

Working title: Highly resolved spatiotemporal simulations for exploring mixed fishery dynamics

Paul J. Dolder^{a,b,*}, C  il  n Minto^a, Jean-Marc Guarini^c, Jan Jaap Poos^d

^a*Galway-Mayo Institute of Technology (GMIT), Dublin Road, Galway, Ireland*

^b*Centre for Environment, Fisheries and Aquaculture Science (Cefas), Pakefield Road, Lowestoft, UK*

^c*Sorbonne Universit  , Faculty of Sciences, 4 Place Jussieu, 75005 Paris, France*

^d*Wageningen Marine Research, Haringkade 1 1976 CP IJmuiden, Netherlands*

Abstract

Most fisheries exploit a variety of spatially and temporally heterogeneous fish populations using species-unselective gear. This can result in unintended, unwanted catch of low quota or protected species and reducing these catches is crucial for biological and economic sustainability of ‘mixed fisheries’.

If fisheries are to avoid unwanted catch, an in-depth understanding of spatiotemporal fishery dynamics is required. However, traditional scientific advice is limited by a lack of highly resolved knowledge of population distributions and movement, and how fishers interact with different fish populations. Because data on fish location at high temporal and spatial resolutions is expensive and difficult to collect proxies are usually inferred from scientific surveys or commercial catches with limited spatial and temporal resolution.

To understand how data resolution impacts inference on mixed fisheries interactions, we developed a highly resolved spatiotemporal event-based simulation model incorporating: i) delay-difference population dynamics, ii) population movement using Gaussian Random Fields to simulate patchy, heterogeneously distributed populations, and iii) fishery dynamics for multiple fleet characteristics based on species targeting under an explore-exploit strategy. This is implemented via a mix of correlated random walk movement (for exploration) and

*Corresponding author

Email address: paul.dolder@gmit.ie (Paul J. Dolder)

learned behaviour (for exploitation) phases of the fisheries.

Fifty years of sub-daily fishing was simulated and used to draw inference on the underlying community structures. We compared inferences based on: commercial catch, a simulated fixed-site sampling survey design and the true underlying community. We i) establish the potential limitations of fishery-dependent data in providing a robust picture of spatiotemporal distributions; and then ii) simulated an area closure based on areas defined from the different data sources at a range of temporal and spatial resolutions. We conclude from our example framework application that commercial data, while containing bias, provide a useful tool for managing catches in mixed fisheries if applied at the correct spatiotemporal scale. [NEED A LITTLE MORE DETAIL OF THE RESULTS HERE - 2 MORE SENTENCES ON KEY TAKE-HOME RESULTS]

Keywords: Some, keywords, here. Max 6

2010 MSC: 00-01, 99-00

1. Introduction

Fishers exploit a variety of fish populations that are heterogeneously distributed in space and time, with varying knowledge of species distributions. In doing so fisheries catch an assemblage of species and may discard over-quota catch when managed by single species quotas and fishers exhaust one or more quota. This may lead to overexploitation of fish populations (Ulrich et al., 2011; Batsleer et al., 2015). Discarding of fish in excess of quota limits the ability to maintain fishing mortality within sustainable limits (Alverson et al., 1994; Crowder et al., 1998; Rijnsdorp et al., 2007) and the ability to manage for the biological and economic sustainability of fisheries. As such, there is increasing interest in technical solutions such as gear and spatial closures as measures to reduce unwanted catch (Kennelly and Broadhurst, 2002; Catchpole and Revill, 2008; Bellido et al., 2011; Cosgrove et al., 2019).

14

Adaptive spatial management strategies have been proposed as a way of reducing over-quota discards (Holmes et al., 2011; Little et al., 2014; Dunn et al., 2014). However, implementation is restricted by lack of knowledge of fish and fishery spatiotemporal dynamics and understanding of the scale at which processes become important for management. Understanding the correct scale for spatial measures is crucial for implementing effective solutions which minimising economic impact (Dunn et al., 2016). For example, the problem can be to identify a scale that promotes species avoidance for vulnerable or low quota species while allowing continuance of sustainable fisheries for available quota species.

Identifying appropriate spatial scales for fisheries closures has been a challenge in the past but is crucial to their success (Costello et al., 2010; Dunn et al., 2016). Inference is hampered where spatial information is coarse due to low resolution reporting of fisheries catch which is aggregated across larger gridded areas (Branch et al., 2005). Further, if data does not allow identification of spatial features it may lead to poorly sited closures which are ineffectual or have unintended consequences. For example, increased benthic impact on previously unexploited areas from the cod closure in the North Sea were observed without the intended effect of reducing cod exploitation (Rijnsdorp et al., 2001; Dinmore et al., 2003)). More refined spatiotemporal information has since become available through the combination of logbook and Vessel Monitoring System (VMS) data (Lee et al., 2010; Bastardie et al., 2010; Gerritsen et al., 2012; Mateo et al., 2016) and more real-time spatial management has been possible (e.g. Holmes et al., 2011). However, fishers establish favoured fishing grounds through an explore-exploit strategy (Bailey et al., 2018) where they search for areas with high catches and then use experience to return to areas where they’ve experienced high catch in the past. This leads to an inherently biased sampling where target species are over-represented in the catch as fishers exploit areas of high abundance.

46 To understand the effect of spatiotemporal aggregation of data and fishery
47 targeting we ask two fundamental questions regarding inference derived from
48 observational data:

- 49 1. How does sampling-derived fisheries data reflects the underlying commu-
50 nity structure?
- 51 2. How does data aggregation and source impact on spatial fisheries man-
52 agement measures?

53 To answer these questions we i) develop a simulation model where popu-
54 lation dynamics are highly-resolved in space and time by use of a Gaussian
55 spatial process to define suitable habitat for different populations. Precise lo-
56 cations of the fish being known directly rather than inferred from sampling or
57 commercial catch, we can use the population model to validate how inference
58 from fisheries-dependent and fisheries independent sampling relates to the real
59 community structure in a way we could not with real data. We ii) compare, at
60 different spatial and temporal aggregations, the ‘real population’ distributions
61 to samples from fisheries-dependent and fisheries independent catches to test if
62 these are a true reflection of the relative density of the populations. We then
63 iii) simulate a fishery closure to protect a species based on different spatial and
64 temporal data aggregations.

65
66 We use these evaluations to draw inference on the utility of commercial data
67 in supporting management decisions.

68 **2. Materials and Methods**

69 An event-based simulation model of a hypothetical fishery was developed
70 as a software package (‘MixFishSim’). The modular approach enabled efficient
71 computation by allowing for sub-modules implemented on time-scales appro-
72 priate to capture the characteristic of the different processes (Figure 1). The
73 following sub-modules were included to capture the full system: 1) Population

74 dynamics, 2) Recruitment dynamics, 3) Population movement, 4) fishery dy-
 75 namics.

76

77 Population dynamics operate on a daily time-step, while population move-
 78 ment occurs on a weekly time-step, with the fishing module operating on a
 79 tow-by-tow basis (i.e. multiple events a day).

80 2.1. Population dynamics

81 The basic population level processes were simulated using a modified two-
 82 stage Deriso-Schnute delay difference model which models the fish populations in
 83 terms of aggregate biomass of recruits and mature components rather than keep-
 84 ing track of individuals (Deriso, 1980; Schnute, 1985; Dichmont et al., 2003). A
 85 daily time-step was chosen to discretise continuous population processes on a bi-
 86 ologically relevant and computationally tractable timescale. Population biomass
 87 growth was modelled as a function of previous recruited biomass, intrinsic pop-
 88 ulation growth and recruitment functionally linked to the adult population size.
 89 Biomass for each cell c was incremented each day d as follows (the full parameter
 90 list is detailed in Table 1):

$$\begin{aligned}
 B_{c,d+1} = & \\
 & (1 + \rho)B_{c,d} \cdot e^{-Z_{c,d}} - \rho \cdot e^{-Z_{c,d}} \quad \times \\
 & (B_{c,d-1} \cdot e^{-Z_{c,d-1}} + Wt_{R-1} \cdot \alpha_{d-1} \cdot R_{\tilde{y}(c,y,d-1)}) \quad + \\
 & Wt_R \cdot \alpha_d \cdot R_{\tilde{y}(c,y,d)}
 \end{aligned} \tag{1}$$

91 where ρ is Brody's coefficient, shown to be equal to e^{-K} when K is the growth
 92 rate from a von Bertalanffy logistic growth model (Schnute, 1985). Wt_{R-1} is
 93 the average weight of fish prior to recruitment, while Wt_R is the average re-
 94 cruited weight. α_d represents the proportion of fish recruited during that day
 95 for the year, while $R_{c,\tilde{y}}$ is the annual recruits in cell c for year y .

