

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,e}

^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*

^e*Aquaculture and Fisheries Group, Wageningen University & Research, Zodiac Building 122, De Elst 1, 6708 WD Wageningen, the Netherlands*

Abstract

To understand how data resolution impacts inference on mixed fisheries interactions we developed a highly resolved spatiotemporal discrete-event simulation model ('MixFishSim') 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 (simulated) 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

*Corresponding author

Email address: paul.dolder@cefas.co.uk (Paul J. Dolder)

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.

Keywords: spatiotemporal, mixed fisheries, individual based, spatial management, heterogeneity, preferential sampling

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. 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 Reville, 2008; Bellido et al., 2011; Cosgrove et al., 2019) and

15 adaptive spatial management strategies have been proposed as a way of reduc-
16 ing over-quota discards (Holmes et al., 2011; Little et al., 2015; 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.

19

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.

32

33

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)).

44

45 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., 2017) 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., 2019) 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 reflect 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

75 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.

78

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.

89

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):

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

where ρ 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. α_d represents the proportion of fish recruited during that day for the year, while $R_{c,\tilde{y}(c)}$ is the annual recruits in year y for cell c .

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 FL the fleet and total number of fleets, v and V the vessel and total number of vessels 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.

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 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. The stochastic Ricker form (Ricker, 1954) is:

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

where α is the maximum productivity per spawner and β 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 which are affected by the suitability of habitat, temperature in a cell and the thermal tolerance of a population to that temperature.

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

149 To simulate fish population distribution in space and time a Gaussian spa-
 150 tial process was employed to model habitat suitability for each of the popula-
 151 tions on a 2d grid. We first defined a Gaussian random field process, $\{S(c) :$
 152 $c \in \mathbb{R}^2\}$, where for any set of cells c_1, \dots, c_n , the joint distribution of $S =$
 153 $\{S(c_1), \dots, S(c_n)\}$ is multivariate Gaussian with a *Matérn* covariance structure,
 154 where the correlation strength weakens with distance controlled by two param-
 155 eters, with ν a scale parameter in the units of distance and κ a shape parameter
 156 which determines the smoothness of the process. We use the most commonly
 157 used Matérn covariance structure as it is a flexible form that under certain
 158 conditions is of the same form as an exponential function and itThis enables
 159 us to model the spatial autocorrelation observed in animal populations where
 160 density is more similar in nearby locations, but that correlation decreases non-
 161 linearly (Tobler, 1970; F. Dormann et al., 2007; Poos and Rijnsdorp, 2007b).
 162 We change the parameters to implement different spatial structures for the dif-
 163 ferent populations using the *RandomFields* R package (Schlather et al., 2015).
 164 We define a stationary habitat field with an anisotropic pattern (to simulate a
 165 depth gradient) and combine it with a temporally dynamic thermal tolerance
 166 field to imitate two key drivers of population dynamics without modelling the
 167 processes explicitly. Each population was initialised at a single location, and
 168 subsequently moved across the entire space according to a probabilistic distri-
 169 bution based on habitat suitability (represented by the normalised values from
 170 the GRFs), temperature tolerance and distance from current cell:

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

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

175
 176 During pre-defined weeks of the year the habitat suitability is modified with

177 user-defined spawning habitat locations, resulting in each population having
 178 concentrated areas where spawning takes place. The populations then move to-
 179 wards these cells in the weeks prior to spawning, resulting in directional move-
 180 ment towards the spawning grounds.

181

182 A time-varying temperature covariate changes the interaction between time
 183 and suitable habitat on a weekly time-step. Each population p was assigned a
 184 thermal tolerance with mean, μ_p and standard deviation, σ_p so that each cell
 185 and population temperature tolerance is defined that:

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

186 Where $Tol_{c,p,wk}$ is the tolerance of population p for cell c in week wk , $T_{c,wk}$ is
 187 the temperature in the cell given the week and μ_p and σ_p the mean and standard
 188 deviation of the population temperature tolerance.

