metcalfe, O'Brien,
530 et al., 2004; Righton, Quayle, Hetherington, & Burt, 2007).

531

532 One limitation of our method is the way in which we deal with individual variation. Currently we
533 assume that by analysing the movements of a finite sample of data-rich pathways (n=34) we gain

534 sufficient information about how the mean movement of each state is distributed throughout the
535 population. We then expect the movements of all other individuals to be drawn from one of these
536 distributions and make no attempt to explain any deviance away from this ‘expected’ process. One
537 way to improve our approach and make it more generic would be the inclusion of covariate
538 information (e.g. Phillips, Patterson, Leroy, Pilling, & Nicol, 2015). For example, 4 Atlantic cod
539 were unexpectedly classified solely to a resident state even through their movements occurred
540 throughout the winter (November – April). *Post-hoc* investigations reveal an average body length
541 of ~56cm which lies within the predicted range of length at first maturity (31-74cm; Froese &
542 Pauly, 2017). It is likely that immature fish act differently to their mature conspecifics (Sippel et
543 al., 2015) and that tagging programmes like the one considered here include fish of differing sex
544 and age (Carter et al., 2016). Consideration of these factors is beyond the scope of this paper.
545 However we believe that the inclusion of body length (see Towner et al., 2016 for an ecological
546 example) or other individual covariates within the HMMs likelihood function would provide a
547 fruitful avenue for future research.

548

549 Technological advancements in telemetry devices have led to huge efforts to track the movements
550 of free-roaming marine animals (Hussey et al., 2015; Hays et al., 2016). Tagging data is now seen
551 as a valuable information source for stock assessment models (Sippel et al., 2015), monitoring the
552 effectiveness of conservation efforts (e.g. Raymond et al., 2015; McGowan et al., 2017) and
553 understanding population dynamics across vast spatial scales (e.g. Block et al., 2011; Hindell et
554 al., 2016). However, there is no avoiding the fact that tags are expensive (McGowan et al., 2017),
555 liable to occasional failure and often produce individual pathways that are of limited use (data-
556 poor or a low number of observations). Here we have introduced a methodology that makes the

557 process of scaling up inference about movement behaviours from individuals to population more
558 readily achievable. Moreover, we illustrate how the adoption of our approach can make tagging
559 studies more cost-effective, as inference can still be gained from data-poor movement paths
560 without resorting to redeployment or a renewed effort to secure further funding.

561
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569
570 **Authors' contributions**

571
572 C.A.G, T.A.P. and P.G.B. designed the methodology; C.A.G., P.G.B., J.L.B. and D.A.R.
573 interpreted and analysed the model's output; movement paths were derived and analysed by
574 D.A.R. and S.R.W.; C.A.G., J.L.B., P.G.B., D.A.R. and J.W.P. led the writing of the manuscript;
575 C.A.G. and S.R.W. designed the figures. All authors contributed critically to the drafts and gave
576 final approval for publication.

577
578 **Data and R Code**

579

580 The collated datasets for each fish species including estimated state sequences, geolocation
581 estimates (latitude and longitude) and date stamps can be found on the CEFAS Data Hub
582 (<https://doi.org/10.14466/CefasDataHub.54>). Example R code to run our HMM is included in
583 Supplementary Information document 2 or can be downloaded from GitHub
584 (https://github.com/cagriffiths1/Fish_HMM).

585

586 **Conflict of Interest**

587

588 Authors declare no conflicts of interest.

589

590 **References**

591

592 Bainbridge, B. Y. R. (1957). The speed of swimming of fish as related to size and the frequency
593 and amplitude of the tail beat. *The Journal of Experimental Biology*, 35(1937), 109–133.

594 doi:10.1098/rspb.1971.0085

595 Bestley, S., Jonsen, I. D., Hindell, M. A., Harcourt, R. G., & Gales, N. J. (2015). Taking animal
596 tracking to new depths : synthesizing horizontal-vertical movement relationships for four

597 marine predators. *Ecology*, 96(2), 417–427.

598 Block, B. A., Jonsen, I. D., Jorgensen, S. J., Winship, A. J., Shaffer, S. A., Bograd, S. J., ...

599 Costa, D. P. (2011). Tracking apex marine predator movements in a dynamic ocean. *Nature*,
600 475(7354), 86–90. doi:10.1038/nature10082

601 Breed, G. A., Bowen, W. D., & Leonard, M. L. (2013). Behavioral signature of intraspecific
602 competition and density dependence in colony-breeding marine predators. *Ecology and*

603 *Evolution*, 3(11), 3838–3854. doi:10.1002/ece3.754

604 Carter, M. I. D., Bennett, K. A., Embling, C. B., Hosegood, P. J., & Russell, D. J. F. (2016).
605 Navigating uncertain waters : a critical review of inferring foraging behaviour from location
606 and dive data in pinnipeds. *Movement Ecology*, 4–25. doi:10.1186/s40462-016-0090-9

607 Costa, D. P., Breed, G. A., & Robinson, P. W. (2012). New Insights into Pelagic Migrations:
608 Implications for Ecology and Conservation. *Annual Review of Ecology, Evolution, and*
609 *Systematics*, 43(1), 73–96. doi:10.1146/annurev-ecolsys-102710-145045

610 DeRuiter, S. L., Langrock, R., Skirbutas, T., Goldbogen, J. A., Chalambokidis, J., Friedlaender,
611 A. S., & Southall, B. L. (2016). A multivariate mixed hidden Markov model to analyze blue
612 whale diving behaviour during controlled sound exposures, *arXiv, arX*, 1–26.
613 doi:10.1214/16-AOAS1008

