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

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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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1. **Introduction**

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

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

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169   2. **Materials & Methods**

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171   *2.1.Case study data*

172

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

179

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

186

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

$$\Gamma = \begin{pmatrix} \gamma_{R \to R} & \gamma_{R \to M} \\ \gamma_{M \to R} & \gamma_{M \to M} \end{pmatrix} \qquad [1]$$

220   and

$$\gamma_{j \to k} = \Pr(S_{t+1} = k \mid S_t = j) \qquad [2]$$

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):

$$x_t \sim MVN\left(\mu_j, \Sigma_j\right) \qquad [3]$$

226   with

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

228   and

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

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 $S_1, \ldots, S_T$ is

233

$$\omega_{S_1} \phi_{S_1}(x_1) \gamma_{S_1 \to S_2} \phi_{S_2}(x_2) \ldots \gamma_{S_{T-1} \to S_T} \phi_{S_T}(x_T) \qquad [6]$$

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 $i = 1, \ldots, 107$, 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 (Metcalfe 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    $$\gamma_{11} \sim beta(\alpha, \beta) \tag{7}$$

256   and

257    $$\gamma_{22} \sim beta(\alpha, \beta) \tag{8}$$

258

259   where α = 99 and β =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.

2.3.Classifying fish movements

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
$$\prod_{j}\prod_{d}\phi(\mu_{jd} \mid m_{jd}, \delta_{jd})$$
[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 $5km^2$ 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

17

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 assiocated with longer dive durations, whereas an inverted relationship is noted in blue whales

474 (*Balaenoptera musculus*) with percieved shallow foraging behaviours being characteried 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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563

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**

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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	
	Sub-Stock	*Horizontal movement (km)*	*Vertical movement (m)*	*Horizontal movement (km)*	*Vertical movement (m)*
Atlantic cod (*Gadus morhua)*	Southern North Sea	9.2	31.5	13.9	158.3
	English Channel	9.6	53.5	13.4	125.4
European plaice (*Pleuronectes platessa*)	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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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.