189

190 ~~The final combined process results in a population structure and movement~~
 191 ~~pattern unique to each population, with population movement occurring on a~~
 192 ~~weekly basis. The decision to model population movement on a weekly timescale~~
 193 ~~was to reflect that fish tend to aggregate in species specific locations that have~~
 194 ~~been observed to last around one to two weeks (Poos and Rijnsdorp, 2007b).~~
 195 ~~Therefore this process approximated the demographic shifts in fish populations~~
 196 ~~throughout a year with seasonal spawning patterns (Figure S5).~~

197 2.4. Fleet dynamics

198 Fleet dynamics ~~werecan be~~ broadly categorised into three components. *Fleet*
 199 *targeting* ~~determineddetermines~~ the fleet catch efficiency and preference to-
 200 wards a particular population; *trip-level decisions* ~~determinedthat determines~~
 201 the initial location to be fished at the beginning of a trip; and *within-trip deci-*
 202 *sions*~~determined fishing locations; that determines movement from one fishing~~
 203 ~~spot to another~~ within a trip. This results in an explore-exploit strategy ~~was~~
 204 ~~implemented in the model that combined these three components~~ for individual

205 vessels to maximise their catch from an unknown resource distribution (Bailey
 206 et al., 2019). The decision to use an individual based model for fishing vessels
 207 was taken because fishers are heterogeneous in their location choice behaviour
 208 due to different objectives, risk preference and targeting preference (Van Putten
 209 et al., 2012; Boonstra and Hentati-Sundberg, 2016). Therefore fleet dynamics
 210 are emergent from individual dynamics rather than pre-defined group dynamics.

211 *2.4.1. Fleet targeting*

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

219 *2.4.2. Decision about where to fish at the start of a trip*

220 Several studies (for a review see Girardin et al., 2017) have confirmed past
 221 activity and past catch rates are strong predictors of fishing location choice.
 222 For this reason, the fleet dynamics sub-model included a learning component,
 223 where a vessel's initial fishing location in a trip was based on selecting from
 224 previously successful fishing locations. This was achieved by calculating an
 225 expected revenue based on the catches from locations fished in the preceding
 226 trip as well as the same month periods in previous years and the travel costs
 227 from the port to the fishing grounds. Then a vessel chooses randomly from the
 228 top 70 % of fishing events (defined as the 'threshold') in terms of expected profit
 229 within that season.

230 *2.4.3. Decision about where to fish within a trip*

231 Fishing locations within a trip are initially determined by a modified ran-
 232 dom walk process. As the simulation progresses the within-trip decision become
 233 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 heterogeneously 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).

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 relating recent fishing success, measured as the summed value of fish caught (revenue, Rev);

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

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

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

Where β_1 , β_2 and β_3 are parameters determining the shape of the step function in its relation to revenue, so that, a step from (x_t, y_t) to (x_{t+1}, y_{t+1}) is defined

260 by:

$$\begin{aligned} (x_{t+1}, y_{t+1}) = & x_t + Le \cdot \cos\left(\frac{\pi \cdot Br_{t+1}}{180}\right), \\ & y_t + Le \cdot \sin\left(\frac{\pi \cdot Br_{t+1}}{180}\right) \end{aligned} \quad (9)$$

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

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

261 where Le is the step length, Br_t is the bearing at time t , k the concentration
 262 parameter from the von Mises distribution that we correlate with the revenue so
 263 that $k = (Rev + 1/RefRev) \cdot max_k$, where max_k is the maximum concentration
 264 value, k , and $RefRev$ is parametrised as for β_3 in the step length function.

265 2.4.4. Local population depletion

266 Where several fishing vessels exploit the same fish population competition is
 267 known to play an important role in local distribution of fishing effort (Gillis and
 268 Peterman, 1998). If several vessels are fishing on the same patch of fish, local
 269 depletion and interference competition will affect fishing location choice of the
 270 fleet as a whole (Rijnsdorp, 2000; Poos and Rijnsdorp, 2007a). To account for
 271 this behaviour, the fishing sub-model operates spatially on a daily time-step so
 272 that for future days the biomass available to the fishery is reduced in the areas
 273 fished. The cumulative effect is to make heavily fished areas less attractive as a
 274 future fishing location choice as reduced catch rates will be experienced.