614 Froese, R., & Pauly, D. (2017). FishBase. World Wide Web electronic publication. Retrieved
615 from www.fishbase.org, version (10/2017)

616 GEBCO. (2017). General Bathymetric Chart of the Oceans. Retrieved 17 November 2016, from
617 http://www.bodc.ac.uk/projects/international/gebco/gebco_digital_atlas

618 Hays, G. C., Ferreira, L. C., Sequeira, A. M. M., Meekan, M. G., Duarte, C. M., Bailey, H., ...
619 Thums, M. (2016). Key Questions in Marine Megafauna Movement Ecology. *Trends in*
620 *Ecology and Evolution*, 31(6), 463–475. doi:10.1016/j.tree.2016.02.015

621 Hebblewhite, M., & Haydon, D. T. (2010). Distinguishing technology from biology: a critical
622 review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the*
623 *Royal Society B: Biological Sciences*, 365(1550), 2303–2312. doi:10.1098/rstb.2010.0087

624 Hindell, M. A., McMahon, C. R., Bester, M. N., Boehme, L., Costa, D., Fedak, M. A., ...
625 Charrassin, J. B. (2016). Circumpolar habitat use in the southern elephant seal: Implications

626 for foraging success and population trajectories. *Ecosphere*, 7(5), 1–27.
627 doi:10.1002/ecs2.1213

628 Hobson, V. J., Righton, D., Metcalfe, J. D., & Hays, G. C. (2007). Vertical movements of North
629 Sea cod. *Marine Ecology Progress Series*, 347, 101–110. doi:10.3354/meps07047

630 Hobson, V. J., Righton, D., Metcalfe, J. D., & Hays, G. C. (2009). Link between vertical and
631 horizontal movement patterns of cod in the North Sea. *Aquatic Biology*, 5, 133–142.
632 doi:10.3354/ab00144

633 Hunter, E., Metcalfe, J. D., Arnold, G. P., & Reynolds, J. D. (2004). Impacts of migratory
634 behaviour on population structure in North Sea plaice. *Journal of Animal Ecology*, 73, 377–
635 385.

636 Hunter, E., Metcalfe, J. D., O'Brien, C. M., Arnold, G. P., & Reynolds, J. D. (2004). Vertical
637 activity patterns of free-swimming adult plaice in the southern North Sea. *Marine Ecology
638 Progress Series*, 279, 261–273. doi:10.3354/meps279261

639 Hunter, E., Metcalfe, J. D., & Reynolds, J. D. (2003). Migration route and spawning area fidelity
640 by North Sea plaice. *Proceedings of the Royal Society B: Biological Sciences*, 270, 2097–
641 2103. doi:10.1098/rspb.2003.

642 Hussey, N. E., Kessel, S. T., Aarestrup, K., Cooke, S. J., Cowley, P. D., Fisk, A. T., ...
643 Whoriskey, F. G. (2015). Aquatic animal telemetry: A panoramic window into the
644 underwater world. *Science*, 348(6240), 1255642. doi:10.1126/science.1255642

645 Jonsen, I. D. (2016). Joint estimation over multiple individuals improves behavioural state
646 inference from animal movement data. *Scientific Reports*, 6, 20625. doi:10.1038/srep20625

647 Jonsen, I. D., Basson, M., Bestley, S., Bravington, M. V., Patterson, T. A., Pedersen, M. W., ...
648 Wotherspoon, S. J. (2013). State-space models for bio-loggers: A methodological road map.

649 *Deep Sea Research Part II*, 88–89, 34–46. doi:10.1016/j.dsr2.2012.07.008

650 Jonsen, I. D., Myers, R. A., & James, M. C. (2007). Identifying leatherback turtle foraging
651 behaviour from satellite telemetry using a switching state-space model. *Marine Ecology*
652 *Progress Series*, 337, 255–264.

653 Kahle, D., & Wickham, H. (2013). ggmap: Spatial Visualization with ggplot2. *The R Journal*, 5,
654 144–161.

655 Kie, J. G., Matthiopoulos, J., Fieberg, J., Powell, R. A., Cagnacci, F., Mitchell, M. S., ...
656 Moorcroft, P. R. (2010). The home-range concept: are traditional estimators still relevant
657 with modern telemetry technology? *Philosophical Transactions of the Royal Society B:*
658 *Biological Sciences*, 365, 2221–2231. doi:10.1098/rstb.2010.0093

659 Kranstauber, B., Cameron, A., Weinzerl, R., Fountain, T., Tilak, S., Wikelski, M., & Kays, R.
660 (2011). The Movebank data model for animal tracking. *Environmental Modelling and*
661 *Software*, 26, 834–835. doi:10.1016/j.envsoft.2010.12.005

662 Langrock, R., King, R., Matthiopoulos, J., Thomas, L., Fortin, D., & Morales, J. M. (2012).
663 Flexible and practical modeling of animal telemetry data : hidden Markov models and
664 extensions. *Ecology*, 93(11), 2336–2342.