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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 spilt 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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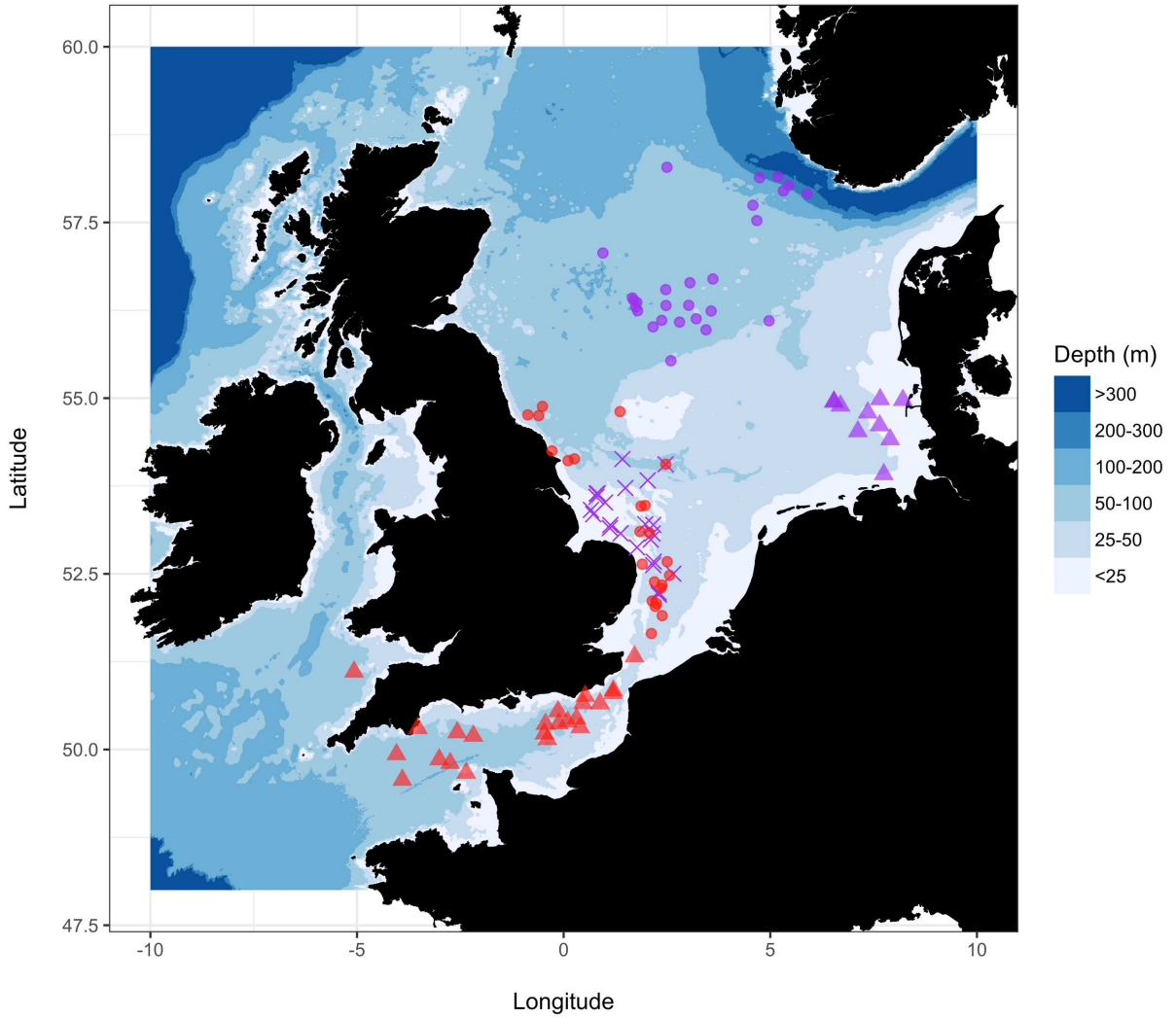
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