

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

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## Abstract

To understand how data resolution impacts inference on mixed fisheries interactions we developed a highly resolved spatiotemporal discrete-event 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 population targeting under an explore-exploit strategy. This is implemented via a mix of correlated random walk movement (for exploration) and learned behaviour (for exploitation) phases of the fisheries.

Fifty years of sub-daily fishing activity 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 populations. 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.

Our framework allows users to explore the assumptions in modelling observational data and evaluate the underlying dynamics of such approaches at a fine

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spatial and temporal scale. In application to a mixed fishery exploiting four different populations we found different spatial patterns were evident and that the effectiveness of the spatial closure reduced when data were aggregated across larger spatial areas. However, aggregation across time periods has less of a negative impact on the closure success and while not as effective as when based on the true population, closures based on high catch rates observed in commercial data could still reduce fishing on a protected species.

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.

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## 1. Introduction

Fishers exploit a variety of fish populations that are heterogeneously distributed in space and time with varying knowledge of species distributions. As fishers do not have full control over what species they select when fishing in ‘mixed fisheries’ it can result in catch of low quota or protected species. If over-quota catch of a species for which they have no quota is discarded without being accounted for it limits our ability to control fishing mortality (Alverson et al., 1994; Crowder et al., 1998; Rijnsdorp et al., 2007) and the ability to manage fisheries for the biological and economic sustainability (Ulrich et al., 2011; Battlesler et al., 2015).

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) and adaptive spatial management strategies have been proposed as a way of reduc-

16 ing over-quota discards (Holmes et al., 2011; Little et al., 2014; Dunn et al.,  
17 2014). However, if fisheries are to reduce unwanted catch through spatial avoid-  
18 ance, an in-depth understanding of spatiotemporal fishery dynamics is required.

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20 Understanding the correct scale for spatial management measures to be effec-  
21 tive is crucial as it enables implementation of effective solutions which minimise  
22 economic impact (Dunn et al., 2016). For example, the problem can be to iden-  
23 tify a scale that promotes species avoidance for vulnerable or low quota species  
24 while allowing continuance of sustainable fisheries for available quota species.  
25 Identifying the correct spatial scale remains a challenge because data on fish  
26 location at high temporal and spatial resolutions is expensive and difficult to  
27 collect and proxies are usually inferred from scientific surveys or commercial  
28 catches with limited spatial and temporal resolution. Thus, implementation of  
29 spatial measures is hampered by a lack of knowledge of fish and fishery spa-  
30 tiotemporal dynamics and understanding of the scale at which these processes  
31 become important for management.

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34 Identifying appropriate spatial scales for fisheries closures has been a high-  
35 lighted as crucial to their success (Costello et al., 2010; Dunn et al., 2016).  
36 Inference on fisheries spatial dynamics is hampered where spatial information  
37 is coarse due to low resolution reporting of fisheries catch which is aggregated  
38 across larger gridded areas (Branch et al., 2005). Further, if data does not allow  
39 identification of spatial features it may lead to poorly sited closures which are  
40 ineffectual or have unintended consequences. For example, increased benthic  
41 impact on previously unexploited areas from the cod closure in the North Sea  
42 were observed without the intended effect of reducing cod exploitation (Rijns-  
43 dorp et al., 2001; Dinmore et al., 2003)).

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45 More refined spatiotemporal information has since become available through  
46 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 (Rijnsdorp et al., 2011; 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. There is a need to understand the influence of these biases on any spatial management measures which are implemented based on inference from commercial landings or catch data.

To understand the effect of spatiotemporal aggregation of data and fishery targeting on our perception of spatial abundance of different fish populations we ask two fundamental questions regarding inference derived from observational data:

1. Do different source of sampling-derived fisheries data reflects the underlying community structure?
2. How does data aggregation and data source impact on the success of spatial fisheries management measures?

To answer these questions we i) develop a simulation model where population dynamics are highly-resolved in space and time, using a Gaussian spatial process to define suitable habitat for different populations. As the precise locations of the fish are known directly rather than inferred from sampling or commercial catch, we can use the population model to validate how inference from fisheries-dependent and fisheries independent sampling relates to the real community structure in a way we could not with real data. We ii) compare, at different spatial and temporal aggregations, the real (simulated) population distributions to samples from fisheries-dependent and fisheries independent catches to test if these are a true reflection of the relative density of the populations.

76 We then iii) simulate a fishery closure to protect a species based on different  
77 spatial and temporal data aggregations.

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79 We use these evaluations to draw inference on the utility of commercial data  
80 in supporting management decisions.

## 81 **2. Materials and Methods**

82 A Discrete-event simulation (DES) model of a hypothetical fishery was de-  
83 veloped as a software package (*MixFishSim*). The modular approach enabled  
84 efficient computation by allowing for sub-modules implemented on time-scales  
85 appropriate to capture the characteristic of the different processes (Figure 1).  
86 The following sub-modules were included to capture the full system: 1) Popu-  
87 lation dynamics, 2) Recruitment dynamics, 3) Population movement, 4) fishery  
88 dynamics.

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

### 93 *2.1. Population dynamics*

94 The basic population level processes were simulated using a modified two-  
95 stage Deriso-Schnute delay difference model which models the fish populations in  
96 terms of aggregate biomass of recruits and mature components rather than keep-  
97 ing track of individuals (Deriso, 1980; Schnute, 1985; Dichmont et al., 2003). A  
98 daily time-step was chosen to discretise continuous population processes on a bi-  
99 ologically relevant and computationally tractable timescale. Population biomass  
100 growth was modelled as a function of previous recruited biomass, intrinsic pop-  
101 ulation growth and recruitment functionally linked to the adult population size.  
102 Biomass for each cell  $c$  was incremented each day  $d$  as follows (the full parameter

list is detailed in Table 1):

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

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

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Mortality  $Z_{c,d}$  can be decomposed to natural mortality,  $M_{c,d}$ , and fishing 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  $F_{c,d}$ :

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

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 is the sum of those across all fleets and vessels,  $C_{c,d} = \sum_{fl=1}^{fl} \sum_{v=1}^v E_{fl,v,c,d} \cdot Q_{fl} \cdot D_{c,d}$  with  $fl$  and  $v$  the fleet and vessel respectively and  $E_{fl,v,c,d}$  and  $Q_{fl}$  fishing effort and catchability of the gear, and  $D_{c,d}$  is the density of the population at the location fished.

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## 2.2. Recruitment dynamics

Recruitment is modelled as a function of adult biomass. In *MixFishSim*, it can either take the form of a stochastic Beverton-Holt stock recruitment relationship, or a stochastic Ricker stock recruitment relationship. The Beverton-Holt

relationship is defined as (Beverton and Holt, 1957):

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

Where  $\alpha$  is the maximum recruitment rate,  $\beta$  the spawning stock biomass (SSB) required to produce half the maximum stock size,  $S$  current stock size and  $\sigma^2$  the variability in the recruitment due to stochastic processes, the stochastic Ricker form (Ricker, 1954):

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

where  $\alpha$  is the maximum productivity per spawner and  $\beta$  the density dependent reduction in productivity as the SSB increases.