665 Leos-Barajas, V., Gangloff, E. J., Adam, T., Langrock, R., van Beest, F. M., Nabe-Nielsen, J., &
666 Morales, J. M. (2017). Multi-scale Modeling of Animal Movement and General Behavior
667 Data Using Hidden Markov Models with Hierarchical Structures. *Journal of Agricultural,*
668 *Biological, and Environmental Statistics*, 22(3), 232–248. doi:10.1007/s13253-017-0282-9

669 Leos-Barajas, V., Photopoulou, T., Langrock, R., Patterson, T. A., Watanabe, Y., Murgatroyd,
670 M., & Papastamatiou, Y. P. (2017). Analysis of animal accelerometer data using hidden
671 Markov models. *Methods in Ecology and Evolution*, 8(2), 161–173. doi:10.1111/2041-

672 210X.12657

673 Lindberg, M. S., & Walker, J. (2007). Satellite Telemetry in Avian Research and Management:
674 Sample Size Considerations. *Journal of Wildlife Management*, 71(3), 1002–1009.
675 doi:10.2193/2005-696

676 Maxwell, S. M., Breed, G. A., Nickel, B. A., Makanga-Bahouna, J., Pemo-Makaya, E., Parnell,
677 R. J., ... Coyne, M. S. (2011). Using satellite tracking to optimize protection of long-lived
678 marine species: Olive ridley sea turtle conservation in central africa. *PLoS ONE*, 6(5),
679 e19905. doi:10.1371/journal.pone.0019905

680 McClintock, B. T., Russell, D. J. F., Matthiopoulos, J., & King, R. (2013). Combining individual
681 animal movement and ancillary biotelemetry data to investigate population-level activity
682 budgets. *Ecology*, 94(4), 838–849. doi:10.1890/12-0954.1

683 McGowan, J., Beger, M., Lewison, R. L., Harcourt, R., Campbell, H., Priest, M., ... Possingham,
684 H. P. (2017). Integrating research using animal-borne telemetry with the needs of
685 conservation management. *Journal of Applied Ecology*, 54(2), 423–429. doi:10.1111/1365-
686 2664.12755

687 McKellar, A. E., Langrock, R., Walters, J. R., & Kesler, D. C. (2015). Using mixed hidden
688 Markov models to examine behavioral states in a cooperatively breeding bird. *Behavioral*
689 *Ecology*, 26(1), 148–157. doi:10.1093/beheco/aru171

690 Metcalfe, J. D., & Arnold, G. (1997). Tracking fish with electronic tags. *Nature*, 387, 665–666.
691 doi:10.1038/42622

692 Metcalfe, J. D., Hunter, E., & Buckley, A. A. (2006). The migratory behaviour of North Sea
693 plaice: Currents, clocks and clues. *Marine and Freshwater Behaviour and Physiology*,
694 39(1), 25–36. doi:10.1080/10236240600563404

695 Michelot, T., Langrock, R., Bestley, S., Jonsen, I. D., Photopoulou, T., & Patterson, T. A.
696 (2017). Estimation and simulation of foraging trips in land-based marine predators.
697 *Ecology*, 98(7), 1932–1944. doi:10.1002/ecy.1880

698 Michelot, T., Langrock, R., & Patterson, T. (2016). moveHMM: An R package for the statistical
699 modelling of animal movement data using hidden Markov models. *Methods in Ecology and*
700 *Evolution*, 7, 1308–1315. doi:10.1111/2041-210X.12578

701 Moustakas, A., Silvert, W., & Dimitromanolakis, A. (2006). A spatially explicit learning model
702 of migratory fish and fishers for evaluating closed areas. *Ecological Modelling*, 192, 245–
703 258. doi:10.1016/j.ecolmodel.2005.07.007

704 Neat, F. C., Bendall, V., Berx, B., Wright, P. J., Cuaig, M., Townhill, B., ... Righton, D. (2014).
705 Movement of Atlantic cod around the British Isles: Implications for finer scale stock
706 management. *Journal of Applied Ecology*, 51, 1564–1574. doi:10.1111/1365-2664.12343

707 Neat, F. C., Wright, P. J., Zuur, A. F., Gibb, I. M., Gibb, F. M., Tulett, D., ... Turner, R. J.
708 (2006). Residency and depth movements of a coastal group of Atlantic cod (*Gadus morhua*
709 *L.*). *Marine Biology*, 148, 643–654. doi:10.1007/s00227-005-0110-6

710 Nguyen, V. M., Brooks, J. L., Young, N., Lennox, R. J., Haddaway, N., Whoriskey, F. G., ...
711 Cooke, S. J. (2017). To share or not to share in the emerging era of big data: perspectives
712 from fish telemetry researchers on data sharing. *Canadian Journal of Fisheries and Aquatic*
713 *Sciences*, 74, 1260–1274. doi:10.1139/cjfas-2016-0261

714 Ogburn, M. B., Harrison, A.-L., Whoriskey, F. G., Cooke, S. J., Mills Flemming, J. E., & Torres,
715 L. G. (2017). Addressing Challenges in the Application of Animal Movement Ecology to
716 Aquatic Conservation and Management. *Frontiers in Marine Science*, 4, 70.
717 doi:10.3389/fmars.2017.00070

718 Patterson, T. A., Basson, M., Bravington, M. V., & Gunn, J. S. (2009). Classifying movement
719 behaviour in relation to environmental conditions using hidden Markov models. *Journal of*
720 *Animal Ecology*, 78(6), 1113–1123. doi:10.1111/j.1365-2656.2009.01583.x

721 Patterson, T. A., Parton, A., Langrock, R., Blackwell, P. G., Thomas, L., & King, R. (2017).
722 Statistical modelling of individual animal movement: an overview of key methods and a
723 discussion of practical challenges. *AStA Advances in Statistical Analysis*, 101, 399–438.
724 doi:10.1007/s10182-017-0302-7

725 Pedersen, M. W., Righton, D., Thygesen, U. H., Andersen, K. H., & Madsen, H. (2008).
726 Geolocation of North Sea cod (*Gadus morhua*) using hidden Markov models and
727 behavioural switching. *Canadian Journal of Fisheries and Aquatic Sciences*, 65, 2367–
728 2377. doi:10.1139/F08-144