275 2.5. Fisheries independent survey

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

283

284 2.6. Software: R-package development

285 The simulation framework is implemented in the statistical software package
286 R (R Core Team, 2017) and available as an R package from the author’s github
287 site (www.github.com/pdolder/MixFishSim).
288

289 3. Model calibration

290 We calibrate *MixFishSim* to investigate the influence of data aggregation on
291 spatial inference.

292 3.1. Population models

293 We calibrated the simulation model for four example populations with dif-
294 ferent demographics, growth rates, natural mortality and recruitment (Table 4).
295 Habitat preference (Figure S1) and temperature (Figures S3, with temperature
296 tolerance S4) defined to be unique to each population resulting in differently
297 weekly distribution patterns (Figures S5-S7). In addition, each of the pop-
298 ulations was assumed to have two defined spawning areas that result in the
299 populations moving towards these areas in pre-defined weeks (Figure S2) with
300 population-specific movement rates (Table 4).

301 3.2. Fleet calibration

302 The fleets were calibrated to reflect five different characteristic fisheries with
303 unique exploitation dynamics (Table 5). By setting different catchability coef-
304 ficients ($Q_{fl,p}$) we create different targeting preferences between the fleets and
305 hence spatial dynamics. The learned random walk process implies that within
306 a fleet different vessels have different spatial distributions based on individual
307 experience. The step function was calibrated dynamically within the simula-
308 tions as the maximum revenue obtainable was not known beforehand. This was
309 implemented so that vessels take smaller steps when fishing at a location that
310 yields landings value in the top 90th percentile of the value experienced in that

311 year so far (as defined per fleet in Table 5).

312

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

322

323 3.3. Survey settings

324 The survey simulation was set up with a fixed gridded station design with
325 100 stations fished each year, starting on day 92 and ending on day 112 (5
326 stations per day) with same catchability parameter ($Q_p = 1$) for all populations
327 p . This approximates a real world survey design with limited seasonal and
328 spatial coverage.

329 3.4. Example research question

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

337

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

340

341 To answer this question we compare different spatial and temporal aggrega-
342 tions of the true population distributions to:

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

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

352

353 The following steps are undertaken to determine closures:

- 354 1. Extract data source (true population, commercial or survey),
- 355 2. Aggregate according to desired spatial and temporal resolution,
- 356 3. Interpolate across entire area at desired resolution using simple bivariate
357 interpolation using the *interp* function from the R package *akima* (Akima
358 and Gebhardt, 2016). This is intended to represent a naive spatial model
359 of catch rates, without knowledge of the spatial population dynamics.
- 360 4. Close area covering top 5 % of catch rates

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

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

Survey closures were on an annual basis only, as this was the most temporally resolved survey data available. We evaluated the factors contributing to the success of the closures through a regression tree (using the R package REEMtree (Sela and Simonoff, 2011)) to identify the factor most contributing to differences in fishing mortality before and after the closure.

4. Results

4.1. Emergent simulation dynamics

Individual habitat preferences and thermal tolerances result in different spatial habitat use for each population (Figure 2) and consequently different seasonal exploitation patterns (Figure 3).

It can be seen from a single vessels movements during a trip that the vessel 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 revenue were experienced, as shown by Figure 4 (D), where several vessels tracks are overlaid on the revenue field, i.e.

$$Rev_c = \sum_{p=1}^P B_{c,p} \cdot Q_{fl,p} \cdot Pr_p$$

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 ~~aggregated at different spatial resolutions~~ from each of the data sources (~~which shows~~ average seasonal patterns over a

ten-year period) 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% (SD = 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.

In most cases the fishery closure was successful in reducing fishing mortality on the species of interest (population 3; Figure 7), 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 (i.e. failed to reduce fishing mortality) with all data sources. As expected, closures based on the “known” population distribution were most effective, with differing degrees of success using the commercial data. Fishing mortality rates on the other species changed in different proportions, depending on whether the displaced fishing effort moved to areas where the populations were found in greater or lesser density.