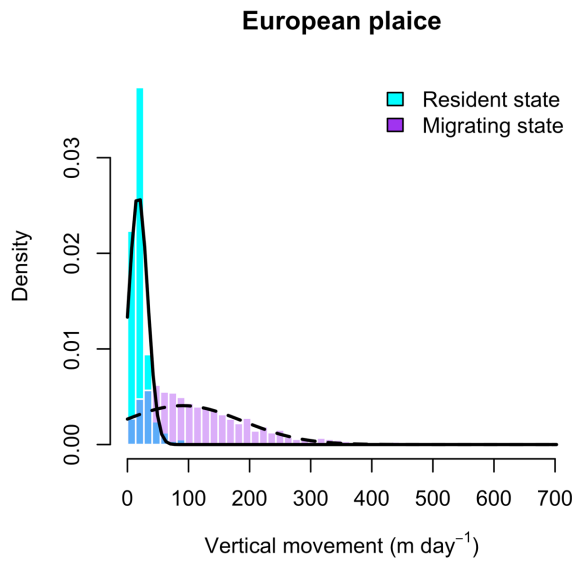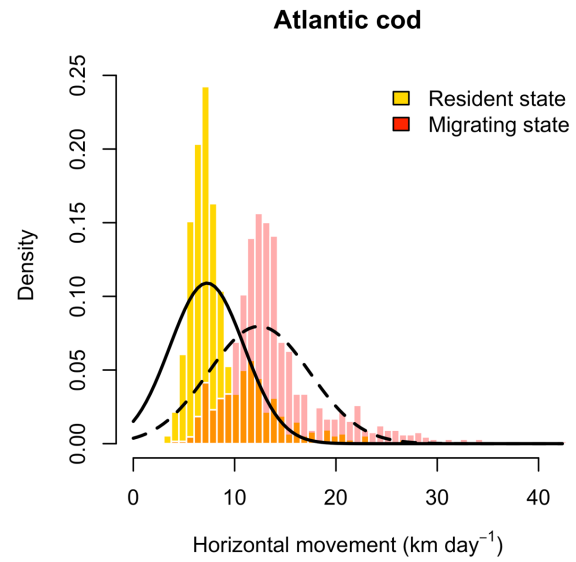
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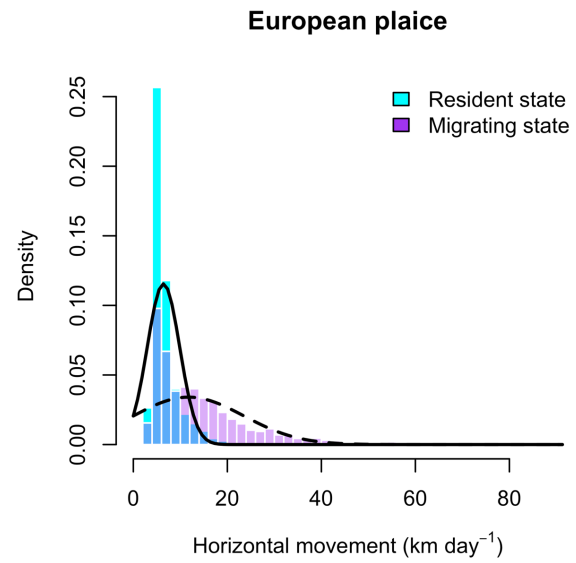
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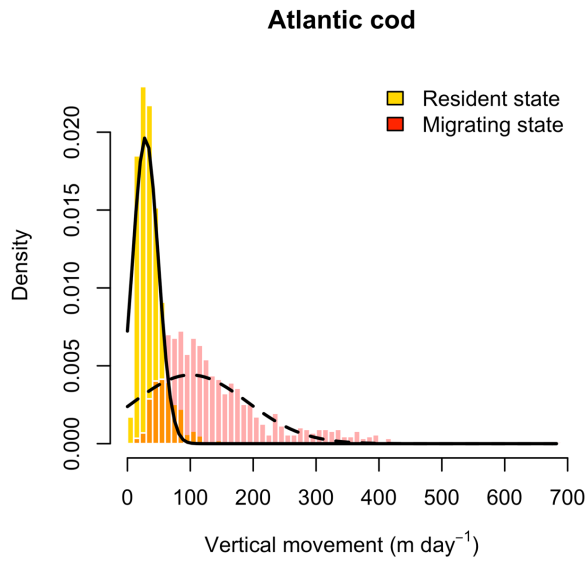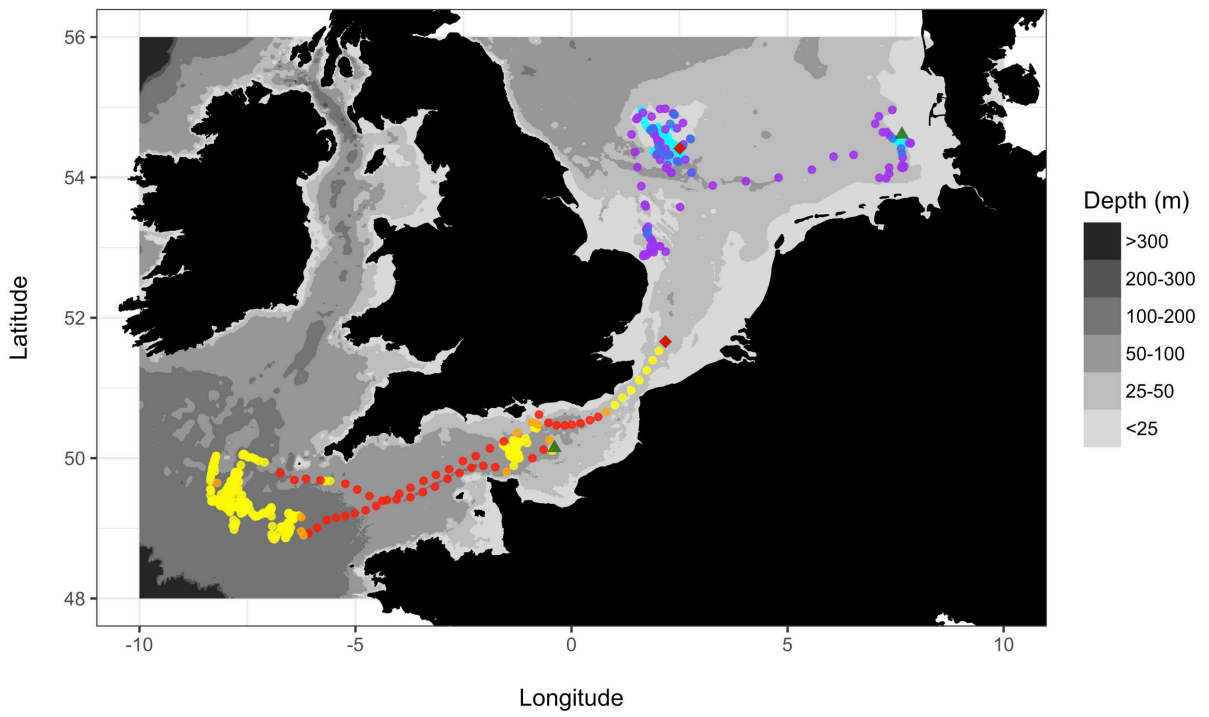