### 2.3. Population movement dynamics

Population movement is a combination of directed (advective) movement where at certain times of year the population moves towards spawning grounds by increasing the probabilities of moving into the spawning grounds from adjacent cells, and random (diffusive) movement, governed by a stochastic process where movement between adjacent cells is described by a set of probabilities.

To simulate fish population distribution in space and time a Gaussian spatial process was employed to model habitat suitability for each of the populations on a 2d grid. We first defined a Gaussian random field process,  $\{S(c) : c \in \mathbb{R}^2\}$ , where for any set of cells  $c_1, \dots, c_n$ , the joint distribution of  $S = \{S(c_1), \dots, S(c_n)\}$  is multivariate Gaussian with a *Matérn* covariance structure, where the correlation strength weakens with distance. This enables us to model the spatial autocorrelation observed in animal populations where density is more similar in nearby locations (Tobler, 1970; F. Dormann et al., 2007; Poos and Rijnsdorp, 2007b) and we change the parameters to implement different spatial structures for the different populations using the *RandomFields* R package

(Schlater et al., 2015). We define a stationary habitat field and combine it with a temporally dynamic thermal tolerance field to imitate two key drivers of population dynamics. Each population was initialised at a single location, and subsequently moved across the entire space according to a probabilistic distribution based on habitat suitability (represented by the normalised values from the GRFs), temperature and distance from current cell:

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

Where  $d_{I,J}$  is the euclidean distance between cell  $I$  and cell  $J$ ,  $\lambda$  is a given rate of decay,  $Hab_{c,p}^2$  is the squared index of habitat suitability for cell  $c$  and population  $p$ , with  $Tol_{c,p,wk}$  the temperature tolerance for cell  $c$  by population  $p$  in week  $wk$  (see below).

During pre-defined weeks of the year the habitat suitability is modified with user-defined spawning habitat locations, resulting in each population having concentrated areas where spawning takes place. The populations then move towards these cells in the weeks prior to spawning, resulting in directional movement towards the spawning grounds.

A time-varying temperature covariate changes the interaction between time and suitable habitat on a weekly time-step. Each population  $p$  was assigned a thermal tolerance with mean,  $\mu_p$  and variance,  $\sigma_p^2$  so that each cell and population temperature suitability is defined that:

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

Where  $Tol_{c,p,wk}$  is the tolerance of population  $p$  for cell  $c$  in week  $wk$ ,  $T_{c,wk}$  is the temperature in the cell given the week and  $\mu_p$  and  $\sigma_p^2$  the mean and standard deviation of the population temperature tolerance.

The final combined process results in a population structure and movement



175 pattern unique to each population, with population movement occurring on a  
 176 weekly basis. The decision to model population movement on a weekly timescale  
 177 was to reflect that fish tend to aggregate in species specific locations that have  
 178 been observed to last around one to two weeks (Poos and Rijnsdorp, 2007b).  
 179 Therefore this process approximated the demographic shifts in fish populations  
 180 throughout a year with seasonal spawning patterns (Figure S5).

#### 181 *2.4. Fleet dynamics*

182 Fleet dynamics can be broadly categorised into three components: fleet tar-  
 183 geting - that determined the fleet catch efficiency and preference towards a  
 184 particular population; trip-level decisions, that determines the initial location  
 185 to be fished at the beginning of a trip; and within-trip decisions, that determines  
 186 movement from one fishing spot to another within a trip. An explore-exploit  
 187 type strategy was implemented in the model that combined these three compo-  
 188 nents for individual vessels to maximise their catch from an unknown resource  
 189 distribution (Bailey et al., 2018). The decision to use an individual based model  
 190 for fishing vessels was taken because fishers are heterogeneous in their location  
 191 choice behaviour due to different objectives, risk preference and targeting prefer-  
 192 ence (Van Putten et al., 2012; Boonstra and Hentati-Sundberg, 2015). Therefore  
 193 fleet dynamics are emergent from individual dynamics rather than pre-defined  
 194 group dynamics.

##### 195 *2.4.1. Fleet targeting*

196 Each fleet of  $n$  vessels was characterised by both a general efficiency,  $Q_{fl}$ ,  
 197 and a population specific efficiency,  $Q_{fl,p}$  which are each bound by  $[0,1]$ . The  
 198 product of these parameters  $[Q_{fl} \cdot Q_{fl,p}]$  affects the overall catch rates for the fleet  
 199 and the preferential targeting of one species over another. This, in combination  
 200 with the parameter choice for the step-function defined below (as well as some  
 201 randomness from the exploratory fishing process) determined the preference of  
 202 fishing locations for the fleet.

203 *2.4.2. Decision about where to fish at the start of the trip*

204 Several studies (Girardin et al., 2016, for a review) have confirmed past  
205 activity and past catch rates are strong predictors of fishing location choice.  
206 For this reason, the fleet dynamics sub-model included a learning component,  
207 where a vessel’s initial fishing location in a trip was based on selecting from  
208 previously successful fishing locations. This was achieved by calculating an  
209 expected revenue based on the catches from locations fished in the preceding  
210 trip as well as the same month periods in previous years and the travel costs  
211 from the port to the fishing grounds. Then a vessel chooses randomly from the  
212 top 75 % of fishing events as defined by the expected profit, that has a seasonal  
213 component.

214 *2.4.3. Decision about where to fish within the trip*

215 Fishing locations within a trip are initially determined by a modified ran-  
216 dom walk process. As the simulation progresses the within-trip decision become  
217 gradually more influenced by experience gained from past fishing locations (as  
218 per the initial trip-level location choice), moving location choice towards areas  
219 of higher perceived profit. A random walk was chosen for the exploratory fishing  
220 process as it is the simplest assumption commonly used in ecology to describe  
221 optimal animal search strategy for exploiting heterogeneously distributed prey  
222 about which there is uncertain knowledge (Viswanathan et al., 1999). In a ran-  
223 dom walk, movement is a stochastic process through a series of steps. These  
224 steps have a length, and a direction that can either be equal in length or take  
225 some other functional form. The direction of the random walk was also cor-  
226 related (known as ‘persistence’) providing some overall directional movement  
227 (Codling et al., 2008).

228

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

233 fishing location) is determined by relating recent fishing success, measured as  
 234 the summed value of fish caught (revenue,  $Rev$ );

$$Rev_{c,d} = \sum_{p=1}^P L_{c,d,p} \cdot Pr_p \quad (7)$$

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

$$Le = e^{\log(\beta_1) + \log(\beta_2) - \left(\log\left(\frac{\beta_1}{\beta_3}\right)\right) \cdot Rev} \quad (8)$$

242 Where  $\beta_1$ ,  $\beta_2$  and  $\beta_3$  are parameters determining the shape of the step function  
 243 in its relation to revenue, so that, a step from  $(x1, y1)$  to  $(x2, y2)$  is defined by:

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

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

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

244 where  $Le$  is the step length,  $k$  the concentration parameter from the von Mises  
 245 distribution that we correlate with the revenue so that  $k = (Rev + 1/RefRev) \cdot$   
 246  $max_k$ , where  $max_k$  is the maximum concentration value,  $k$ , and  $RefRev$  is  
 247 parametrised as for  $\beta_3$  in the step length function.