447 The factor most contributing to differences in fishing mortality before and
 448 after the closure was the population (72 % showing that the closures were ef-
 449 fective for population 3), followed by data resolution (21 %), data type (7 %)
 450 with the least important factor the timescale (< 1 %). In general the finer the
 451 spatial resolution of the data used the greater reduction in fishing mortality for
 452 population 3 after the closures (Figure 8). The notable outliers are the com-
 453 mercial data at the coarsest spatial resolution (20 x 20) at a yearly and weekly
 454 timescale, where closures were nearly as effective as the fine-scale resolution. In
 455 this case the closures were sufficiently large to protect a core area of the habitat
 456 for the population, but this was achieved in a fairly crude manner by closing a
 457 large area - including area where the species was not found (Figure 9) that may
 458 have consequences in terms of restricting the fishery in a much larger area than
 459 necessary. We found that these trade-offs existed, with high catches maintained
 460 with an effective closure when the highest resolution data was used, with the
 461 effect being linear when the true population distribution was known and also
 462 persisting for closures based on commercial information (Figure 10).

463

464 5. Discussion

465 Our study presents a new highly resolved fisheries simulation framework to
 466 evaluate the importance of data scaling and considers potential bias introduced
 467 through data aggregation when using fisheries data to infer spatiotemporal dy-
 468 namics of fish populations. Understanding how fishers exploit multiple hetero-
 469 geneously distributed fish populations with different catch limits or conservation
 470 status requires detailed understanding of the overlap of resources; this is difficult
 471 to achieve using conventional modelling approaches due to species targeting in
 472 fisheries resulting in preferential sampling (Martínez-Minaya et al., 2018). Of-
 473 ten data are aggregated or extrapolated which requires assumptions about the
 474 spatial and temporal scale of processes. Our study explores the assumptions
 475 behind such aggregation and preferential sampling to identify potential impacts

476 on management advice. With modern management approaches increasingly
477 employing more nuanced spatiotemporal approaches to maximise productivity
478 while taking account of both the biological and human processes operating on
479 different time-frames (Dunn et al., 2016), understanding assumptions behind
480 the data used - increasingly a combination of logbook and positional informa-
481 tion from vessel monitoring systems - is vital to ensure measures are effective.

483 5.1. *Simulation dynamics*

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

489
490 Our approach is unique in that it captures fine scale population and fish-
491 ery dynamics and their interaction in a way not usually possible with real data
492 and thus not usually considered in fisheries simulations. While other simulation
493 frameworks seek to model individual vessel dynamics based on inferred dynam-
494 ics from VMS and logbook records (Bastardie et al., 2010), or as a system to
495 identify measures to meet particular management goals (Bailey et al., 2019), our
496 framework allows users to explore the assumptions in modelling observational
497 data and evaluate the underlying dynamics of such approaches at a fine spatial
498 and temporal scale. This offers the advantage that larger scale fishery patterns
499 are emergent properties of the system and results can be compared to those
500 obtained under a statistical modelling framework.

501
502 Typically, simulation models that treat fish as individuals are focussed on
503 exploring the inter- and intra- specific interactions among fish populations (e.g.
504 OSMOSE; Shin et al. (2004)) in order to understand how they vary over space
505 and time. Our focus was on understanding the strengths and limitations of in-

506 ference from catch data obtained through commercial fishing activity with fleets
 507 exploiting multiple fish populations and realising catch distributions that may
 508 differ from the underlying populations, as identified by Gillis et al. (2008). As
 509 such, we favoured a minimum realistic model of the fish populations (Plagányi
 510 et al., 2014) taking account of environmental but not demographic stochastic-
 511 ity, while incorporating detailed fishing dynamics that take account of different
 512 drivers in a mechanistic way.

513

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

521

522 We take account of heterogeneity in fleet dynamics due to different prefer-
 523 ences and drivers similarly to other approaches (Fulton et al., 2011), but at an
 524 individual vessel rather than fleet level. We do not explicitly define fleets as
 525 rational profit maximisers at the outset, but consider there are several stages
 526 to development of the fishery; information gathering through search where the
 527 resource location is not known, followed by individual learnt behaviour of prof-
 528 itable locations. This provides a realistic model of how fishing patterns are
 529 established and maintained to exploit an uncertain resource through an explore-
 530 exploit strategy (Mangel and Clark, 1983; Bailey et al., 2019).