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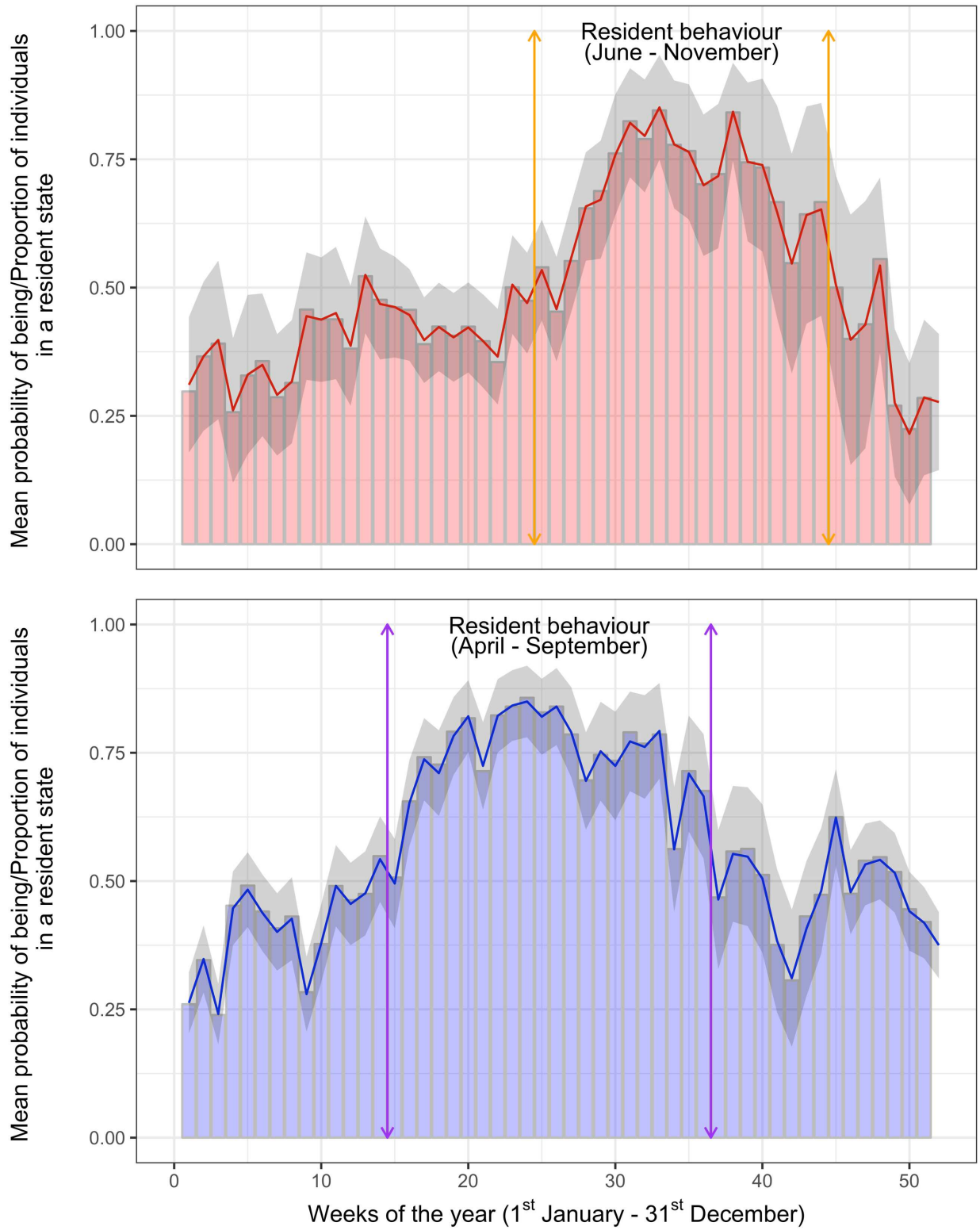
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879   **Figure 3.**