96

97 Mortality $Z_{c,d}$ can be decomposed to natural mortality, $M_{c,d}$, and fishing
 98 mortality, $F_{c,d}$, where both $M_{c,d}$ and $F_{c,d}$ are instantaneous rates with $M_{c,d}$

fixed and $F_{c,d}$ calculated by solving the Baranov catch equation (Hilborn and Walters, 1992) for $F_{c,d}$:

$$C_{c,d} = \frac{F_{c,d}}{F_{c,d} + M_{c,d}} \left(1 - e^{-(F_{c,d} + M_{c,d})} \right) \cdot B_{c,d} \quad (2)$$

where $C_{c,d}$ is the summed catch from the fishing model across all fleets and vessels in cell c for the population during the day d , and $B_{c,d}$ the daily biomass for the population in the cell. Here, catch and fishing mortality are the sum of those across all fleets and vessels, where $F_{fl,v,c,d,p} = E_{fl,v,c,d} \cdot Q_{fl,p} \cdot D_{c,d,p}$ with fl , v and p the fleet, vessel and population respectively and E and Q fishing effort and catchability of the gear, and D is the density of the population at the location fished.

2.2. Recruitment dynamics

Recruitment is modelled through a function relating to adult biomass. In *MixFishSim*, it can be either as a stochastic Beverton-Holt stock-recruit form (Beverton and Holt, 1957):

$$\begin{aligned} \bar{R}_{c,d} &= \frac{(\alpha \cdot S_{c,d})}{(\beta + S_{c,d})} \\ R_{c,d} &\sim \log N[(\log(\bar{R}_{c,d}), \sigma^2)] \end{aligned} \quad (3)$$

Where α is the maximum recruitment rate, β the spawning stock biomass (SSB) required to produce half the maximum stock size, S current stock size and σ^2 the variability in the recruitment due to stochastic processes, or a stochastic Ricker form (Ricker, 1954):

$$\begin{aligned} \bar{R}_{c,d} &= B_{c,d} \cdot e^{(\alpha - \beta \cdot B_{c,d})} \\ R_{c,d} &\sim \log N[(\log(\bar{R}_{c,d}), \log(\sigma^2))] \end{aligned} \quad (4)$$

where α is the maximum productivity per spawner and β the density dependent reduction in productivity as the SSB increases.

119 2.3. Population movement dynamics

120 Population movement is a combination of random (diffusive) movement,
 121 governed by a stochastic process where movement between adjacent cells is
 122 described by a set of probabilities, and directed (advective) movement where
 123 at certain times of year the population moves towards spawning grounds by
 124 increasing the probabilities of moving into the spawning grounds from adjacent
 125 cells. We characterise a set of different fishing fleet dynamics exploiting four fish
 126 populations with different spatial and population demographics. The following
 127 describes the implementation of each of the sub-modules.

128 To simulate fish population distribution in space and time a Gaussian spatial
 129 process was employed to model habitat suitability for each of the populations
 130 on a 2d grid.

131 We first defined a Gaussian random field process, $\{S(c) : c \in \mathbb{R}^2\}$, where
 132 for any set of cells c_1, \dots, c_n , the joint distribution of $S = \{S(c_1), \dots, S(c_n)\}$ is
 133 multivariate Gaussian with a *Matérn* covariance structure, where the correlation
 134 strength weakens with distance. This enables us to model the spatial autocor-
 135 relation observed in animal populations where density is more similar in nearby
 136 locations (Tobler, 1970; F. Dormann et al., 2007) and we change the parameters
 137 to implement different spatial structures for the different populations using the
 138 *RandomFields* R package (Schlatter et al., 2015). We define a stationary habitat
 139 field and combine with a temporally dynamic thermal tolerance field to imitate
 140 two key drivers of population dynamics. Each population was initialised at a
 141 single location, and subsequently moved according to a probabilistic distribu-
 142 tion based on habitat suitability (represented by the normalised values from the
 143 GRFs), temperature and distance from current cell:

$$Pr(C_{wk+1} = J | C_{wk} = I) = \frac{e^{-\lambda * d_{IJ}} \cdot (Hab_{J,p}^2 \cdot Tol_{J,p,wk})}{\sum_{c=1}^C e^{-\lambda * d} \cdot (Hab_{c,p}^2 \cdot Tol_{c,p,wk})} \quad (5)$$

144 Where d_{IJ} is the euclidean distance between cell I and cell J , λ is a given
 145 rate of decay, $Hab_{J,p}^2$ is the squared index of habitat suitability for cell J and
 146 population p , with $Tol_{J,p,wk}$ the temperature tolerance for cell J by population

147 p in week wk (see below).

148 During pre-defined weeks of the year the habitat suitability is modified with
149 user-defined spawning habitat locations, resulting in each population having
150 concentrated areas where spawning takes place. In the simulations the popu-
151 lations move towards these cells in the weeks prior to spawning, resulting in
152 directional movement towards the spawning grounds.

153 An advection-diffusion process controls population movement, with a time-
154 varying temperature covariate used to change the interaction between time and
155 suitable habitat on a weekly time-step. Each population p was assigned a ther-
156 mal tolerance with mean, μ_p and variance, σ_p^2 so that each cell and population
157 temperature suitability is defined that:

$$Tol_{c,p,wk} = \frac{1}{\sqrt{(2\pi \cdot \sigma_p^2)}} \cdot \exp\left(-\frac{(T_{c,wk} - \mu_p)^2}{2 \cdot \sigma_p^2}\right) \quad (6)$$

158 Where $Tol_{c,p,wk}$ is the tolerance of population p for cell c in week wk , $T_{c,wk}$ is
159 the temperature in the cell given the week and μ_p and σ_p^2 the mean and standard
160 deviation of the population temperature tolerance.

161 The final combined process results in a population structure and movement
162 pattern unique to each species, with population movement occurring on a weekly
163 basis. The decision to model population movement on a weekly timescale was
164 to reflect that fish tend to aggregate in species specific locations that have
165 been observed to last around one to two weeks (Poos and Rijnsdorp, 2007b).
166 Therefore this process approximated the demographic shifts in fish populations
167 throughout a year with seasonal spawning patterns (Figure ??).

168 2.4. Fleet dynamics

169 Fleet dynamics can be broadly categorised into three components: fleet tar-
170 geting - that determined the fleet catch efficiency and preference towards a
171 particular species; trip-level decisions, that determines the initial location to
172 be fished at the beginning of a trip; and within-trip decisions, that determines
173 movement from one fishing spot to another within a trip. Together, these ele-
174 ments implement an explore-exploit type strategy for individual vessels to max-

175 imise their catch from an unknown resource distribution (Bailey et al., 2018).
 176 The decision to use an individual based model for fishing vessels was taken
 177 because fishers are heterogeneous in their location choice behaviour due to dif-
 178 ferent objectives, risk preference and targeting preference (Van Putten et al.,
 179 2012). Therefore in the simulations fleet dynamics reflect individual experiences
 180 rather than pre-defined group dynamics.

181 2.4.1. Fleet targeting

182 Each fleet of n vessels was characterised by both a general efficiency, Q_{fl} ,
 183 and a population specific efficiency, $Q_{fl,p}$. Thus, the product of these parame-
 184 ters $[Q_{fl} \cdot Q_{fl,p}]$ affects the overall catch rates for the fleet and the preferential
 185 targeting of one population over another. This, in combination with the param-
 186 eter choice for the step-function defined below (as well as some randomness from
 187 the exploratory fishing process) determined the preference of fishing locations
 188 for the fleet.

189 2.4.2. Trip-level decisions

190 Several studies (e.g. Hutton et al., 2004; Tidd et al., 2012; Girardin et al.,
 191 2015) have confirmed past activity and past catch rates are strong predictors of
 192 fishing location choice. For this reason, the fleet dynamics sub-model included a
 193 learning component, where a vessel’s initial fishing location in a trip was based
 194 on selecting from previously successful fishing locations. This was achieved by
 195 calculating an expected revenue based on the catches from locations fished in
 196 the preceding trip as well as the same month periods in previous years and the
 197 travel costs from the port to the fishing grounds, and choosing randomly from
 198 the top 75 % of fishing events as defined by the expected profit, that has a
 199 seasonal component.

200 2.4.3. Within-trip decisions

201 Fishing locations within a trip are initially determined by a modified ran-
 202 dom walk process. As the simulation progresses the within-trip decision become
 203 gradually more influenced by experience gained from past fishing locations (as

per the initial trip-level location choice), moving location choice towards areas of higher perceived profit. A random walk was chosen for the exploratory fishing process as it is the simplest assumption commonly used in ecology to describe optimal animal search strategy for exploiting homogeneously distributed prey about which there is uncertain knowledge (Viswanathan et al., 1999). In a random walk, movement is a stochastic process through a series of steps. These steps have a length, and a direction that can either be equal in length or take some other functional form. The direction of the random walk was also correlated (known as ‘persistence’) providing some overall directional movement (Codling et al., 2008).