729 Peel, D., & Good, N. M. (2011). A hidden Markov model approach for determining vessel
730 activity from vessel monitoring system data. *Canadian Journal of Fisheries and Aquatic*
731 *Sciences*, 68, 1252–1264. doi:10.1139/f2011-055

732 Phillips, J. S., Patterson, T. A., Leroy, B., Pilling, G. M., & Nicol, S. J. (2015). Objective
733 classification of latent behavioral states in bio-logging data using multivariate-normal
734 hidden Markov models. *Ecological Applications*, 25(5), 1244–1258. doi:10.1890/14-
735 0862.1.sm

736 Pittman, S. J., Monaco, M. E., Friedlander, A. M., Legare, B., Nemeth, R. S., Kendall, M. S., ...
737 Caldwell, C. (2014). Fish with chips: Tracking reef fish movements to evaluate size and
738 connectivity of Caribbean marine protected areas. *PLoS ONE*, 9(5), e96028.
739 doi:10.1371/journal.pone.0096028

740 R Development Core Team. (2016). A Language and Environment for Statistical Computing. R

741 Foundation for Statistical Computing, Vienna.

742 Raymond, B., Lea, M. A., Patterson, T., Andrews-Goff, V., Sharples, R., Charrassin, J. B., ...
743 Hindell, M. A. (2015). Important marine habitat off east Antarctica revealed by two decades
744 of multi-species predator tracking. *Ecography*, *38*, 121–129. doi:10.1111/ecog.01021

745 Righton, D. A., Andersen, K. H., Neat, F., Thorsteinsson, V., Steingrund, P., Svedäng, H., ...
746 Metcalfe, J. D. (2010). Thermal niche of Atlantic cod *Gadus morhua*: Limits, tolerance and
747 optima. *Marine Ecology Progress Series*, *420*, 1–13. doi:10.3354/meps08889

748 Righton, D. A., Metcalfe, J. D., & Connolly, P. (2001). Different behaviour of North and Irish
749 Sea cod. *Nature*, *411*(90), 2001.

750 Righton, D. A., Quayle, V. A., Hetherington, S., & Burt, G. (2007). Movements and distribution
751 of cod (*Gadus morhua*) in the southern North Sea and English Channel: Results from
752 conventional and electronic tagging experiments. *Journal of the Marine Biological*
753 *Association of the United Kingdom*, *87*, 599–613. doi:10.1017/S0025315407054641

754 Righton, D. A., Townhill, B., & Van Der Kooij, J. (2009). Catch me if you can: archival tagging
755 studies can help assess changes in the accessibility of Atlantic cod (*Gadus morhua*) to trawl
756 gears. ICES CM 2009/J:08. *ICES CM*, J:08.

757 Scott, R., Hodgson, D. J., Witt, M. J., Coyne, M. S., Adnyana, W., Blumenthal, J. M., ... Godley,
758 B. J. (2012). Global analysis of satellite tracking data shows that adult green turtles are
759 significantly aggregated in Marine Protected Areas. *Global Ecology and Biogeography*, *21*,
760 1053–1061. doi:10.1111/j.1466-8238.2011.00757.x

761 Sippel, T., Paige Eveson, J., Galuardi, B., Lam, C., Hoyle, S., Maunder, M., ... Nicol, S. (2015).
762 Using movement data from electronic tags in fisheries stock assessment: A review of
763 models, technology and experimental design. *Fisheries Research*, *163*, 152–160.

764 doi:10.1016/j.fishres.2014.04.006

765 Towner, A. V., Leos-Barajas, V., Langrock, R., Schick, R. S., Smale, M. J., Kaschke, T., ...
766 Hopkins, W. (2016). Sex-specific and individual preferences for hunting strategies in white
767 sharks. *Functional Ecology*, *30*(8), 1397–1407. doi:10.1111/1365-2435.12613

768 Vermard, Y., Rivot, E., Mahévas, S., Marchal, P., & Gascuel, D. (2010). Identifying fishing trip
769 behaviour and estimating fishing effort from VMS data using Bayesian Hidden Markov
770 Models. *Ecological Modelling*, *221*, 1757–1769. doi:10.1016/j.ecolmodel.2010.04.005

771 Videler, J. J., & Wardle, C. S. (1991). Fish swimming stride by stride: speed limits and
772 endurance. *Reviews in Fish Biology and Fisheries*, *1*, 23–40. doi:10.1007/BF00042660

773 Wakefield, E. D., Phillips, R. A., Trathan, P. N., Arata, J., Gales, R., Huin, N., ... Matthiopoulos,
774 J. (2011). Habitat preference , accessibility , and competition limit the global distribution of
775 breeding Black-browed Albatrosses. *Ecological Monographs*, *81*(1), 141–167.

776 Wickham, H. (2009). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York.

777 Womble, J. N., & Gende, S. M. (2013). Post-Breeding Season Migrations of a Top Predator, the
778 Harbor Seal (*Phoca vitulina richardii*), from a Marine Protected Area in Alaska. *PLoS ONE*,
779 *8*(2), e55386. doi:10.1371/journal.pone.0055386

780 Worton, B. J. (1989). Kernel Methods for Estimating the Utilization Distribution in Home-Range
781 Studies. *Ecology*, *70*(1), 164–168.

782 Zucchini, W., MacDonald, I. L., & Langrock, R. (2016). *Hidden Markov models for time series:*
783 *an introduction using R (second edition)*. Chapman and Hall/CRC.