531 *5.2. How does sampling-derived fisheries data reflect the underlying population* 532 *structure?*

533 Our results demonstrate the importance of considering data scale and resolu-
 534 tion when using observational data to support management measures. We find
 535 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).

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

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

The yearly data assumes the same proportion of each population caught at any time of the year due to the data aggregation. This assumption introduces ‘aggregation bias’ as the data may only be representative of some point (or no point) in time. The monthly data shows some consistency between the real population and commercial data for population 2 - 4, though population 1 remains under-represented. On an annual basis, interestingly the commercial data un-

der represents the first species (in red) while the survey over represents species
1. This is likely due to the biases in commercial sampling, with the fisheries
not targeting the areas where population 1 are present and the survey sampling
areas where population 1 is more abundant than on average. This indicates that
fixed closures, at the right resolution, when based on commercially derived data
have the potential to reduced fishing mortality. The likely cost of poor spatial
and temporal resolution is associated with reduced effectiveness and potentially
closing fishing opportunities for other fisheries (Figure 10).

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

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

5.4. Model assumptions and caveats

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

596 Fish populations in our simulations move in pre-defined timescales and ac-
 597 cording to fixed habitat preferences and temperature gradients (Figures S1, S3).
 598 Our assumptions in calibrating the model (movement rates, temperature toler-
 599 ances) will have a direct impact on our conclusions on the relative importance
 600 of spatial and temporal processes. These assumptions could be explored in a
 601 future study by varying the parameters and assessing the robustness of our con-
 602 clusions. For our example application we have chosen movement rates to reflect
 603 aggregation periods observed in past studies (Poos and Rijnsdorp, 2007b).

604
 605 In addition, we have assumed that fishing vessels are not restricted by quota
 606 and therefore discarding of species for which vessels have no quota or that are
 607 unwanted is not taken into account. This is likely to be a significant source of
 608 bias in any inference using commercial data and should also be explored. For
 609 example, *MixFishSim* could be altered to allow for spatiotemporal appraisal of
 610 the impact of discarding on fisher behaviour and underlying populations via in-
 611 clusion as discarding behaviour, or through move-on rules or cessation of fishing
 612 activity when quota is exhausted.

613 614 5.5. Future applications of *MixFishSim*

615 We consider that the increased availability of high resolution catch and lo-
 616 cational information from commercial fisheries will require it to be a key source
 617 of data for ensuring management is implemented at the right scale in future.
 618 For example, identifying hot-spots for bycatch reduction or identifying spatial
 619 overlaps in mixed fisheries (Dolder et al., 2018; Gardner et al., 2008; Little
 620 et al., 2015; Dedman et al., 2015; Ward et al., 2015). Our simulation model has
 621 the potential to test some of the assumptions behind the modelling approaches
 622 in identifying such hotspots and indeed behind spatiotemporal modelling in
 623 general, (e.g. comparing GAMs, GLMMs, Random Forests and geostatistical
 624 models under different data generation processes as exemplified by Stock et al.
 625 (2019)deleted).

626

627 Other novel applications of our framework could be: testing different sur-
 628 vey designs given multiple species and data generating assumptions (Xu et al.,
 629 2015); commercial index standardisation methods and approaches and under-
 630 standing of appropriate scales and data aggregations and non-proportionality
 631 in catch rate and abundance (Harley et al., 2001; Maunder and Punt, 2004);
 632 exploring assumptions about the distribution of natural mortality and fishing
 633 mortality throughout the year and importance of capturing in-year dynamics
 634 in estimating stock status (Liu and Heino, 2014); at sea sampling scheme de-
 635 signs to deliver unbiased estimates of population parameters (Cotter and Pilling,
 636 2007; Kimura and Somerton, 2006); adaptive management (Walters, 2007; Dunn
 637 et al., 2016); testing the ability of commonly employed fleet dynamics models
 638 such as Random Utility Models to capture fine scale dynamics and understand
 639 their importance (Girardin et al., 2017); and as a detailed operating model in a
 640 management strategy evaluation (Mahévas and Pelletier, 2004).