We use a *Lévy flight* which is a particular form of random walk characterised by a heavy-tailed distribution of step-length. The Lévy flight has received a lot of attention in ecological theory in recent years as having shown to have very similar characteristics as those observed by animals in nature, and being a near optimum searching strategy for predators pursuing patchily distributed prey (Viswanathan et al., 1999; Bartumeus et al., 2005; Sims et al., 2008). Bertrand et al. (2007) showed that Peruvian anchovy fishermen have a stochastic search pattern similar to that observed with a Lévy flight. However, it remains a subject of debate (e.g. see Edwards et al., 2011; Reynolds, 2015), with the contention that search patterns may be more simply characterised as random walks (Sakiyama and Gunji, 2013) with specific patterns related to the characteristics of the prey field (Sims et al., 2012).

For our implementation of a random walk directional change is based on a negatively correlated circular distribution where a favourable fishing ground is likely to be “fished back over” by the vessel returning in the direction it came from. The step length (i.e. the distance travelled from the current to the next fishing location) is determined by recent fishing success, measured as the

233 summed value of fish caught (revenue, Rev),

$$Rev = \sum_{p=1}^P L_p \cdot Pr_p \quad (7)$$

234 where L_p is landings of a population p , and Pr_p price of a population. All
 235 species prices were kept the same across fleets and seasons. Here, when fishing
 236 is successful vessels remain in a similar location and continue to exploit the local
 237 fishing grounds. When unsuccessful, they move some distance away from the
 238 current fishing location. The movement distance retains some degree of stochasticity,
 239 that can be controlled separately, but is determined by the relationship:

$$StepL = e^{\log(\beta_1) + \log(\beta_2) - (\log(\frac{\beta_1}{\beta_3}))} * Rev \quad (8)$$

241 Where β_1 , β_2 and β_3 are parameters determining the shape of the step function
 242 in its relation to revenue, so that, a step from $(x1, y1)$ to $(x2, y2)$ is defined by:

$$\begin{aligned} (x2, y2) = & x1 + StepL \cdot \cos\left(\frac{\pi \cdot Br}{180}\right), \\ & y1 + StepL \cdot \sin\left(\frac{\pi \cdot Br}{180}\right) \end{aligned} \quad (9)$$

with $Br_{t-1} < 180, Br_t = 180 + \sim vm[(0, 360), k]$
 $Br_{t-1} > 180, Br_t = 180 - \sim vm[(0, 360), k]$

243 where k the concentration parameter from the von Mises distribution that we
 244 correlate with the revenue so that $k = (Rev + 1/RefRev) * max_k$, where max_k
 245 is the maximum concentration value, k , and $RefRev$ is parametrised as for β_3
 246 in the step length function. A realised example of the step length and turning
 247 angle relationships to revenue can be seen at Figure ??.

248 2.4.4. Local population depletion

249 Where several fishing vessels exploit the same fish population competition is
 250 known to play an important role in local distribution of fishing effort (Gillis and
 251 Peterman, 1998). If several vessels are fishing on the same patch of fish, local
 252 depletion and interference competition will affect fishing location choice of the
 253 fleet as a whole (Rijnsdorp, 2000; Poos and Rijnsdorp, 2007a). To account for

254 this behaviour, the fishing sub-model operates spatially on a daily time-step so
255 that for future days the biomass available to the fishery is reduced in the areas
256 fished. The cumulative effect is to make heavily fished areas less attractive as a
257 future fishing location choice as reduced catch rates will be experienced.

258 2.5. Fisheries independent survey

259 A fisheries-independent survey is simulated where fishing on a regular grid
260 begins each year at the same time for a given number of stations (a fixed station
261 survey design). Catches of the populations at each station are recorded but not
262 removed from the population (catches are assumed to have negligible impact
263 on population dynamics). This provides a fishery independent snapshot of the
264 populations at a regular spatial intervals each year, similar to scientific surveys
265 undertaken by fisheries research agencies.

267 2.6. Software: R-package development

268 The simulation framework is implemented in the statistical software package
269 R (R Core Team, 2017) and available as an R package from the author’s github
270 site (www.github.com/pdolder/MixFishSim).

272 3. Parameterisation

273 We parameterise *MixFishSim* to investigate the influence of data aggregation
274 on spatial inference.

275 3.1. Population models

276 We parametrised the simulation model for four example populations with
277 different demographics, growth rates, natural mortality and recruitment pa-
278 rameters (Table 4). Habitat preference (Figure ??) and temperature tolerances
279 (Figures ??, ??) were defined to be unique to each population resulting in dif-
280 ferently weekly distribution patterns (Figures ??-??). In addition, each of the

281 populations was assumed to have two defined spawning areas that result in the
 282 populations moving towards these areas in pre-defined weeks (Figure ??) with
 283 population-specific movement rates (Table 4). In such a configuration, the in-
 284 dividual habitat preferences and thermal tolerances result in different spatial
 285 habitat use for each population (Figure ??) and consequently different seasonal
 286 exploitation patterns (Fishing mortality in Figure ??).

287 3.2. Fleet parametrisation

288 The fleets were parametrised to reflect five different characteristic fisheries
 289 with unique exploitation dynamics (Table 5). By setting different catchability
 290 parameters ($Q_{fl,p}$) we create different targeting preferences between the fleets
 291 and hence spatial dynamics. The learned random walk process implies that
 292 within a fleet different vessels have different spatial distributions based on indi-
 293 vidual experience. The step function was parametrised dynamically within the
 294 simulations as the maximum revenue obtainable was not known beforehand.
 295 This was implemented so that vessels take smaller steps when fishing at a loca-
 296 tion that yields landings value in the top 90th percentile of the value experienced
 297 in that year so far (as defined per fleet in Table 5).

298
 299 With increasing probability throughout the simulation, fishing locations were
 300 chosen based on experience of profitable catches built up in the same month from
 301 previous years and from the previous trip. 'Profitable' in this context was de-
 302 fined as the locations where the top 70 % of expected profit would be found
 303 given revenue from previous trips and cost of movement to the new fishing lo-
 304 cation. This probability was based on a logistic sigmoid function with a lower
 305 asymptote of 0 and upper asymptote of 0.95, and a growth rate that ensures
 306 the upper asymptote (where decisions are mainly based on past knowledge) is
 307 reached approximately halfway through the simulation.

308

309 3.3. Survey settings

310 The survey simulation was set up with a fixed gridded station design with
311 100 stations fished each year, starting on day 92 and ending on day 112 (5
312 stations per day) with same catchability parameters for all populations ($Q_p =$
313 1). This approximates a real world survey design with limited seasonal and
314 spatial coverage.

315 3.4. Example research question

316 To illustrate the capabilities of *MixFishSim*, we investigate the influence of
317 the temporal and spatial resolution of different data sources on the reduction in
318 catches of a population given spatial closures. To do so, we set up a simulation
319 to run for 50 years based on a 100×100 square grid (undetermined units), with
320 five fleets of 20 vessels each and four fish populations. Fishing takes place four
321 times a day per vessel and five days a week, while population movement is every
322 week.

323 We allow the simulation to run unrestricted for 30 years, then implement
324 spatial closed areas for the last 20 years of the simulation based on data (either
325 derived from the commercial catches, fisheries-independent survey or the 'real
326 population') used at different spatial and temporal scales.

327

328 The following steps are undertaken to determine closures:

- 329 1. Extract data source
- 330 2. Aggregate according to desired spatial and temporal resolution
- 331 3. Interpolate across entire area at desired resolution using simple bivariate
332 interpolation using the *interp* function from the R package *akima* (Akima,
333 2006). This is intended to represent a naive spatial model of catch rates,
334 without knowledge of the spatial population dynamics.
- 335 4. Close area covering top 5 % of catch rates

336 In total 28 closure scenarios were run that represent combinations of:

- 337 • **data types:** commercial logbook data, survey data and ‘real population’,
- 338 • **temporal resolutions:** weekly, monthly and yearly closures,
- 339 • **spatial resolutions:** 1 x 1 grid, 5 x 5 grid, 10 x 10 grid and 20 x 20 grid,
- 340 • **closure basis:** highest 5 % of catch rates for the protected species

341 Survey closures were on an annual basis only, as this was the most temporally
 342 resolved survey data available.

343 4. Results

344 4.1. Emergent simulation dynamics

It can be seen from a single vessels movements during a trip that the vessel exploits four different fishing grounds, three of them multiple times (Figure ??), while across several trips fishing grounds that are further apart are fished (Figure ??). These different locations relate to areas where the highest revenue were experienced, as shown by Figure ??, where several trips for the vessel overlaid on the revenue field, i.e.

$$\sum_{c=1}^c \sum_{s=1}^s B_{s,c} \cdot Q_{s,c}$$

345 Vessels from the same fleet (and therefore targeting preference) may exploit
 346 some shared and some different fishing grounds depending on their own personal
 347 experience during the exploratory phase of the fishery (Figure ??). This results
 348 from the randomness in the correlated random walk step function, with distance
 349 moved during the exploitation phase and the direction stochastically related to
 350 the revenue experienced on the fishing ground (Figure ??).