#### 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](https://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 S1) and temperature tolerances

(Figures S3, S4) were defined to be unique to each population resulting in differently weekly distribution patterns (Figures S5-S7). In addition, each of the populations was assumed to have two defined spawning areas that result in the populations moving towards these areas in pre-defined weeks (Figure S2) with population-specific movement rates (Table 4).

### 3.2. Fleet parametrisation

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

Fishing locations were chosen based on random search and, with increasing proportion as time progressed, experience of profitable catches built up in the same month from previous years and from the previous trip. 'Profitable' in this context was defined as the locations where the top 70 % of expected profit would be found given revenue from previous trips and cost of movement to the new fishing location. This probability was based on a logistic sigmoid function with a lower asymptote of 0 and upper asymptote of 0.95, and a growth rate that ensures the upper asymptote (where decisions are mainly based on past knowledge) is reached approximately halfway through the simulation.

### 3.3. Survey settings

The survey simulation was set up with a fixed gridded station design with 100 stations fished each year, starting on day 92 and ending on day 112 (5

stations per day) with same catchability parameters for all populations ( $Q_p = 1$ ). This approximates a real world survey design with limited seasonal and spatial coverage.

### 3.4. Example research question

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

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

To answer this question we compare different spatial and temporal aggregations of the true population distributions to:

- a) **fisheries-independent data:** the inferred population density from a fixed-site sampling survey design as commonly used for fisheries monitoring purposes;
- b) **fisheries-dependent data:** the inferred population density from our fleet model that includes fishery-induced sampling dynamics.

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

The following steps are undertaken to determine closures:

- 337 1. Extract data source (true population, commercial or survey),
- 338 2. Aggregate according to desired spatial and temporal resolution,
- 339 3. Interpolate across entire area at desired resolution using simple bivariate  
340 interpolation using the *interp* function from the R package *akima* (Akima,  
341 2006). This is intended to represent a naive spatial model of catch rates,  
342 without knowledge of the spatial population dynamics.
- 343 4. Close area covering top 5 % of catch rates

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

- 345 • **data types:** commercial logbook data, survey data and true population,
- 346 • **temporal resolutions:** weekly, monthly and yearly closures,
- 347 • **spatial resolutions:** 1 x 1 grid, 5 x 5 grid, 10 x 10 grid and 20 x 20 grid,
- 348 • **closure basis:** highest 5 % of catch rates for the protected population

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

## 351 4. Results

### 352 4.1. Emergent simulation dynamics

353 Individual habitat preferences and thermal tolerances result in different spa-  
354 tial habitat use for each population (Figure 2) and consequently different sea-  
355 sonal exploitation patterns (Figure 3).

It can be seen from a single vessels movements during a trip that the ves-  
sel exploits three different fishing grounds, each of them multiple times (Figure  
4(A)), while across several trips fishing grounds that are further apart are fished  
(Figure 4 (B)). These different locations relate to areas where the highest rev-  
enue were experienced, as shown by Figure 4 (D), where several vessels tracks

are overlaid on the revenue field, i.e.

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

Vessels from the same fleet (and therefore targeting preference) may exploit some shared and some different fishing grounds depending on their own personal experience during the exploratory phase of the fishery (Figure 4 (C)). This results from the randomness in the correlated random walk step function, with distance moved during the exploitation phase and the direction stochastically related to the revenue experienced on the fishing ground (Figure 4 (D)).

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

The aggregated catch composition from each of the data sources over a ten-year period (which shows average seasonal patterns) at different spatial resolutions highlights different patterns in perceived community structure depending on the data source and aggregation level (Figure 5). The finer spatial grid for the true population (top left) and commercial data (top middle) show visually similar patterns, though there are large unsampled areas in the commercial data from a lack of fishing activity (particularly in the lower left part of the sampling domain). The survey data at this spatial resolution displays very sparse information about the spatial distributions of the populations. The slightly aggregated data on a 5 x 5 grid shows similar patterns and, while losing some of the spatial detail, there remains good consistency between the true population and the commercial data. Survey data starts to pick out some of the similar patterns as the other data sources, but lacks spatiotemporal coverage. The spatial catch information on a 10 x 10 and 20 x 20 grid lose a significant amount of information about the spatial resolutions for all data sources, and some differences between the survey, commercial and true population data emerge.

Different perceptions of the proportion of each stock in an area are seen when we aggregate the data over a smaller geographical region at different timescales,



with weekly (top), monthly (middle) and yearly (bottom) catch compositions from across an aggregated 20 x 20 area (Figure 6). In the true population, the monthly aggregation captures the major patterns of composition seen in the weekly data with the percentage of different populations in the catch having similar mean and standard deviations. In the weekly data population 1 = 9.36 (3.99), population 2 = 83.2 (5.60), population 3 = 3.57 (1.23), population 4 = 3.91 (1.59); in the monthly data population 1 = 9.23 (3.87), population 2 = 83.3 (5.52), population 3 = 3.62 (1.15), population 4 = 3.86 (1.52). While means were similar some of the variation was lost when aggregated to an annual level; population 1 = 9.90 (0.173), population 2 = 82.2 (0.308), population 3 = 3.82 (0.119), population 4 = 4.03 (0.0502).

The commercial data on a weekly basis shows some of the same patterns as the true population, though the population 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 population 1 = 0.0472 (0.0139), population 2 = 94.4 (1.47), population 3 = 3.12 (1.47), population 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; population 1 = 0.372 (0.00473), population 2 = 87.7 (0.193), population 3 = 0.729 (0.0200), population 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 population 3, given availability of data and its use at different resolutions in order to evaluate the trade-offs in data sources.

413 The trend in fishing mortality for each species show that in most cases the  
414 fishery closure was successful in reducing fishing mortality on the species of in-  
415 terest (population 3; Figure 7), though interestingly the largest reductions in  
416 fishing mortality happened immediately after the closures, following which the  
417 fisheries “adapted” to the closures and fishing mortality increased again some-  
418 what. The exception to the success was the closures implemented based on the  
419 coarsest spatial (20 x 20) and temporal resolution (yearly) that was ineffective  
420 with all data sources. As expected, closures based on the “known” population  
421 distribution were most effective, with differing degrees of success using the com-  
422 mercial data. Fishing mortality rates on the other species changed in different  
423 proportions, depending on whether the displaced fishing effort moved to areas  
424 where the populations were found in greater or lesser density.