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891   **Figure 4.**
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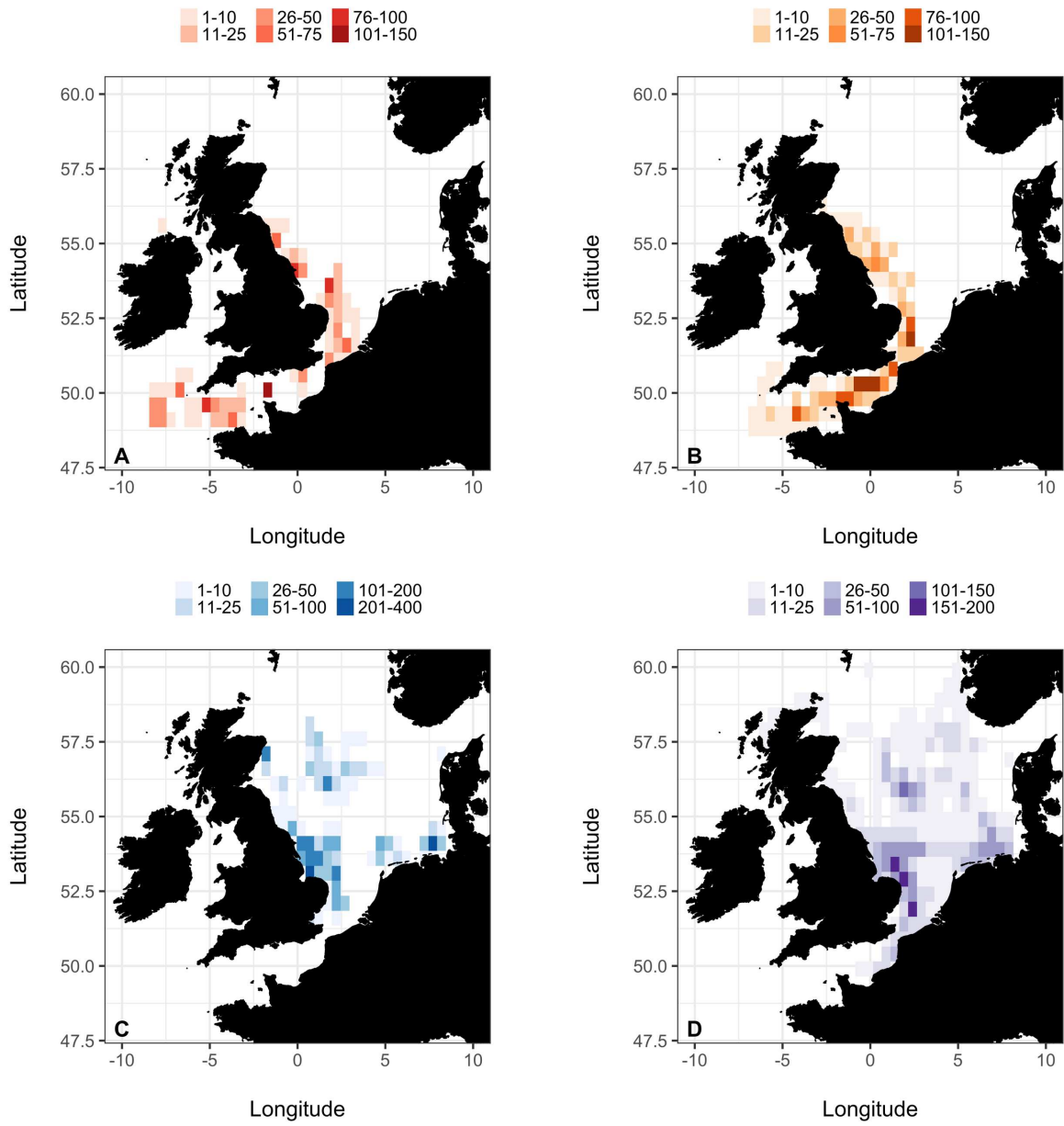**Figure 5.**