351 4.2. How does sampling-derived fisheries data reflect the underlying population 352 structure?

353 To answer this question we compare different spatial and temporal aggrega-
 354 tions of the real population distributions to:

- 355 a) **fisheries-independent data:** the inferred population from a fixed-site
356 sampling survey design as commonly used for fisheries monitoring pur-
357 poses;
- 358 b) **fisheries-dependent data:** the inferred population from our fleet model
359 that includes fishery-induced sampling dynamics.

360 Figure ?? shows the aggregated catch composition from each of the data
361 sources over a ten-year period (to average seasonal patterns) at different spa-
362 tial resolutions. The finer spatial grid for the real population (top left) and
363 commercial data (top middle) show visually similar patterns, though there are
364 large unsampled areas in the commercial data from a lack of fishing activity
365 (particularly in the lower left part of the sampling domain). The survey data at
366 this spatial resolution displays very sparse information about the spatial distri-
367 butions of the populations. The slightly aggregated data on a 5 x 5 grid shows
368 similar patterns and, while losing some of the spatial detail, there remains good
369 consistency between the real population and the commercial data. Survey data
370 starts to pick out some of the similar patterns as the other data sources, but
371 lacks spatiotemporal coverage. The spatial catch information on a 10 x 10 and
372 20 x 20 grid lose a significant amount of information about the spatial resolu-
373 tions for all data sources, and some differences between the survey, commercial
374 and 'real population' data emerge.

375
376 Figure ?? shows the consequences of different temporal aggregations of the
377 data over a ten-year period, with weekly (top), monthly (middle) and yearly
378 (bottom) catch compositions from across an aggregated 20 x 20 area. In the
379 real population, the monthly aggregation captures the major patterns of com-
380 position seen in the weekly data with similar mean and standard deviations. In
381 the weekly data species 1 = 9.36 (3.99), species 2 = 83.2 (5.60), species 3 =
382 3.57 (1.23), species 4 = 3.91 (1.59); in the monthly data species 1 = 9.23 (3.87),
383 species 2 = 83.3 (5.52), species 3 = 3.62 (1.15), species 4 = 3.86 (1.52). While
384 means were similar some of the variation was lost when aggregated to an annual

level; species 1 = 9.90 (0.173), species 2 = 82.2 (0.308), species 3 = 3.82 (0.119), species 4 = 4.03 (0.0502).

The commercial data on a weekly basis shows some of the same patterns as the real population, though the species 1 (in red) is less well represented and some weeks are missing catches from the area. Here, weekly and monthly compositions were nearly identical, with monthly composition of species 1 = 0.0472 (0.0139), species 2 = 94.4 (1.47), species 3 = 3.12 (1.47), species 4 = 2.40 (0.444). Again, yearly values head a similar mean but smaller standard deviation.

The survey data was only available on an annual basis, and showed again a slightly different composition; species 1 = 0.372 (0.00473), species 2 = 87.7 (0.193), species 3 = 0.729 (0.0200), species 4 = 11.2 (0.172).

4.3. How does data aggregation and source impact on spatial fisheries management measures?

We implemented a spatial closure using the different data sources and spatial and temporal aggregations as outlined in the protocol in Section 3.4. We used this to assess the efficacy of a closure in reducing fishing mortality on species 3, given availability of data and its use at different resolutions in order to evaluate the trade-offs in data sources.

The trend in fishing mortality for each species show that in most cases the fishery closure was successful in reducing fishing mortality on the species of interest (species 3; Figure ??), though interestingly the largest reductions in fishing mortality happened immediately after the closures, following which the fisheries “adapted” to the closures and fishing mortality increased again somewhat. The exception to the success was the closures implemented based on the coarsest spatial (20 x 20) and temporal resolution (yearly) that was ineffective with all data sources. As expected, closures based on the “known” population distribution were most effective, with differing degrees of success using the com-

415 mercial data. Fishing mortality rates on the other species changed in different
416 proportions, depending on whether the displaced fishing effort moved to areas
417 where the populations were found in greater or lesser density.

418

419 A regression tree (using the R package REEMtree (Sela and Simonoff, 2012))
420 highlights that the factor most contributing to differences in fishing mortality
421 before and after the closure was the population (72 % showing that the clo-
422 sures were effective for population 3), followed by data resolution (21 %), data
423 type (7 %) with the least important factor the timescale (< 1 %). In general
424 the finer the spatial resolution of the data used the greater reduction in fishing
425 mortality for population 3 after the closures (Figure ??). The notable outliers
426 are the commercial data at the coarsest spatial resolution (20 x 20) at a yearly
427 and weekly timescale, where closures were nearly as effective as the fine-scale
428 resolution. In this case the closures were sufficiently large to protect a core area
429 of the habitat for the population, but this was achieved in a fairly crude manner
430 by closing a large area - including area where the species was not found (Figure
431 ??) that may have consequences in terms of restricting the fishery in a much
432 larger area than necessary.

433

434 5. Discussion

435 Our study presents a new highly resolved fisheries simulation framework,
436 evaluates the importance of data scaling and considers potential bias introduced
437 through data aggregation when using fisheries data to infer spatiotemporal dy-
438 namics of fish populations. Understanding how fishers exploit multiple hetero-
439 geneously distributed fish populations with different catch limits or conservation
440 status requires detailed understanding of the overlap of resources; this is difficult
441 to achieve using conventional modelling approaches due to species targeting in
442 fisheries resulting in preferential sampling (Martínez-Minaya et al., 2018). Of-
443 ten data are aggregated or extrapolated which requires assumptions about the

444 spatial and temporal scale of processes. Our study explores the assumptions
445 behind such aggregation and preferential sampling to identify potential impacts
446 on management advice. With modern management approaches increasingly
447 employing more nuanced spatiotemporal approaches to maximise productivity
448 while taking account of both the biological and human processes operating on
449 different time-frames (Dunn et al., 2016), understanding assumptions behind
450 the data used - increasingly a combination of logbook and positional informa-
451 tion from vessel monitoring systems - is vital to ensure measures are effective.

453 5.1. *Simulation dynamics*

454 We employ a simulation approach to model each of the population and fish-
455 ery dynamics in a hypothetical ‘mixed fishery’, allowing us to i) evaluate the
456 consequences of different aggregation assumptions on our understanding of the
457 spatiotemporal distribution of the underlying fish populations, and ii) evaluate
458 the effectiveness of a spatial closure given those assumptions.

459
460 Our approach is unique in that it captures fine scale population and fish-
461 ery dynamics and their interaction in a way not usually possible with real data
462 and thus not usually considered in fisheries simulations. While other simulation
463 frameworks seek to model individual vessel dynamics based on inferred dynam-
464 ics from VMS and logbook records (Bastardie et al., 2010), or as a system to
465 identify measures to meet particular management goals (Bailey et al., 2018), our
466 framework allows users to explore the assumptions in modelling observational
467 data and evaluate the underlying dynamics of such approaches at a fine spatial
468 and temporal scale. This offers the advantage that larger scale fishery patterns
469 are emergent properties of the system and results can be compared to those
470 obtained under a statistical modelling framework.

471
472 Typically, simulation models that treat fish as individuals are focussed on
473 exploring the inter- and intra- specific interactions among fish populations (e.g.

OSMOSE Shin et al. (2004)) in order to understand how they vary over space and time. Our focus was on understanding the strengths and limitations of inference from catch data obtained through commercial fishing activity with fleets exploiting multiple fish populations and realising catch distributions that may differ from the underlying populations. As such, we favoured a minimum realistic model of the fish populations (Plagányi et al., 2014) taking account of environmental but not demographic stochasticity, while incorporating detailed fishing dynamics that take account of different drivers in a mechanistic way.

Demographic stochasticity arises due to individual-level variability in time to reproduction and death. This form of stochasticity is often modelled by drawing random time intervals from a given distribution (Gillespie, 1977). The impact of demographic stochasticity depends on the population size, with the effects expected to decrease with increasing population size (Lande et al., 2010). This contrasts with environmental stochasticity, which affects all population sizes and is present at the population level in our model by variability in recruitment.

We take account of heterogeneity in fleet dynamics due to different preferences and drivers similarly to other approaches (Fulton et al., 2011), but at an individual vessel rather than fleet level. We do not explicitly define fleets as rational profit maximisers at the outset, but consider there are several stages to development of the fishery; information gathering through search where the resource location is not known, followed by individual learnt behaviour of profitable locations. This provides a realistic model of how fishing patterns are established and maintained to exploit an uncertain resource through an explore-exploit strategy (Mangel and Clark, 1983; Bailey et al., 2018).

5.2. *How does sampling-derived fisheries data reflect the underlying population structure?*

Our results demonstrate the importance of considering data scale and resolution when using observational data to support management measures. We find

504 that understanding of the community composition dynamics will depend on the
505 level of data aggregation and its important to consider the scale of processes;
506 including population movement rates, habitat uniformity and fishing targeting
507 practices if potential biases in data are to be understood and taken into account
508 (Figures X,Y,Z).