425  
426 A regression tree (using the R package REEMtree (Sela and Simonoff, 2012))  
427 highlights that the factor most contributing to differences in fishing mortality  
428 before and after the closure was the population (72 % showing that the closures  
429 were effective for population 3), followed by data resolution (21 %), data type  
430 (7 %) with the least important factor the timescale (< 1 %). In general the finer  
431 the spatial resolution of the data used the greater reduction in fishing mortality  
432 for population 3 after the closures (Figure 8). The notable outliers are the com-  
433 mercial data at the coarsest spatial resolution (20 x 20) at a yearly and weekly  
434 timescale, where closures were nearly as effective as the fine-scale resolution. In  
435 this case the closures were sufficiently large to protect a core area of the habitat  
436 for the population, but this was achieved in a fairly crude manner by closing a  
437 large area - including area where the species was not found (Figure 9) that may  
438 have consequences in terms of restricting the fishery in a much larger area than  
439 necessary.

440

## 441 5. Discussion

442 Our study presents a new highly resolved fisheries simulation framework,  
443 evaluates the importance of data scaling and considers potential bias introduced  
444 through data aggregation when using fisheries data to infer spatiotemporal dy-  
445 namics of fish populations. Understanding how fishers exploit multiple hetero-  
446 geneously distributed fish populations with different catch limits or conservation  
447 status requires detailed understanding of the overlap of resources; this is difficult  
448 to achieve using conventional modelling approaches due to species targeting in  
449 fisheries resulting in preferential sampling (Martínez-Minaya et al., 2018). Of-  
450 ten data are aggregated or extrapolated which requires assumptions about the  
451 spatial and temporal scale of processes. Our study explores the assumptions  
452 behind such aggregation and preferential sampling to identify potential impacts  
453 on management advice. With modern management approaches increasingly  
454 employing more nuanced spatiotemporal approaches to maximise productivity  
455 while taking account of both the biological and human processes operating on  
456 different time-frames (Dunn et al., 2016), understanding assumptions behind  
457 the data used - increasingly a combination of logbook and positional informa-  
458 tion from vessel monitoring systems - is vital to ensure measures are effective.

### 460 5.1. Simulation dynamics

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

466  
467 Our approach is unique in that it captures fine scale population and fish-  
468 ery dynamics and their interaction in a way not usually possible with real data  
469 and thus not usually considered in fisheries simulations. While other simulation

frameworks seek to model individual vessel dynamics based on inferred dynamics from VMS and logbook records (Bastardie et al., 2010), or as a system to identify measures to meet particular management goals (Bailey et al., 2018), our framework allows users to explore the assumptions in modelling observational data and evaluate the underlying dynamics of such approaches at a fine spatial and temporal scale. This offers the advantage that larger scale fishery patterns are emergent properties of the system and results can be compared to those obtained under a statistical modelling framework.

Typically, simulation models that treat fish as individuals are focussed on 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 identified by Gillis et al. (2008). 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 that understanding of the community composition dynamics will depend on the level of data aggregation and its important to consider the scale of processes; including population movement rates, habitat uniformity and fishing targeting practices if potential biases in data are to be understood and taken into account (Figures 2, 4).

Our simulation shows that, despite biases introduced through the fishing process, the commercially derived data could still inform on the key spatial patterns in the community structures where the fisheries occurred, which was spatially limited due to the “hotspots” of commercially valuable species being fished. Similarly, despite the even spatial coverage the survey was able to capture some of the same spatial patterns as the true population, but missed others due to gaps between survey stations limiting spatial and temporal coverage (Figure 5). This provides a challenge when modelling unsampled areas in inferring species distribution maps, though these limitations may be overcome by understanding the relationship between the species and habitat covariates where these are known at unsampled locations (Robinson et al., 2011).

530 *5.3. How does data aggregation and source impact on spatial fisheries manage-*  
531 *ment measures?*

532 From our simulations spatial disaggregation was more important than the  
533 temporal disaggregation of the commercial data. This reflects the fact that there  
534 was greater spatial heterogeneity over the spatial domain than experienced in  
535 individual locations over the course of the year (Figure 2).

536  
537 The yearly data assumes the same proportion of each population caught at  
538 any time of the year due to the data aggregation. This assumption introduces  
539 ‘aggregation bias’ as the data may only be representative of some point (or no  
540 point) in time. The monthly data shows some consistency between the real pop-  
541 ulation and commercial data for population 2 - 4, though population 1 remains  
542 under-represented. On an annual basis, interestingly the commercial data un-  
543 der represents the first species (in red) while the survey over represents species  
544 1. This is likely due to the biases in commercial sampling, with the fisheries  
545 not targeting the areas where population 1 are present and the survey sampling  
546 areas where population 1 is more abundant than on average. This indicates that  
547 fixed closures, at the right resolution, when based on commercially derived data  
548 have the potential to reduced fishing mortality. The likely cost of poor spatial  
549 and temporal resolution is associated with reduced effectiveness and potentially  
550 closing fishing opportunities for other fisheries.

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

561

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

#### 567 *5.4. Model assumptions and caveats*

568       We model the population and fleet dynamic processes to draw inference on  
569 the importance of data scale and aggregation in understanding and managing  
570 mixed fisheries and their impact on multiple fish populations. In doing so, we  
571 have necessarily had to make a number of simplifying assumptions.

572

573       Fish populations in our simulations move in pre-defined timescales and ac-  
574 cording to fixed habitat preferences and temperature gradients (Figures S1, S3).  
575 Our assumptions in parameterising the model (movement rates, temperature  
576 tolerances) will have a direct impact on our conclusions on the relative impor-  
577 tance of spatial and temporal processes. These assumptions could be explored  
578 in a future study by varying the parameters and assessing the robustness of our  
579 conclusions. For our example application we have chosen movement rates to re-  
580 flect aggregation periods observed in past studies (Poos and Rijnsdorp, 2007b).

581

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

590

### 591 5.5. *Future applications of MixFishSim*

592 We consider that the increased availability of high resolution catch and lo-  
593 cational information from commercial fisheries will require it to be a key source  
594 of data for ensuring management is implemented at the right scale in future.  
595 For example, identifying hot-spots for bycatch reduction or identifying spatial  
596 overlaps in mixed fisheries (Dolder et al., 2018; Gardner et al., 2008; Little et al.,  
597 2014; Dedman et al., 2015; Ward et al., 2015). Our simulation model has the  
598 potential to test some of the assumptions behind the modelling approaches in  
599 identifying such hotspots and indeed behind spatiotemporal modelling in gen-  
600 eral (e.g. comparing GAMs, GLMMs, Random Forests and geostatistical mod-  
601 els under different data generation processes as exemplified by Stock et al. (2019)).