641

642 6. Conclusions

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

651

652 Our application shows that inference on community dynamics may change
 653 depending on the scale of data aggregation. There is an important balance in
 654 ensuring that the data are sufficiently spatially and temporally disaggregated

655 that the main features of the data are captured, yet maintaining enough data
656 coverage that the features can be distinguished. We found in our application
657 that there was greater spatial heterogeneity than temporal heterogeneity and
658 that when using aggregated data to define spatial closures coarser temporal reso-
659 lution (months instead of weeks) could still achieve the same results in reducing
660 exploitation rates of a vulnerable species at the highest temporal resolution
661 data. Conversely, reducing the spatial resolution had a negative effect on the
662 effectiveness of the measures (though importantly, there was still some benefit
663 even with coarse spatial resolution).

664

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

670

671 *MixFishSim* has numerous potential additional applications as it enables
672 the user to apply methods to a fisheries system where there is detailed under-
673 standing of underlying spatiotemporal dynamics. This enables identification of
674 weaknesses or limitations which would not be possible otherwise. In future, we
675 recommend use of the framework to test hypotheses that are otherwise unable
676 to be analysed using real world data due to limitations of data collection. That
677 way the knowledge gained through simulation can inform the future design of
678 management measures.

679 **Funding**

680 This work was supported by the MARES doctoral training program (MARES_14_15)
681 and the Centre for Environment, Fisheries and Aquaculture Science seedcorn
682 program (DP227AC). The authors declare no competing interests.

Table 1: Description of variables for population and recruitment dynamics sub-modules.

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	-
$R_{c,\tilde{y}}$	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}
$B_{c,d}$	biomass in cell c for day d	d^{-1}
α	the maximum recruitment rate (Beverton Holt) or maximum productivity per spawner (Ricker)	kg
β	the stock size required to produce half the maximum rate of recruitment (Beverton Holt) or density dependent reduction in productivity per capita of SSB	kg

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

Variable	Meaning	Units
<i>Thermal tolerance</i>		
$T_{c,wk}$	Temperature for cell c in week wk	$^{\circ}\text{C}$
μ_p	Mean of the thermal tolerance for population p	$^{\circ}\text{C}$
σ_p	Standard deviation of thermal tolerance for population p	$^{\circ}\text{C}$
<i>Population movement model</i>		
λ	Decay rate for population movement	-
$Hab_{c,p}$	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
Rev	Revenue from fishing tow	€
L_p	Landings of population p	kg
Pr_p	Average price of population p	€ kg^{-1}
Le	Step length for vessel	-
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 settings.

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				
Movement $\lambda = 0.1$				
Population dynamics				
Starting Biomass	1e5	2e5	1e5	1e4
Beverton-Holt Recruit α	6	27	18	0.3
Beverton-Holt Recruit β	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
$K = 0.3$				
$wt = 1$				
$wt_{d-1} = 0.1$				
M (annual)	0.2	0.1	0.2	0.1
Movement dynamics				
μ_p	12	15	17	14
σ_p^2	8	9	7	10

Table 5: Fleet dynamics parameter setting.

Parameter	Fleet 1	Fleet 2	Fleet 3	Fleet 4	Fleet 5
Targeting preferences	pop 2/4	pop 1/3	-	pop 4	pop 2/3
Price $Pr_p1 = 100$					
Price $Pr_p2 = 200$					
Price $Pr_p3 = 350$					
Price $Pr_p4 = 600$					
Q_p	0.01	0.02	0.02	0.01	0.01
Q_p	0.02	0.01	0.02	0.01	0.03
Q_p	0.01	0.02	0.02	0.01	0.02
Q_p	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 , the land- ings value n th quantile	90	90	85	90	80
step function $rate$	20	30	25	35	20
Past Knowledge = TRUE					
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 on population 3 (ordered by most effective first). The fishing mortality rate before the closure was 1.08.

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

53	1.06	-1.64	true Population	yearly	20.00
49	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.