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787 **Tables**

788 **Table 1.** State dependent movement rates (horizontal: km day⁻¹, vertical: m day⁻¹) by sub-stock in
 789 Atlantic cod and European plaice. All values are taken from collated model output and are
 790 averaged across all individuals.

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| | | Resident state | | Migrating state | |
|--|--------------------|---------------------------------|------------------------------|---------------------------------|------------------------------|
| <i>Sub-Stock</i> | | <i>Horizontal movement (km)</i> | <i>Vertical movement (m)</i> | <i>Horizontal movement (km)</i> | <i>Vertical movement (m)</i> |
| Atlantic cod (<i>Gadus morhua</i>) | Southern North Sea | 9.2 | 31.5 | 13.9 | 158.3 |
| | English Channel | 9.6 | 53.5 | 13.4 | 125.4 |
| European plaice (<i>Pleuronectes platessa</i>) | Southern North Sea | 6.4 | 20.0 | 12.9 | 115.6 |
| | German Bight | 6.6 | 26.1 | 14.9 | 125.8 |
| | Central North Sea | 12.9 | 26.2 | 19.5 | 121.0 |

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804 **Figure Legends**

805 **Figure 1.** Release locations of all tagged fish. Atlantic cod, *Gadus morhua* (n=46) are shown in
806 red, fish are either separated into the English Channel sub-stock (triangles, n=23) or the Southern
807 North Sea sub-stock (circles, n=23). European plaice, *Pleuronectes platessa* (n=61) are shown in
808 purple, fish are grouped into three sub-stocks: Central North Sea (circles, n=27), German Bight
809 (triangles, n=10) or Southern North Sea (crosses, n=24).

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811 **Figure 2.** Estimated state-dependent distributions (bars) for vertical (left) and horizontal (right)
812 movements of all 34-selected fish. Black lines illustrate the movement parameter prior
813 distributions $N(m, \delta)$ that were constructed based on collective model output. Prior distributions
814 are state (resident, solid line; migratory, dashed line), species (Atlantic cod, top; European plaice,
815 bottom) and dimension (horizontal or vertical) specific.

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817 **Figure 3.** State dependent movement behaviour of two individual fish. Shown in a color scale
818 from red to yellow is the movement behaviour of one Atlantic cod tagged on the 25th March 2005
819 (duration = 300 days). Red points represent a migrating state, yellow a resident state and those
820 points shown in orange illustrate times when the model was uncertain of state classification (i.e.
821 the daily probability of state classification was less than 0.85). Shown in a scale from purple to
822 cyan is the movement behaviour of one European plaice tagged on the 14th November 1997
823 (duration = 253 days). Purple points represent a migrating state, cyan a resident state and those
824 points shown in royal blue illustrate times when the model was uncertain of state classification.
825 The start and end point of each individual's movement path are shown as a green triangle and a
826 red diamond, respectively.

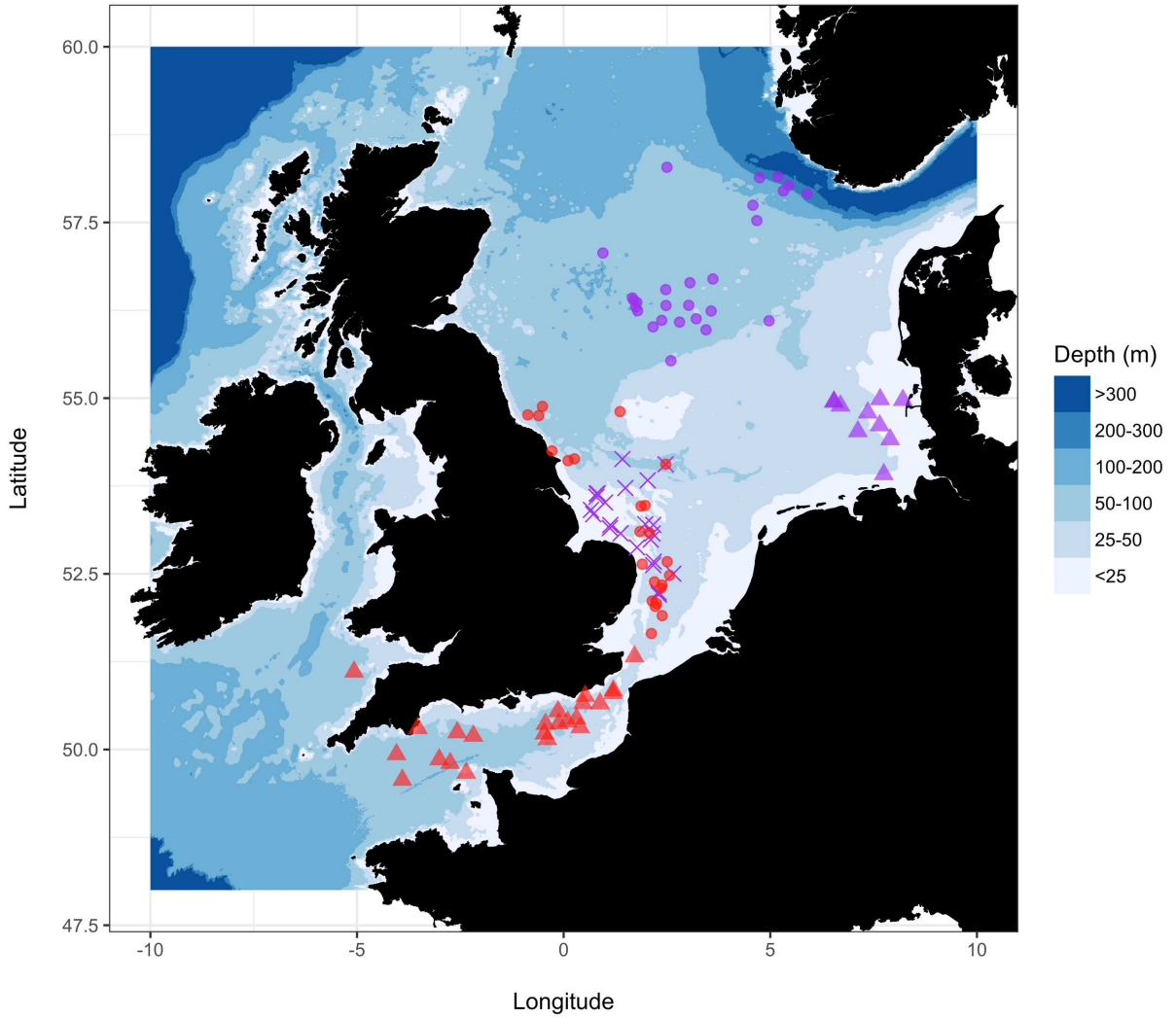
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828 **Figure 4.** Annual temporal distributions of the resident state in Atlantic cod (red) and European
829 plaice (blue). The plotted line in either graph illustrates the mean probability of observing a
830 resident state (± 1 SE – grey shading). The underlying barplots demonstrate the proportion of
831 individual fish that are in a resident state during each week. Periods of time when the mean
832 probability of observing a resident state is continually >0.5 are illustrated in either species.