602  
603 Other novel applications of our framework could be: testing different sur-  
604 vey designs given multiple species and data generating assumptions (Xu et al.,  
605 2015); commercial index standardisation methods and approaches and under-  
606 standing of appropriate scales and data aggregations and non-proportionality  
607 in catch rate and abundance (Harley et al., 2001; Maunder and Punt, 2004);  
608 exploring assumptions about the distribution of natural mortality and fishing  
609 mortality throughout the year and importance of capturing in-year dynamics  
610 in estimating stock status (Liu and Heino, 2013); at sea sampling scheme de-  
611 signs to deliver unbiased estimates of population parameters (Cotter and Pilling,  
612 2007; Kimura and Somerton, 2006); adaptive management (Walters, 2007; Dunn  
613 et al., 2016); testing the ability of commonly employed fleet dynamics models  
614 such as Random Utility Models to capture fine scale dynamics and understand  
615 their importance (Girardin et al., 2016); and as a detailed operating model in a  
616 management strategy evaluation (Mahévas and Pelletier, 2004).

617



## 618 6. Conclusions

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

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

640  
641 While any findings are likely to be case specific, our findings emphasise the  
642 need to understand population demographics, habitat use and movement rates  
643 in designing any closure scenario based on observational sampling. This infor-  
644 mation can then be used to set the bounds on data aggregation used in modelling  
645 studies aimed at informing the management measures.

646  
647 *MixFishSim* has numerous potential additional applications as it enables

648 the user to apply methods to a fisheries system where there is detailed under-  
649 standing of underlying spatiotemporal dynamics. This enables identification of  
650 weaknesses or limitations which would not be possible otherwise. In future, we  
651 recommend use of the framework to test hypothesis that are otherwise unable  
652 to be analysed using real world data due to limitations of data collection. That  
653 way the knowledge gained through simulation can inform the future design of  
654 management measures.

## 655 **Abbreviations**

656     Detail any unusual ones used.

## 657 **Acknowledgements**

658     those providing help during the research..

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661 and the Centre for Environment, Fisheries and Aquaculture Science seedcorn  
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## 663 **Appendices**

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

Variable	Meaning	Units
<b>Population dynamics</b>		
<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 <sup>-1</sup>
$\rho$	Brody's growth coefficient	yr <sup>-1</sup>
$Wt_R$	Weight of a fully recruited fish	kg
$Wt_{R-1}$	Weight of a pre-recruit fish	kg
$\alpha_d$	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
<b>Recruitment dynamics</b>		
$\tilde{R}_{c,d}$	is the recruitment in cell $c$ for day $d$	$d^{-1}$
$S_{c,d}$	is the stock size in cell $c$ for day $d$	$d^{-1}$
$\alpha$	the maximum recruitment rate	kg
$\beta$	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
<b>Population movement dynamics</b>		
<i>Habitat model</i>		
a	b	c
<i>Thermal tolerance</i>		
$T_{c,wk}$	Temperature for cell in week	°C
$\mu_p$	Mean of the thermal tolerance for population	°C
$\sigma_p^2$	Standard deviation of thermal tolerance for the population	°C
<i>Population movement model</i>		
$\lambda$	decay rate for population movement	-
$Hab_{c,p}^2$	Square of habitat suitability for cell $c$ and population $p$	-
$Tol_{c,wk,p}$	Thermal tolerance for in cell $c$ at week $wk$ for population $p$	-
$d_{I,J}$	euclidean distance between cell $I$ and cell $J$	-

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

Variable	Meaning	Units
<b>Short-term fleet dynamics</b>		
$Rev$	Revenue from fishing tow	€
$L_p$	Landings of population $p$	kg
$Pr_p$	Average price of population $p$	€ kg <sup>-1</sup>
Le	Step length for vessel	euclidean distance
Br	Bearing	degrees
$k$	Concentration parameter for Von mises distribution	-
$\beta_1$	shape parameter for step function	-
$\beta_2$	shape parameter for step function	-
$\beta_3$	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 $\nu$	1/0.015	1/0.05	1/0.01	1/0.005
Matérn $\kappa$	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 $\lambda$	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 $\sigma^2$	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				
$\mu$	12	15	17	14
$\sigma^2$	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 $\beta_1$	1	2	1	2	3
step function $\beta_2$	10	15	8	12	7
step function $\beta_3$	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 (ordered by most effective first)

Scenario No	Population	F before	F after	% F change	data type	timescale	resolution
9	Population 3	1.08	0.29	-73.47	True Population	weekly	1.00
10	Population 3	1.08	0.29	-72.94	True Population	monthly	1.00
11	Population 3	1.08	0.35	-68.04	True Population	yearly	1.00
45	Population 3	1.08	0.58	-46.70	commercial	yearly	20.00
1	Population 3	1.08	0.58	-46.21	commercial	weekly	1.00
23	Population 3	1.08	0.59	-45.27	True Population	weekly	5.00
2	Population 3	1.08	0.59	-45.06	commercial	monthly	1.00
7	Population 3	1.08	0.60	-44.48	survey	yearly	1.00
24	Population 3	1.08	0.61	-43.20	True Population	monthly	5.00
3	Population 3	1.08	0.64	-40.82	commercial	yearly	1.00
25	Population 3	1.08	0.65	-39.94	True Population	yearly	5.00
17	Population 3	1.08	0.67	-38.11	commercial	yearly	5.00
15	Population 3	1.08	0.71	-34.38	commercial	weekly	5.00
43	Population 3	1.08	0.71	-34.31	commercial	weekly	20.00
16	Population 3	1.08	0.73	-32.58	commercial	monthly	5.00
51	Population 3	1.08	0.78	-27.92	True Population	weekly	20.00
37	Population 3	1.08	0.78	-27.76	True Population	weekly	10.00
39	Population 3	1.08	0.79	-26.98	True Population	yearly	10.00
38	Population 3	1.08	0.81	-25.47	True Population	monthly	10.00
21	Population 3	1.08	0.81	-25.21	survey	yearly	5.00
35	Population 3	1.08	0.81	-25.05	survey	yearly	10.00
44	Population 3	1.08	0.87	-19.91	commercial	monthly	20.00
52	Population 3	1.08	0.88	-18.39	True Population	monthly	20.00
30	Population 3	1.08	0.96	-11.06	commercial	monthly	10.00
29	Population 3	1.08	0.98	-9.80	commercial	weekly	10.00
31	Population 3	1.08	1.03	-4.36	commercial	yearly	10.00
53	Population 3	1.08	1.06	-1.64	True Population	yearly	20.00
49	Population 3	1.08	1.07	-1.01	survey	yearly	20.00

Table 7: Mean and standard deviation of proportions of each species at different levels of temporal aggregation

Data type	Timescale	Population 1	Population 2	Population 3	Population 4
-----------	-----------	--------------	--------------	--------------	--------------



commercial	monthly	0.047(0.014)	94.435(1.47)	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)
True Population	monthly	9.225(3.872)	83.287(5.522)	3.624(1.151)	3.864(1.519)
True Population	weekly	9.358(3.992)	83.165(5.596)	3.567(1.233)	3.91(1.592)
True Population	yearly	9.899(0.173)	82.25(0.308)	3.821(0.119)	4.031(0.05)
survey	yearly	0.372(0.005)	87.667(0.193)	0.729(0.02)	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.