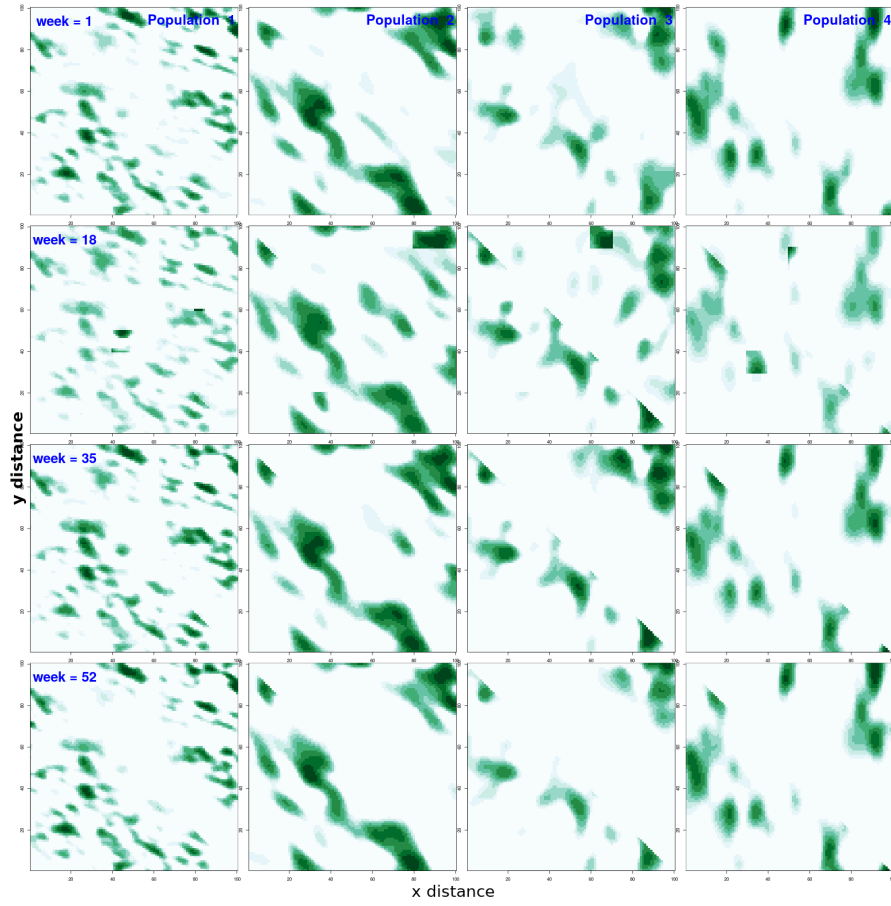


Figure 2: Spatial density (log abundance) for each of the four populations at four time steps. The darker the colour the greater the density of the population. Note that a diagonal anisotropic pattern (mimicking a depth gradient) can be clearly seen in populations 2 and 3. The concentrated spawning areas are also visible in the second row of the panels ($t=18$).