833
834 **Figure 5.** Annual state dependent space use patterns of Atlantic cod (A and B) and European plaice
835 (C and D) in the North Sea and English Channel. Plots are split into periods of resident dominant
836 (A and C) and migrating dominant (B and D), defined by a mean probability of observing a given
837 state at a given time being > 0.5 . All grid cells (5km^2) are illustrated in a color gradient so as to
838 illustrate the sum total number of days spent in a certain state in a given grid cell within a specified
839 time period.

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855 **Figure 1.**
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867 **Figure 2.**

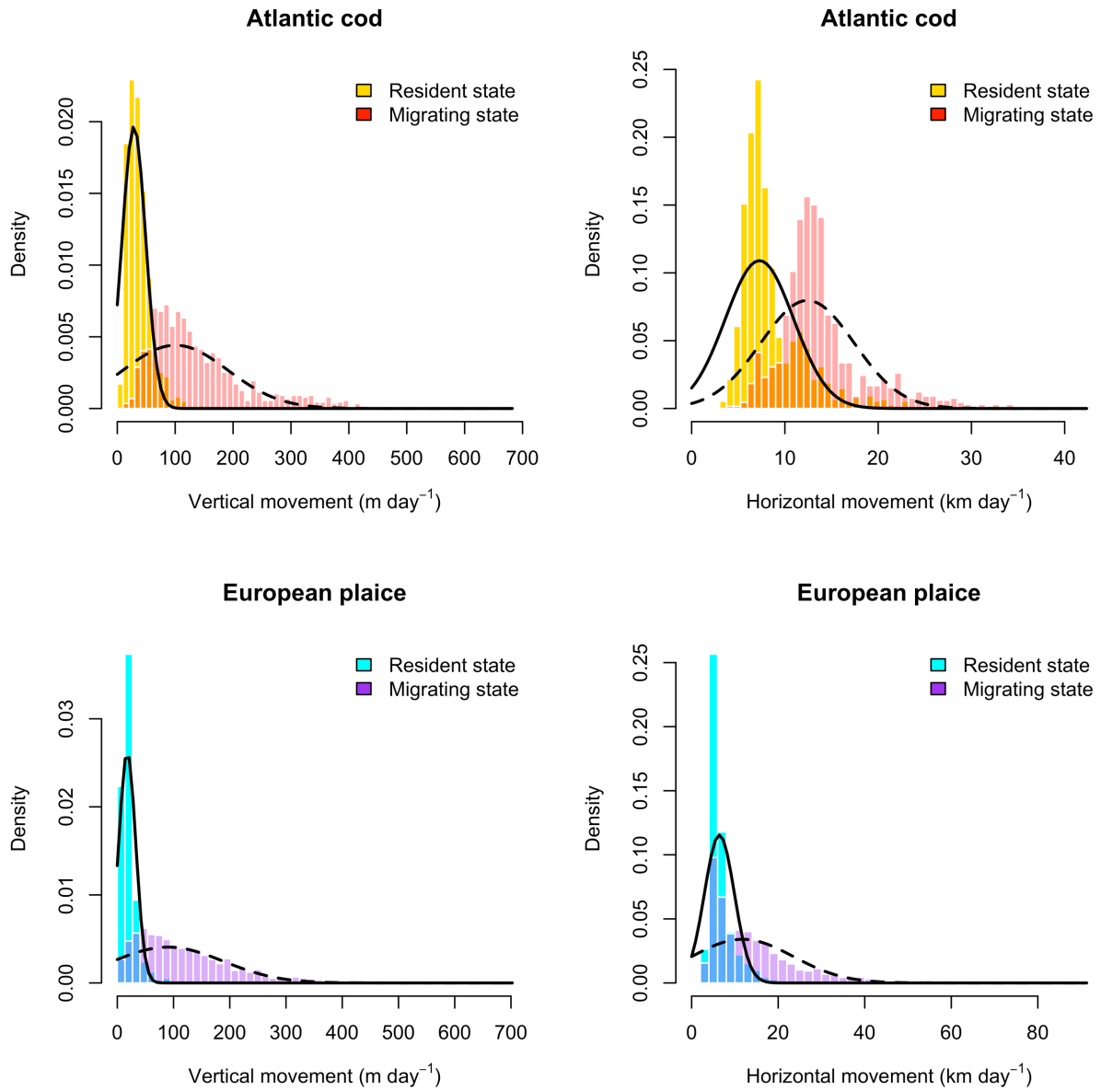
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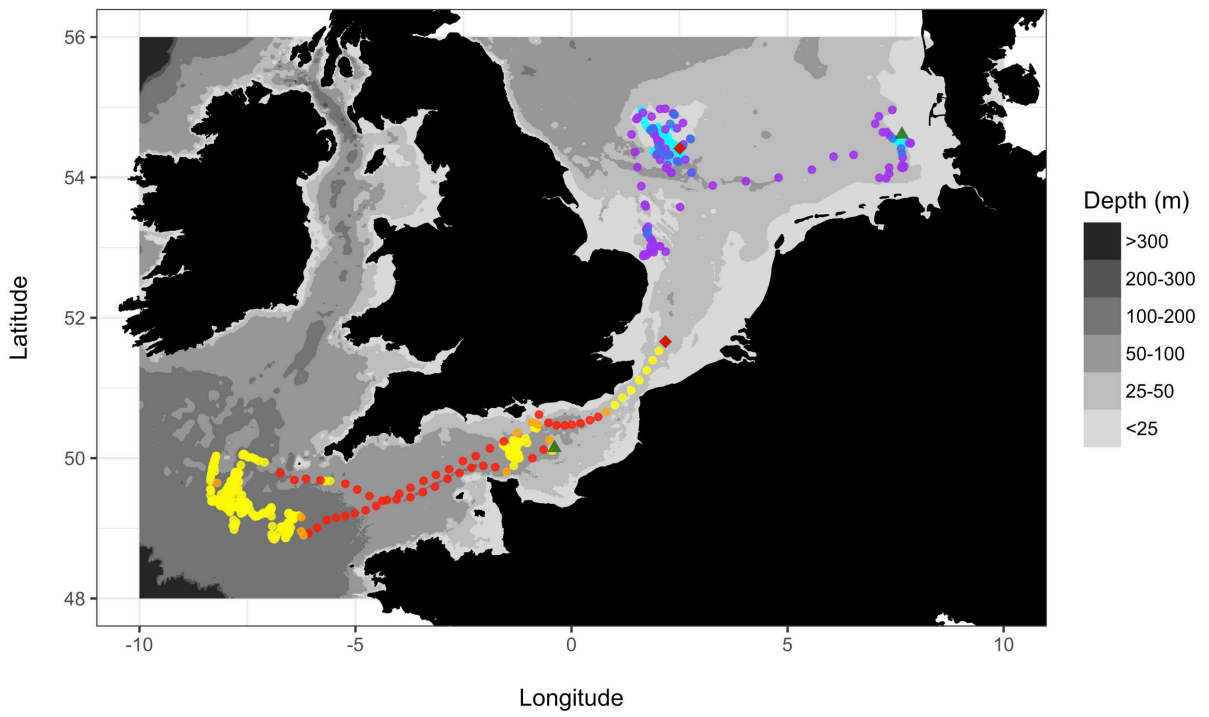
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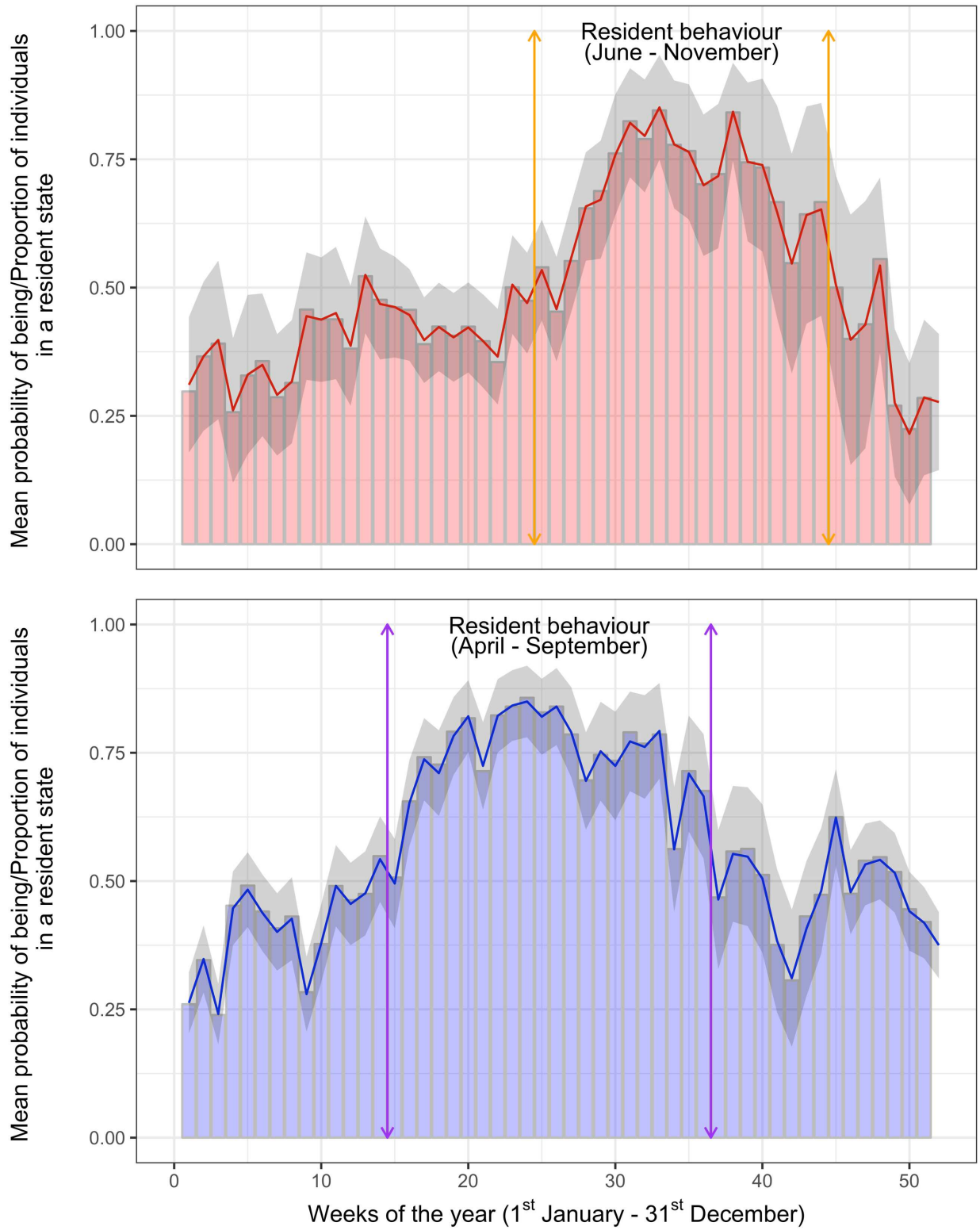
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879 **Figure 3.**
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891 **Figure 4.**
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895 **Figure 5.**