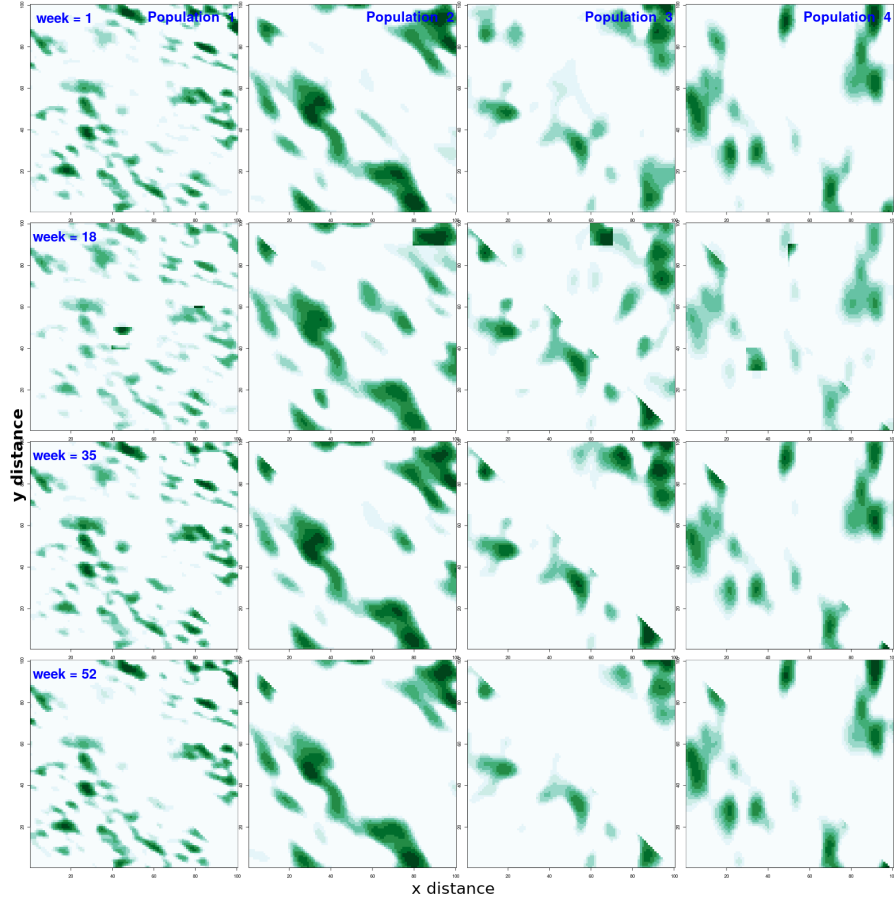


Figure 2: Spatial density (log abundance) for each of the four populations at four time steps. The darker the colour the greater the density of the population. Note that you can see the diagonal isotropic patterns in populations 2 and 3 and concentrated spawning areas in the second row of the panels ( $t=18$ ).

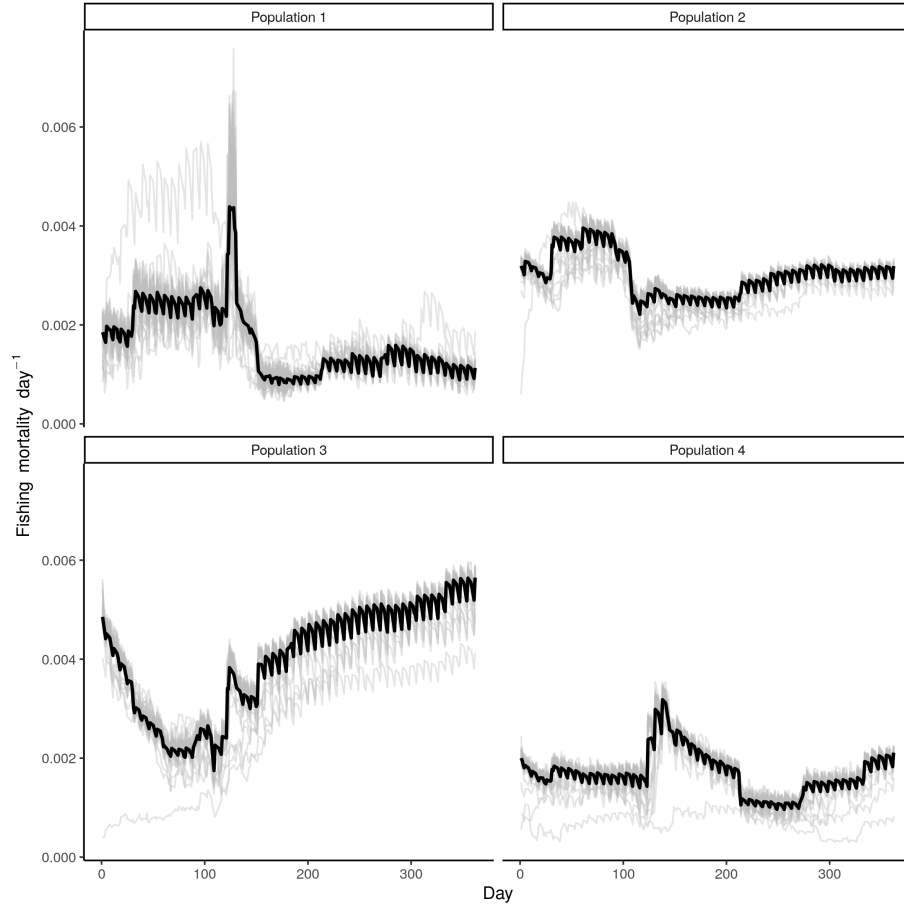


Figure 3: Fishing mortality dynamics - the daily fishing mortalities across the entire spatial domain showing weekly and seasonal patterns in exploitation. Individual years and the light grey lines, the mean of all years the thick black line.