509

510 Our simulation shows that, despite biases introduced through the fishing pro-
511 cess, the commercially derived data could still inform on the key spatial patterns
512 in the community structures where the fisheries occurred, which was spatially
513 limited due to the “hotspots” of commercially valuable species being fished.
514 Similarly, despite the even spatial coverage the survey was able to capture some
515 of the same spatial patterns as the ‘real population’, but missed others due to
516 gaps between survey stations limiting spatial and temporal coverage (Figures
517 X,Y,Z). This provides a challenge when modelling unsampled areas in inferring
518 species distribution maps, though these limitations may be overcome by un-
519 derstanding the relationship between the species and habitat covariates where
520 these are known at unsampled locations (Robinson et al., 2011).

521

522 *5.3. How does data aggregation and source impact on spatial fisheries manage-* 523 *ment measures?*

524 From our simulations spatial disaggregation was more important than the
525 temporal disaggregation of the commercial data. This reflects the fact that there
526 was greater spatial heterogeneity over the spatial domain than experienced in
527 individual locations over the course of the year (Figure ??).

528

529 The yearly data assumes the same proportion of each population caught at
530 any time of the year due to the data aggregation. This assumption introduces
531 ‘aggregation bias’ as the data may only be representative of some point (or no
532 point) in time. The monthly data shows some consistency between the ‘real
533 population’ and commercial data for species 2 - 4, though species 1 remains

534 under-represented. On an annual basis, interestingly the commercial data un-
535 der represents the first species (in red) while the survey over represents species
536 1. This is likely due to the biases in commercial sampling, with the fisheries not
537 targeting the areas where species 1 are present and the survey sampling areas
538 where species 1 is more abundant than on average.

539

540 This indicates that fixed closures, at the right resolution, when based on
541 commercially derived data have the potential to reduced fishing mortality. The
542 likely cost of poor spatial and temporal resolution is associated with reduced
543 effectiveness and potentially closing fishing opportunities for other fisheries.

544

545 Two contrasting real world approaches in this respect were the spatial clo-
546 sures to protect cod in the North Sea. In one example, large scale spatial closures
547 were implemented with little success due to effort displacement to previously
548 unfished areas (Dinmore et al., 2003), while in another small scale targeted
549 spatiotemporal closures were considered to have some effect in reducing cod
550 mortality without having to disrupt other fisheries significantly (Needle and
551 Catarino, 2011). These examples emphasise the importance of considering the
552 right scale and aggregation of data when identifying area closures and the need
553 to consider changing dynamics in the fisheries in response to such closures.

554

555 Our study showed that fishing rates on other populations also changed (both
556 up and down) as a side-effect of closures to protect one species. This indicates
557 the importance in considering fishing effort reallocation following spatial clo-
558 sures, and our simulation allows us to consider the spatiotemporal reasons for
559 these changes.

560 5.4. *Model assumptions and caveats*

561 We model the population and fleet dynamic processes to draw inference on
562 the importance of data scale and aggregation in understanding and managing
563 mixed fisheries and their impact on multiple fish populations. In doing so, we

564 have necessarily had to make a number of simplifying assumptions.

565

566 Fish populations in our simulations move in pre-defined timescales and ac-
567 cording to fixed habitat preferences and temperature gradients (Figures ??,
568 ??). Our assumptions in parameterising the model (movement rates, temper-
569 ature tolerances) will have a direct impact on our conclusions on the relative
570 importance of spatial and temporal processes. These assumptions could be ex-
571 plored in a future study by varying the parameters and assessing the robustness
572 of our conclusions. For our example application we have chosen movement rates
573 to reflect aggregation periods observed in past studies (Poos and Rijnsdorp,
574 2007b).

575

576 In addition, we have assumed that fishing vessels are not restricted by quota
577 and therefore discarding of species for which vessels have no quota or that are
578 unwanted is not taken into account. This is likely to be a significant source of
579 bias in any inference using commercial data and should also be explored. For
580 example, MixFishSim could be altered to allow for spatiotemporal appraisal of
581 the impact of discarding on fisher behaviour and underlying populations via in-
582 clusion as discarding behaviour, or through move-on rules or cessation of fishing
583 activity when quota is exhausted.

584

585 5.5. Future applications of *MixFishSim*

586 We consider that the increased availability of high resolution catch and lo-
587 cational information from commercial fisheries will require it to be a key source
588 of data for ensuring management is implemented at the right scale in future.
589 For example, identifying hot-spots for bycatch reduction or identifying spatial
590 overlaps in mixed fisheries (Dolder et al., 2018; Gardner et al., 2008; Little et al.,
591 2014; Dedman et al., 2015; Ward et al., 2015). Our simulation model has the
592 potential to test some of the assumptions behind the modelling approaches in
593 identifying such hotspots and indeed behind spatiotemporal modelling in gen-

594 eral (e.g. comparing GAMs, GLMMs, Random Forests and geostatistical mod-
595 els under different data generation processes as exemplified by Stock et al. (2019)).

596

597 Other novel applications of our framework could be: testing different sur-
598 vey designs given multiple species and data generating assumptions (Xu et al.,
599 2015); commercial index standardisation methods and approaches and under-
600 standing of appropriate scales and data aggregations and non-proportionality
601 in catch rate and abundance (Harley et al., 2001; Maunder and Punt, 2004);
602 exploring assumptions about the distribution of natural mortality and fishing
603 mortality throughout the year and importance of capturing in-year dynamics
604 in estimating stock status (Liu and Heino, 2013); at sea sampling scheme de-
605 signs to deliver unbiased estimates of population parameters (Cotter and Pilling,
606 2007; Kimura and Somerton, 2006); adaptive management (Walters, 2007; Dunn
607 et al., 2016); testing the ability of commonly employed fleet dynamics models
608 such as Random Utility Models to capture fine scale dynamics and understand
609 their importance (Girardin et al., 2016); and as a detailed operating model in a
610 management strategy evaluation (Mahévas and Pelletier, 2004).

611

612 **6. Conclusions**

613 MixFishSim provides a detailed simulation framework to explore the inter-
614 action of multiple fisheries exploiting different fish populations. The framework
615 enables users to evaluate assumptions in modelling commercially derived data
616 through comparison to the true underlying dynamics at a fine spatial and tem-
617 poral scale. Understanding these dynamics, the limitations of the data and any
618 potential biases that may be introduced when making inference on spatiotempo-
619 ral interactions will enable users to identify weaknesses in modelling approaches
620 and identify where data collection is needed to strengthen inference.

621

622 Our application shows that inference on community dynamics may change

623 depending on the scale of data aggregation. There is an important balance in
624 ensuring that the data are sufficiently spatially and temporally disaggregated
625 that the main features of the data are captured, yet maintaining enough data
626 coverage that the features can be distinguished. We found in our application
627 that there was greater spatial heterogeneity than temporal heterogeneity and
628 that when using aggregated data to define spatial closures coarser temporal reso-
629 lution (months instead of weeks) could still achieve the same results in reducing
630 exploitation rates of a vulnerable species at the highest temporal resolution
631 data. Conversely, reducing the spatial resolution had a negative effect on the
632 effectiveness of the measures (though importantly, there was still some benefit
633 even with coarse spatial resolution).

634

635 While any findings are likely to be case specific, our findings emphasise the
636 need to understand population demographics, habitat use and movement rates
637 in designing any closure scenario based on observational sampling. This infor-
638 mation can then be used to set the bounds on data aggregation used in modelling
639 studies aimed at informing the management measures.

640

641 MixFishSim has numerous potential additional applications as it enables
642 the user to apply methods to a fisheries system where there is detailed under-
643 standing of underlying spatiotemporal dynamics. This enables identification of
644 weaknesses or limitations which would not be possible otherwise. In future, we
645 recommend use of the framework to test hypothesis that are otherwise unable
646 to be analysed using real world data due to limitations of data collection. That
647 way the knowledge gained through simulation can inform the future design of
648 management measures.

649 **Abbreviations**

650 Detail any unusual ones used.

651 Acknowledgements

652 those providing help during the research..

653 Funding

654 This work was supported by the MARES doctoral training program (MARES_14_15)
655 and the Centre for Environment, Fisheries and Aquaculture Science seedcorn
656 program (DP227AC).