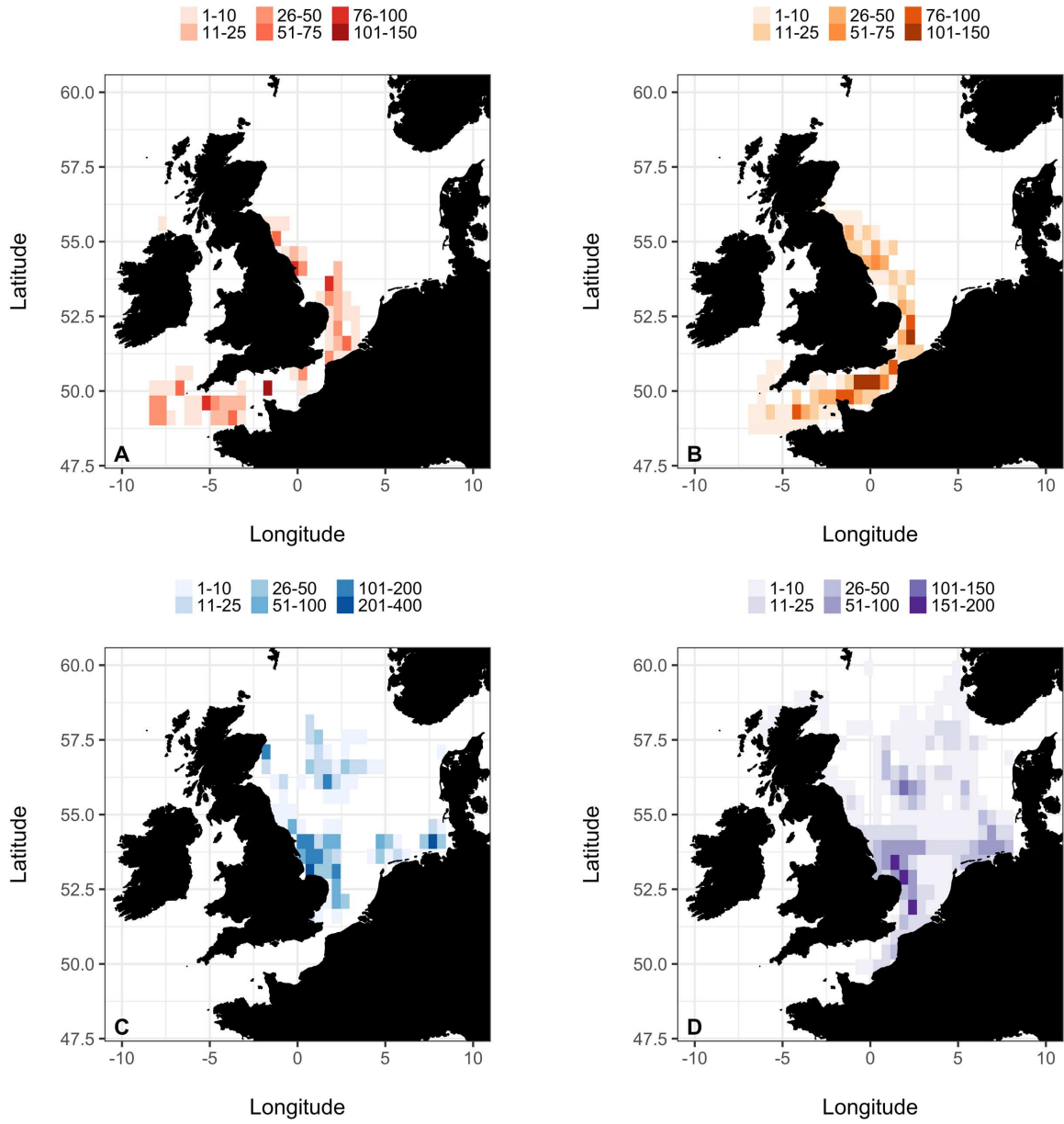
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