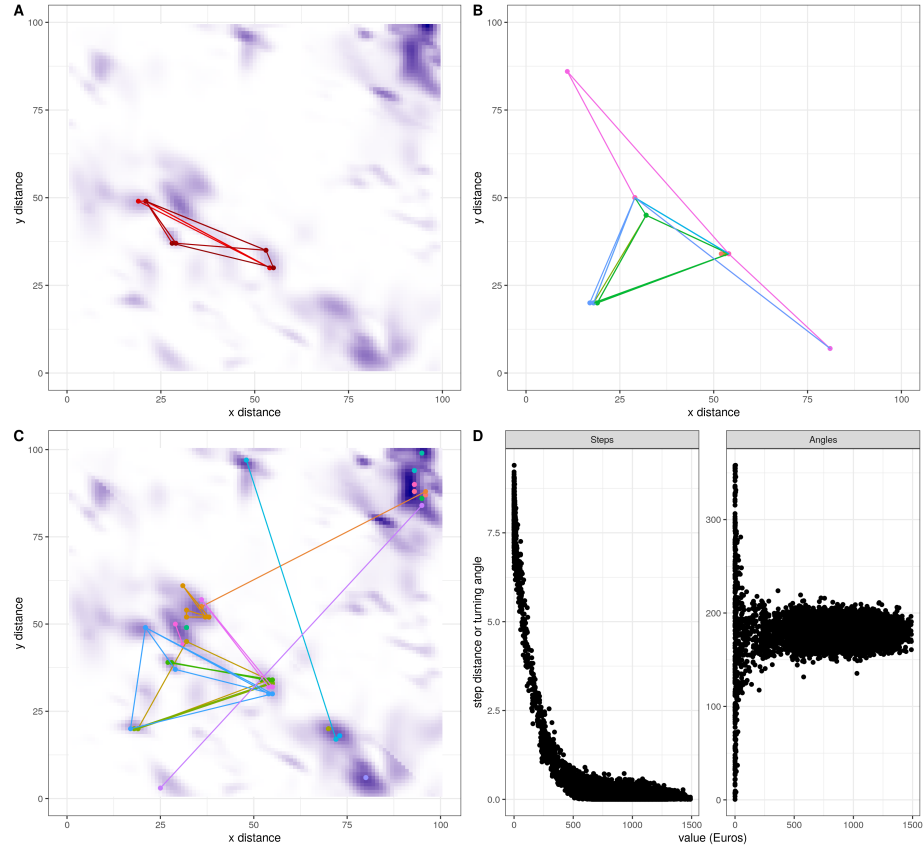


Figure 4: (A) The fishing locations (points) and movements (lines) of a single vessel during a trip overlaid on the revenue of a fishing site (catch  $\times$  price); (B) the fishing locations of the vessel over several trips (value field changes over the period so not shown). Note that the field is wrapped on a torus so that distances between opposite side of the spatial domain are considered next to each other, hence apparent large movements; (C) the locations of multiple vessels from the same fleet overlaid on the value field, (D) the realised step distance and turning angles for a single vessel over the simulation.

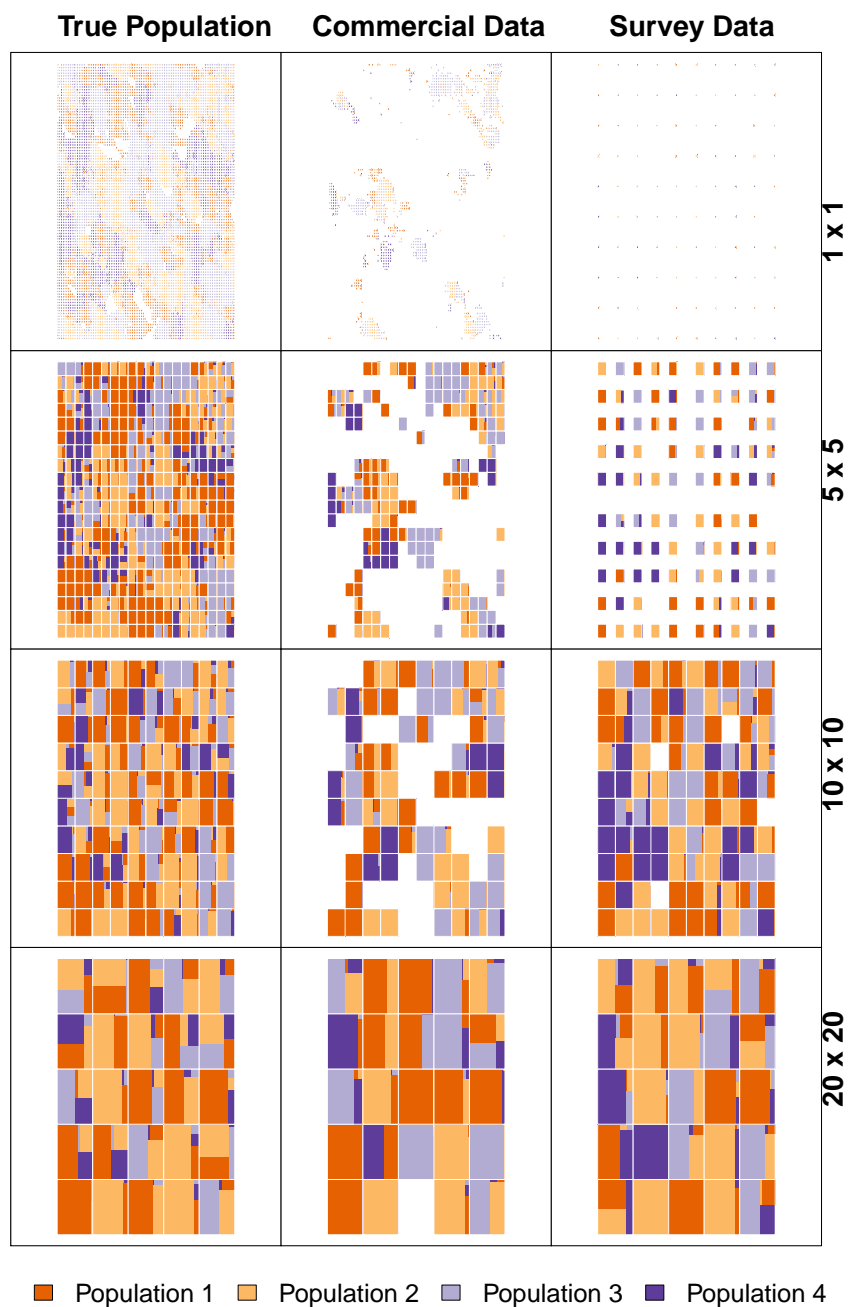


Figure 5: Data aggregation at different spatial resolutions over a ten year period.



Figure 6: Proportion of each population (y axis) for data aggregated at different temporal resolutions. Data is aggregated over a ten-year period for an area 20 x 20. Each bar represents either a week, month or year respectively.