657 Appendices

Table 1: Description of variables for population dynamics sub-module

Variable	Meaning	Units
Population dynamics		
<i>Delay-difference model</i>		
$B_{c,d}$	Biomass in cell c and day d	kg
$Z_{c,d}$	Total mortality in cell c for day d	-
$R_{c,\bar{y}}$	Annually recruited fish in cell	yr ⁻¹
ρ	Brody's growth coefficient	yr ⁻¹
Wt_R	Weight of a fully recruited fish	kg
Wt_{R-1}	Weight of a pre-recruit fish	kg
α_d	Proportion of annually recruited fish recruited during day d	-
<i>Baranov catch equation</i>		
$C_{c,d}$	Catch from cell c for day d	kg
$F_{c,d}$	Instantaneous rate of fishing mortality in cell c on day d	-
$M_{c,d}$	Instantaneous rate of natural mortality in cell c on day d	-
$B_{c,d}$	Biomass in cell c on day d	kg
Recruitment dynamics		
$\tilde{R}_{c,d}$	is the recruitment in cell c for day d	d^{-1}
$S_{c,d}$	is the stock size in cell c for day d	d^{-1}
α	the maximum recruitment rate	kg
β	the stock size required to produce half the maximum rate of recruitment	kg

Table 2: Description of variables for population movement sub-module

Variable	Meaning	Units
Population movement dynamics		
<i>Habitat model</i>		
a	b	c
<i>Thermal tolerance</i>		
$T_{c,wk}$	Temperature for cell in week	°C
μ_p	Mean of the thermal tolerance for population	°C
σ_p^2	Standard deviation of thermal tolerance for the population	°C
<i>Population movement model</i>		
λ	decay rate for population movement	-
$Hab_{c,p}^2$	Square of habitat suitability for cell c and population p	-
$Tol_{c,p,wk}$	Thermal tolerance for population p in cell c at week wk	-
d_{IJ}	euclidean distance between cell I and cell J	-

Table 3: Description of variables for fleet dynamics sub-module

Variable	Meaning	Units
Short-term fleet dynamics		
Rev	Revenue from fishing tow	€
L_p	Landings of population p	kg
Pr_p	Average price of population p	€ kg ⁻¹
StepL	Step length for vessel	euclidean distance
Br	Bearing	degrees
k	Concentration parameter for Von mises distribution	-
β_1	shape parameter for step function	-
β_2	shape parameter for step function	-
β_3	shape parameter for step function	-

Table 4: Population dynamics and movement parameter setting

Parameter	Pop 1	Pop 2	Pop 3	Pop 4
Habitat quality				
Matérn ν	1/0.015	1/0.05	1/0.01	1/0.005
Matérn κ	1	2	1	1
Anisotropy	1.5,3,-3,4	1,2,-1,2	2.5,1,-1,2	0.1,2,-1,0.2
Spawning areas (bound box)	40,50,40,50; 80,90,60,70	50,60,30,40; 80,90,90,90	30,34,10,20; 60,70,20,30	50,55,80,85; 30,40,30,40
Spawning multiplier	10	10	10	10
Movement λ	0.1	0.1	0.1	0.1
Population dynamics				
Starting Biomass	1e5	2e5	1e5	1e4
Beverton-Holt Recruit 'a'	6	27	18	0.3
Beverton-Holt Recruit 'b'	4	4	11	0.5
Beverton-Holt Recruit σ^2	0.7	0.6	0.7	0.6
Recruit week	13-16	12-16	14-16	16-20
Spawn week	16-18	16-19	16-18	18-20
K	0.3	0.3	0.3	0.3
wt	1	1	1	1
wt_{d-1}	0.1	0.1	0.1	0.1
M (annual)	0.2	0.1	0.2	0.1
Movement dynamics				
μ	12	15	17	14
σ^2	8	9	7	10

Table 5: Fleet dynamics parameter setting

Parameter	Fleet	Fleet	Fleet	Fleet	Fleet
	1	2	3	4	5
Targeting preferences	pop	pop	-	pop 4	pop
	2/4	1/3			2/3
Price Pop1	100	100	100	100	100
Price Pop2	200	200	200	200	200
Price Pop3	350	350	350	350	350
Price Pop4	600	600	600	600	600
Q Pop1	0.01	0.02	0.02	0.01	0.01
Q Pop2	0.02	0.01	0.02	0.01	0.03
Q Pop3	0.01	0.02	0.02	0.01	0.02
Q Pop4	0.02	0.01	0.02	0.05	0.01
Exploitation dynamics					
step function β_1	1	2	1	2	3
step function β_2	10	15	8	12	7
step function β_3	Q90	Q90	Q85	Q90	Q80
step function $rate$	20	30	25	35	20
Past Knowledge	T	T	T	T	T
Past Year & Month	T	T	T	T	T
Past Trip	T	T	T	T	T
Threshold	0.7	0.7	0.7	0.7	0.7
Fuel Cost	3	2	5	2	1

Table 6: Fishing mortality effects of the closure scenarios. Results show the fishing mortality before the closure (f.before) and after the closure (f.after) and the percentage change in f (f.change). The results are ordered by most effective scenario first, least effective last.)

scenario	metric	pop	f.before	f.after	f.change	timescale	basis	data_type	resolution
9	F	spp_3	1.08	0.29	-73.47	weekly	high_pop	real_pop	1.00
10	F	spp_3	1.08	0.29	-72.94	monthly	high_pop	real_pop	1.00
11	F	spp_3	1.08	0.35	-68.04	yearly	high_pop	real_pop	1.00
45	F	spp_3	1.08	0.58	-46.70	yearly	high_pop	commercial	20.00
1	F	spp_3	1.08	0.58	-46.21	weekly	high_pop	commercial	1.00
23	F	spp_3	1.08	0.59	-45.27	weekly	high_pop	real_pop	5.00
2	F	spp_3	1.08	0.59	-45.06	monthly	high_pop	commercial	1.00
7	F	spp_3	1.08	0.60	-44.48	yearly	high_pop	survey	1.00
24	F	spp_3	1.08	0.61	-43.20	monthly	high_pop	real_pop	5.00
3	F	spp_3	1.08	0.64	-40.82	yearly	high_pop	commercial	1.00
25	F	spp_3	1.08	0.65	-39.94	yearly	high_pop	real_pop	5.00
17	F	spp_3	1.08	0.67	-38.11	yearly	high_pop	commercial	5.00
15	F	spp_3	1.08	0.71	-34.38	weekly	high_pop	commercial	5.00
43	F	spp_3	1.08	0.71	-34.31	weekly	high_pop	commercial	20.00
16	F	spp_3	1.08	0.73	-32.58	monthly	high_pop	commercial	5.00
51	F	spp_3	1.08	0.78	-27.92	weekly	high_pop	real_pop	20.00
37	F	spp_3	1.08	0.78	-27.76	weekly	high_pop	real_pop	10.00
39	F	spp_3	1.08	0.79	-26.98	yearly	high_pop	real_pop	10.00
38	F	spp_3	1.08	0.81	-25.47	monthly	high_pop	real_pop	10.00
21	F	spp_3	1.08	0.81	-25.21	yearly	high_pop	survey	5.00
35	F	spp_3	1.08	0.81	-25.05	yearly	high_pop	survey	10.00
44	F	spp_3	1.08	0.87	-19.91	monthly	high_pop	commercial	20.00
52	F	spp_3	1.08	0.88	-18.39	monthly	high_pop	real_pop	20.00
30	F	spp_3	1.08	0.96	-11.06	monthly	high_pop	commercial	10.00
29	F	spp_3	1.08	0.98	-9.80	weekly	high_pop	commercial	10.00
31	F	spp_3	1.08	1.03	-4.36	yearly	high_pop	commercial	10.00
53	F	spp_3	1.08	1.06	-1.64	yearly	high_pop	real_pop	20.00
49	F	spp_3	1.08	1.07	-1.01	yearly	high_pop	survey	20.00

Table 7: Proportions of each species at different levels of temporal aggregation

data_type	timescale	spp1	sd_spp1	spp2	sd_spp2	spp3	sd_spp3	spp4	sd_spp4
commercial	monthly	0.047	0.014	94.435	1.470	3.122	1.468	2.396	0.444
commercial	weekly	0.047	0.016	94.426	1.514	3.117	1.563	2.411	0.498
commercial	yearly	0.051	0.001	94.388	0.205	3.021	0.175	2.539	0.046
real_pop	monthly	9.225	3.872	83.287	5.522	3.624	1.151	3.864	1.519
real_pop	weekly	9.358	3.992	83.165	5.596	3.567	1.233	3.910	1.592
real_pop	yearly	9.899	0.173	82.250	0.308	3.821	0.119	4.031	0.050
survey	yearly	0.372	0.005	87.667	0.193	0.729	0.020	11.232	0.172



Figure 1: Schematic overview of the simulation model. Blue boxes indicate fleet dynamics processes, the green boxes population dynamics processes while the white boxes are the time steps at which processes occur; $t = \text{tow}$, t_{max} is the total number of tows; (Rec), (Pop Movement), (Pop Dynamics) logic gates for recruitment periods, population movement and population dynamics for each of the populations, (Past Knowledge) a switch whether to use a random (exploratory) or past knowledge (exploitation) fishing strategy.

658 References

- 659 Akima, H., 2006. Interpolation of irregularly spaced data, The akima Package. Interpolation
660 of Irregularly and Regularly Spaced Data .
- 661 Alverson, D.L., Freeberg, M.H., Murawski, S.A., Pope, J., 1994. A global assessment of
662 fisheries bycatch and discards.
- 663 Bailey, R.M., Carrella, E., Axtell, R., Burgess, M.G., Cabral, R.B., Drexler, M., Dorsett, C.,
664 Madsen, J.K., Merkl, A., Saul, S., 2018. A computational approach to managing coupled
665 human–environmental systems: the POSEIDON model of ocean fisheries.
- 666 Bartumeus, F., Da Luz, M.G.E., Viswanatham, G.M., Catalan, J., 2005. Animal Search
667 Strategies: A Quantitative Random Walk Analysis. *Ecological Society of America* 86,
668 3078–3087.
- 669 Bastardie, F., Nielsen, J.R., Ulrich, C., Egekvist, J., Degel, H., 2010. Detailed mapping
670 of fishing effort and landings by coupling fishing logbooks with satellite-recorded vessel
671 geo-location. *Fisheries Research* 106, 41–53.
- 672 Batsleer, J., Hamon, K.G., Overzee, H.M.J., Rijnsdorp, A.D., Poos, J.J., 2015. High-grading
673 and over-quota discarding in mixed fisheries. *Reviews in Fish Biology and Fisheries* 25,
674 715–736.
- 675 Bellido, J.M., Santos, M.B., Pennino, M.G., Valeiras, X., Pierce, G.J., 2011. Fishery discards
676 and bycatch: Solutions for an ecosystem approach to fisheries management? *Hydrobiologia*
677 670, 317–333.
- 678 Bertrand, S., Bertrand, A., Guevara-Carrasco, R., Gerlotto, F., 2007. Scale-invariant move-
679 ments of fishermen: The same foraging strategy as natural predators. *Ecological Applica-*
680 *tions* 17, 331–337.
- 681 Beverton, R.J., Holt, S.J., 1957. On the Dynamics of Exploited Fish Populations , 533.
- 682 Branch, T., Hilborn, R., Bogazzi, E., 2005. Escaping the tyranny of the grid: a more realistic
683 way of defining fishing opportunities. *Canadian Journal of Fisheries and Aquatic Sciences*
684 642, 631–642.
- 685 Catchpole, T.L., Revill, A.S., 2008. Gear technology in Nephrops trawl fisheries. *Reviews in*
686 *Fish Biology and Fisheries* 18, 17–31.
- 687 Codling, E.A., Plank, M.J., Benhamou, S., Interface, J.R.S., 2008. Random walk models in
688 biology. *Journal of the Royal Society, Interface / the Royal Society* 5, 813–34.

689 Cosgrove, R., Browne, D., Minto, C., Tyndall, P., Oliver, M., Montgomerie, M., McHugh,
690 M., 2019. A game of two halves: Bycatch reduction in Nephrops mixed fisheries. *Fisheries*
691 *Research* 210, 31–40.

692 Costello, C., Rassweiler, A., Siegel, D., De Leo, G., Micheli, F., Rosenberg, A., 2010. The
693 value of spatial information in MPA network design. *Proceedings of the National Academy*
694 *of Sciences* .

695 Cotter, A.J., Pilling, G.M., 2007. Landings, logbooks and observer surveys: Improving the
696 protocols for sampling commercial fisheries. *Fish and Fisheries* 8, 123–152.

697 Crowder, B.L.B., Murawski, S.a., Crowder, L.B., Murawski, S.a., 1998. Fisheries Bycatch:
698 Implications for Management. *Fisheries* 23, 8–17.

699 Dedman, S., Officer, R., Brophy, D., Clarke, M., Reid, D.G., 2015. Modelling abundance
700 hotspots for data-poor Irish Sea rays. *Ecological Modelling* 312, 77–90.

701 Deriso, R.B., 1980. Harvesting Strategies and Parameter Estimation for an Age-Structured
702 Model. *Canadian Journal of Fisheries and Aquatic Sciences* 37, 268–282. [arXiv:1410.7455v3](#).
703 7455v3.

704 Dichmont, C.M., Punt, A.E., Deng, A., Dell, Q., Venables, W., 2003. Application of a weekly
705 delay-difference model to commercial catch and effort data for tiger prawns in Australia ’
706 s Northern Prawn Fishery. *Fisheries Research* 65, 335–350.

707 Dinmore, T.A., Duplisea, D.E., Rackham, B.D., Maxwell, D.L., Jennings, S., 2003. Impact
708 of a large-scale area closure on patterns of fishing disturbance and the consequences for
709 benthic communities. *ICES Journal of Marine Science* 60, 371–380.

710 Dolder, P.J., Thorson, J.T., Minto, C., 2018. Spatial separation of catches in highly mixed
711 fisheries. *Scientific Reports* .

712 Dunn, D.C., Boustany, A.M., Roberts, J.J., Brazer, E., Sanderson, M., Gardner, B., Halpin,
713 P.N., 2014. Empirical move-on rules to inform fishing strategies: A New England case
714 study. *Fish and Fisheries* 15, 359–375.

715 Dunn, D.C., Maxwell, S.M., Boustany, A.M., Halpin, P.N., 2016. Dynamic ocean management
716 increases the efficiency and efficacy of fisheries management. *Proceedings of the National*
717 *Academy of Sciences* , 201513626.

718 Edwards, A.M., Station, P.B., Canada, O., 2011. Overturning conclusions of Lévy flight
719 movement patterns by fishing boats and foraging animals. *Ecology* 92, 1247–1257.

720 F. Dormann, C., M. McPherson, J., B. Araújo, M., Bivand, R., Bolliger, J., Carl, G., G.
721 Davies, R., Hirzel, A., Jetz, W., Daniel Kissling, W., Kühn, I., Ohlemüller, R., R. Peres-
722 Neto, P., Reineking, B., Schröder, B., M. Schurr, F., Wilson, R., 2007. Methods to account
723 for spatial autocorrelation in the analysis of species distributional data: A review. *Ecogra-*
724 *phy* 30, 609–628.

725 Fulton, E.A., Link, J.S., Kaplan, I.C., Savina-Rolland, M., Johnson, P., Ainsworth, C., Horne,
726 P., Gorton, R., Gamble, R.J., Smith, A.D., Smith, D.C., 2011. Lessons in modelling and
727 management of marine ecosystems: The Atlantis experience. *Fish and Fisheries* .

728 Gardner, B., Sullivan, P.J., Morreale, S.J., Epperly, S.P., 2008. Spatial and temporal statistical
729 analysis of bycatch data: patterns of sea turtle bycatch in the North Atlantic. *Canadian*
730 *Journal of Fisheries and Aquatic Sciences* 65, 2461–2470.

731 Gerritsen, H.D., Lordan, C., Minto, C., Kraak, S.B.M., 2012. Spatial patterns in the re-
732 tained catch composition of Irish demersal otter trawlers: High-resolution fisheries data as
733 a management tool. *Fisheries Research* 129-130, 127–136.

734 Gillespie, D.T., 1977. Exact stochastic simulation of coupled chemical reactions, in: *Journal*
735 *of Physical Chemistry*.

736 Gillis, D.M., Peterman, R.M., 1998. Implications of interference among fishing vessels and
737 the ideal free distribution to the interpretation of CPUE. *Canadian Journal of Fisheries*
738 *and Aquatic Sciences* 55, 37–46.

739 Girardin, R., Hamon, K.G., Pinnegar, J., Poos, J.J., Thébaud, O., Tidd, A., Vermard, Y.,
740 Marchal, P., 2016. Thirty years of fleet dynamics modelling using discrete-choice models:
741 What have we learned? *Fish and Fisheries* , 1–18.

742 Girardin, R., Vermard, Y., Thébaud, O., Tidd, A., Marchal, P., 2015. Predicting fisher
743 response to competition for space and resources in a mixed demersal fishery. *Ocean &*
744 *Coastal Management* 106, 124–135.

745 Harley, S.J., Myers, R.A., Dunn, A., 2001. Is catch-per-unit-effort proportional to abundance?
746 *Canadian Journal of Fisheries and Aquatic Sciences* 58, 1760–1772.

747 Hilborn, R., Walters, C., 1992. Quantitative fisheries stock assessment: Choice, dynamics and
748 uncertainty. volume 2. [arXiv:1011.1669v3](https://arxiv.org/abs/1011.1669v3).

749 Holmes, S.J., Bailey, N., Campbell, N., Catarino, R., Barratt, K., Gibb, A., Fernandes, P.G.,
750 2011. Using fishery-dependent data to inform the development and operation of a co-
751 management initiative to reduce cod mortality and cut discards. *ICES Journal of Marine*
752 *Science* 68, 1679–1688.

753 Hutton, T., Mardle, S., Pascoe, S., Clark, R.a., 2004. Modelling fishing location choice within
754 mixed fisheries: English North Sea beam trawlers in 2000 and 2001. *ICES Journal of Marine*
755 *Science* 61, 1443–1452.