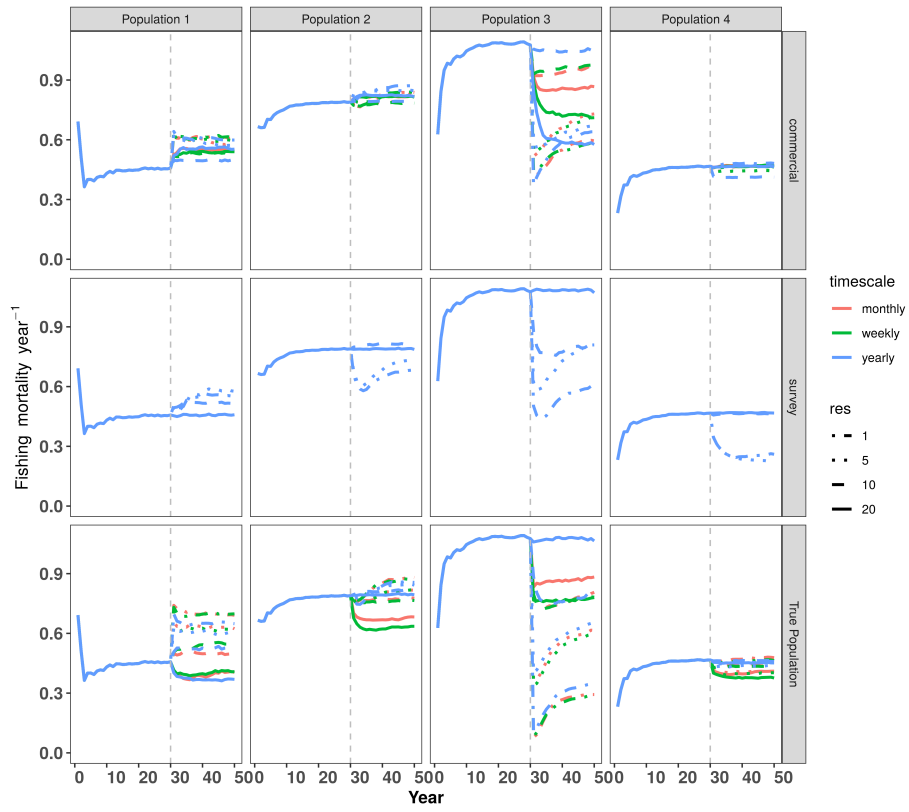


Figure 7: Comparison of closure scenarios effect on fishing mortality trends. Line colour denotes timescale, while linestyle denotes spatial resolution. The vertical dashed line indicates the onset of the spatial closures.





Figure 8: Comparison of closure scenario effectiveness based on different spatial and temporal resolutions.



Figure 9: Closure fishing locations based on annual closures with a coarse spatial resolution. Closure location can be seen in red box in relation to a) before the closure fishing locations, b) after the closure fishing locations, c) population 3 habitat distribution.

## 664 References

- 665 Akima, H., 2006. Interpolation of irregularly spaced data, The akima Package. Interpolation  
666 of Irregularly and Regularly Spaced Data .
- 667 Alverson, D.L., Freeberg, M.H., Murawski, S.A., Pope, J., 1994. A global assessment of  
668 fisheries bycatch and discards.
- 669 Bailey, R.M., Carrella, E., Axtell, R., Burgess, M.G., Cabral, R.B., Drexler, M., Dorsett, C.,  
670 Madsen, J.K., Merkl, A., Saul, S., 2018. A computational approach to managing coupled  
671 human–environmental systems: the POSEIDON model of ocean fisheries.
- 672 Bastardie, F., Nielsen, J.R., Ulrich, C., Egekvist, J., Degel, H., 2010. Detailed mapping  
673 of fishing effort and landings by coupling fishing logbooks with satellite-recorded vessel  
674 geo-location. *Fisheries Research* 106, 41–53.
- 675 Batsleer, J., Hamon, K.G., Overzee, H.M.J., Rijnsdorp, A.D., Poos, J.J., 2015. High-grading  
676 and over-quota discarding in mixed fisheries. *Reviews in Fish Biology and Fisheries* 25,  
677 715–736.
- 678 Bellido, J.M., Santos, M.B., Pennino, M.G., Valeiras, X., Pierce, G.J., 2011. Fishery discards  
679 and bycatch: Solutions for an ecosystem approach to fisheries management? *Hydrobiologia*  
680 670, 317–333.
- 681 Beverton, R.J., Holt, S.J., 1957. On the Dynamics of Exploited Fish Populations , 533.
- 682 Boonstra, W.J., Hentati-Sundberg, J., 2015. Classifying fishers’ behaviour. An invitation to  
683 fishing styles. *Infancy* .
- 684 Branch, T., Hilborn, R., Bogazzi, E., 2005. Escaping the tyranny of the grid: a more realistic  
685 way of defining fishing opportunities. *Canadian Journal of Fisheries and Aquatic Sciences*  
686 642, 631–642.
- 687 Catchpole, T.L., Revill, A.S., 2008. Gear technology in Nephrops trawl fisheries. *Reviews in*  
688 *Fish Biology and Fisheries* 18, 17–31.
- 689 Codling, E.A., Plank, M.J., Benhamou, S., Interface, J.R.S., 2008. Random walk models in  
690 biology. *Journal of the Royal Society, Interface / the Royal Society* 5, 813–34.
- 691 Cosgrove, R., Browne, D., Minto, C., Tyndall, P., Oliver, M., Montgomerie, M., McHugh,  
692 M., 2019. A game of two halves: Bycatch reduction in Nephrops mixed fisheries. *Fisheries*  
693 *Research* 210, 31–40.

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

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

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

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

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

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

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

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

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

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

F. Dormann, C., M. McPherson, J., B. Araújo, M., Bivand, R., Bolliger, J., Carl, G., G. Davies, R., Hirzel, A., Jetz, W., Daniel Kissling, W., Kühn, I., Ohlemüller, R., R. Peres-Neto, P., Reineking, B., Schröder, B., M. Schurr, F., Wilson, R., 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: A review. *Ecography* 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 Gillis, D.M., Rijnsdorp, A.D., Poos, J.J., 2008. Behavioral inferences from the statistical  
740 distribution of commercial catch: patterns of targeting in the landings of the Dutch beam  
741 trawler fleet. *Canadian Journal of Fisheries and Aquatic Sciences* 65, 27–37.

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

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

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

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

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

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

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

767 Mahévas, S., Pelletier, D., 2004. ISIS-Fish, a generic and spatially explicit simulation tool for  
768 evaluating the impact of management measures on fisheries dynamics. *Ecological Modelling*  
769 .

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

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

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

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

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

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

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

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

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

794 Ricker, W.E., 1954. Stock and recruitment. *Journal of the Fisheries Research Board of Canada*  
795 11, 559 – 623.

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

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

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

803 Rijnsdorp, A.D., Poos, J.J., Quirijns, F.J., Grant, J., 2011. Spatial dimension and exploitation  
804 dynamics of local fishing grounds by fishers targeting several flatfish species. *Canadian*  
805 *Journal of Fisheries and Aquatic Sciences* 68, 1064–1076.

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

810 Schlater, M., Malinowski, A., Menck, P.J., 2015. Analysis, Simulation and Prediction of  
811 Multivariate Random Fields with Package RandomFields. *Journal of Statistical Software*  
812 63, 1–25. [arXiv:1501.0228](https://arxiv.org/abs/1501.0228).

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

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

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

819 Stock, B.C., Ward, E.J., Eguchi, T., Jannot, J.E., Thorson, J.T., Feist, B.E., Semmens, B.X.,  
820 2019. Comparing predictions of fisheries bycatch using multiple spatiotemporal species  
821 distribution model frameworks. *Canadian Journal of Fisheries and Aquatic Sciences* .

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

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

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

830 Viswanathan, G.M., Buldyrev, S.V., Havlin, S., Da Luz, M.G.E., Raposo, E.P., Stanley, H.E.,  
831 1999. Optimizing the success of random searches. *Nature* 401, 911–914.

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

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

836 Xu, B., Zhang, C., Xue, Y., Ren, Y., Chen, Y., 2015. Optimization of sampling effort for a  
837 fishery-independent survey with multiple goals. *Environmental Monitoring and Assessment*  
838 .