756 Kennelly, S.J., Broadhurst, M.K., 2002. By-catch begone: Changes in the philosophy of fishing
757 technology. *Fish and Fisheries* 3, 340–355.

758 Kimura, D.K., Somerton, D.A., 2006. Review of statistical aspects of survey sampling for
759 marine fisheries. *Reviews in Fisheries Science* 14, 245–283.

760 Lande, R., Engen, S., Saether, B.E., 2010. Stochastic Population Dynamics in Ecology and
761 Conservation.

762 Lee, J., South, A.B., Jennings, S., 2010. Developing reliable, repeatable, and accessible meth-
763 ods to provide high-resolution estimates of fishing-effort distributions from vessel monitor-
764 ing system (VMS) data. *ICES Journal of Marine Science* 67, 1260–1271.

765 Little, A.S., Needle, C.L., Hilborn, R., Holland, D.S., Marshall, C.T., 2014. Real-time spatial
766 management approaches to reduce bycatch and discards: experiences from Europe and the
767 United States. *Fish and Fisheries* , n/a–n/a.

768 Liu, X., Heino, M., 2013. Overlooked biological and economic implications of within-season
769 fishery dynamics. *Canadian Journal of Fisheries and Aquatic Sciences* .

770 Mahévas, S., Pelletier, D., 2004. ISIS-Fish, a generic and spatially explicit simulation tool for
771 evaluating the impact of management measures on fisheries dynamics. *Ecological Modelling*
772 .

773 Mangel, M., Clark, C.W., 1983. Uncertainty, search, and information in fisheries. *ICES*
774 *Journal of Marine Science* .

775 Martínez-Minaya, J., Cameletti, M., Conesa, D., Pennino, M.G., 2018. Species distribution
776 modeling: a statistical review with focus in spatio-temporal issues.

777 Mateo, M., Pawlowski, L., Robert, M., 2016. Highly mixed fisheries: fine-scale spatial patterns
778 in retained catches of French fisheries in the Celtic Sea. *ICES Journal of Marine Science:*
779 *Journal du Conseil* , fsw129.

780 Maunder, M.N., Punt, A.E., 2004. Standardizing catch and effort data: A review of recent
781 approaches. *Fisheries Research* .

782 Needle, C.L., Catarino, R., 2011. Evaluating the effect of real-time closures on cod targeting.
783 *ICES Journal of Marine Science* 68, 1647–1655.

784 Plagányi, É.E., Punt, A.E., Hillary, R., Morello, E.B., Thébaud, O., Hutton, T., Pillans, R.D.,
785 Thorson, J.T., Fulton, E.A., Smith, A.D.M., Smith, F., Bayliss, P., Haywood, M., Lyne,
786 V., Rothlisberg, P.C., 2014. Multispecies fisheries management and conservation: tactical
787 applications using models of intermediate complexity. *Fish and Fisheries* 15, 1–22.

788 Poos, J.J., Rijnsdorp, A.D., 2007a. An "experiment" on effort allocation of fishing vessels:
789 the role of interference competition and area specialization. *Canadian Journal of Fisheries*
790 *and Aquatic Sciences* 64, 304–313.

791 Poos, J.J., Rijnsdorp, A.D., 2007b. The dynamics of small-scale patchiness of plaice and sole
792 as reflected in the catch rates of the Dutch beam trawl fleet and its implications for the
793 fleet dynamics. *Journal of Sea Research* 58, 100–112.

794 R Core Team, 2017. R Core Team (2017). R: A language and environment for statistical
795 computing. R Foundation for Statistical Computing, Vienna, Austria. URL [http://www.R-](http://www.R-project.org/)
796 [project.org/](http://www.R-project.org/) , R Foundation for Statistical Computing.

797 Reynolds, A., 2015. Liberating Lévy walk research from the shackles of optimal foraging.

798 Ricker, W.E., 1954. Stock and recruitment. *Journal of the Fisheries Research Board of Canada*
799 11, 559 – 623.

800 Rijnsdorp, A., 2000. Competitive interactions among beam trawlers exploiting local patches
801 of flatfish in the North Sea. *ICES Journal of Marine Science* 57, 894–902.

802 Rijnsdorp, a.D., Daan, N., Dekker, W., Poos, J.J., Van Densen, W.L.T., 2007. Sustainable
803 use of flatfish resources: Addressing the credibility crisis in mixed fisheries management.
804 *Journal of Sea Research* 57, 114–125.

805 Rijnsdorp, A.D., Piet, G.J., Poos, J.J., 2001. Effort allocation of the Dutch beam trawl fleet
806 in response to a temporarily closed area in the North Sea. *Ices Cm 2001/N: 01* , 1–17.

807 Robinson, L.M., Elith, J., Hobday, A.J., Pearson, R.G., Kendall, B.E., Possingham, H.P.,
808 Richardson, a.J., 2011. Pushing the limits in marine species distribution modelling: Lessons
809 from the land present challenges and opportunities. *Global Ecology and Biogeography* 20,
810 789–802.

811 Sakiyama, T., Gunji, Y.P., 2013. Emergence of an optimal search strategy from a simple
812 random walk. *Journal of the Royal Society, Interface* 10, 20130486.

813 Schlater, M., Malinowski, A., Menck, P.J., 2015. Analysis, Simulation and Prediction of
814 Multivariate Random Fields with Package RandomFields. *Journal of Statistical Software*
815 63, 1–25. [arXiv:1501.0228](https://arxiv.org/abs/1501.0228).

816 Schnute, J., 1985. A general theory for analysis of catch and effort data. *Canadian Journal of*
817 *Fisheries and Aquatic Sciences* 42, 414–429.

818 Sela, R., Simonoff, J., 2012. Package ‘REEMtree’.

819 Shin, Y.J., Shannon, L.J., Cury, P.M., 2004. Simulations of fishing effects on the southern
820 Benguela fish community using an individual-based model: Learning from a comparison
821 with ECOSIM, in: *African Journal of Marine Science*.

822 Sims, D.W., Humphries, N.E., Bradford, R.W., Bruce, B.D., 2012. Lévy flight and Brownian
823 search patterns of a free-ranging predator reflect different prey field characteristics. *Journal*
824 *of Animal Ecology* 81, 432–442.

825 Sims, D.W., Southall, E.J., Humphries, N.E., Hays, G.C., Bradshaw, C.J.A., Pitchford, J.W.,
826 James, A., Ahmed, M.Z., Brierley, A.S., Hindell, M.A., Morritt, D., Musyl, M.K., Righton,
827 D., Shepard, E.L.C., Wearmouth, V.J., Wilson, R.P., Witt, M.J., Metcalfe, J.D., 2008.
828 Scaling laws of marine predator search behaviour. *Nature* 451, 1098–U5.

829 Stock, B.C., Ward, E.J., Eguchi, T., Jannot, J.E., Thorson, J.T., Feist, B.E., Semmens, B.X.,
830 2019. Comparing predictions of fisheries bycatch using multiple spatiotemporal species
831 distribution model frameworks. *Canadian Journal of Fisheries and Aquatic Sciences* .

832 Tidd, A.N., Hutton, T., Kell, L.T., Blanchard, J.L., 2012. Dynamic prediction of effort
833 reallocation in mixed fisheries. *Fisheries Research* 125–126, 243–253.

834 Tobler, W.R., 1970. A Computer Movie Simulating Urban Growth in the Detroit Region.
835 *Economic Geography* 46, 234. [arXiv:1011.1669v3](#).

836 Ulrich, C., Reeves, S.a., Vermard, Y., Holmes, S.J., Vanhee, W., 2011. Reconciling single-
837 species TACs in the North Sea demersal fisheries using the Fcube mixed-fisheries advice
838 framework. *ICES Journal of Marine Science* 68, 1535–1547.

839 Van Putten, I.E., Kulmala, S., Thébaud, O., Dowling, N., Hamon, K.G., Hutton, T., Pascoe,
840 S., 2012. Theories and behavioural drivers underlying fleet dynamics models. *Fish and*
841 *Fisheries* 13, 216–235.

842 Viswanathan, G.M., Buldyrev, S.V., Havlin, S., Da Luz, M.G.E., Raposo, E.P., Stanley, H.E.,
843 1999. Optimizing the success of random searches. *Nature* 401, 911–914.

844 Walters, C.J., 2007. Is adaptive management helping to solve fisheries problems? *Ambio* .

845 Ward, E.J., Jannot, J.E., Lee, Y.W., Ono, K., Shelton, A.O., Thorson, J.T., 2015. Using spa-
846 tiotemporal species distribution models to identify temporally evolving hotspots of species
847 co-occurrence. *Ecological Applications* 25, 2198–2209.

848 Xu, B., Zhang, C., Xue, Y., Ren, Y., Chen, Y., 2015. Optimization of sampling effort for a
849 fishery-independent survey with multiple goals. *Environmental Monitoring and Assessment*
850 .