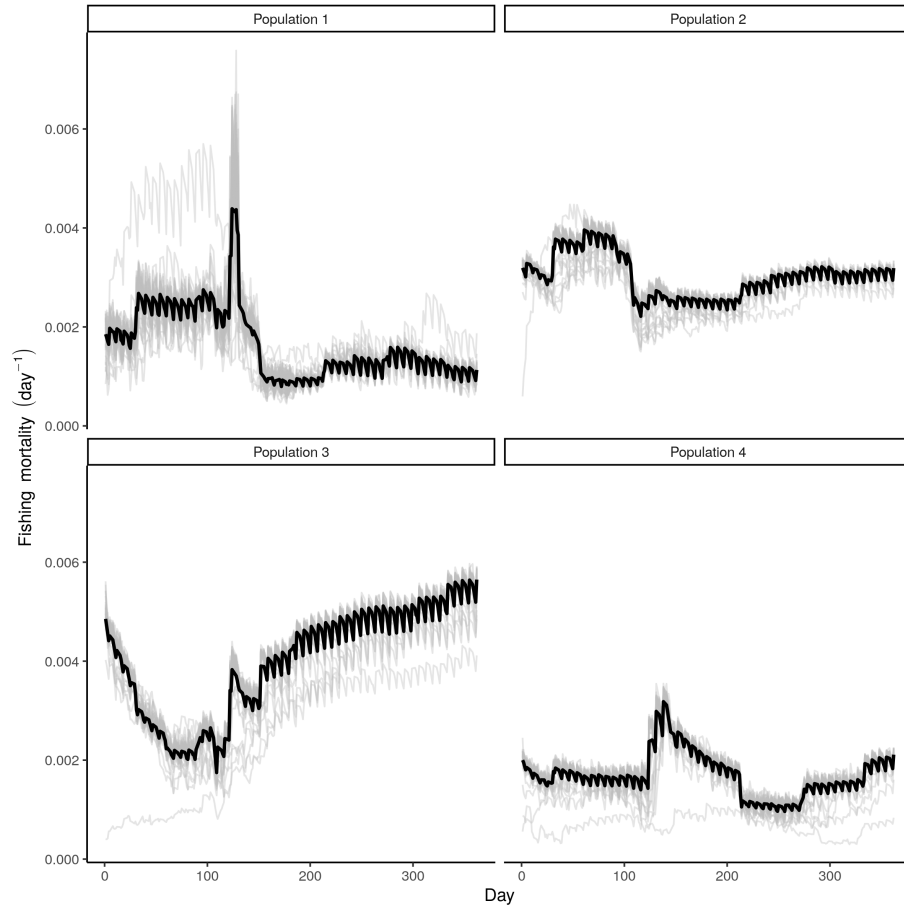


Figure 3: Fishing mortality dynamics - the daily fishing mortalities across the entire spatial domain showing weekly and seasonal patterns in exploitation. Individual years are the light grey lines, the mean of all years the thick black line.

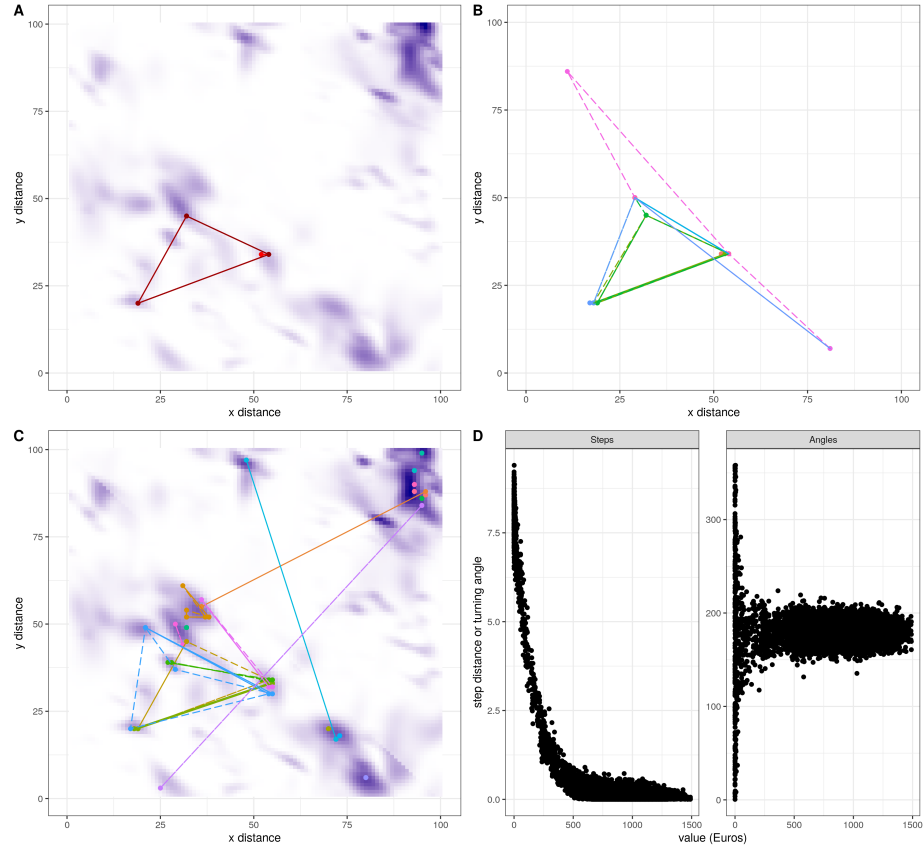


Figure 4: (A) The fishing locations (points) and movements (lines) of a single vessel during a trip overlaid on the revenue of a fishing site (landings \times price); (B) the fishing locations of the vessel over several trips (value field changes over the period so not shown). Note that movements are a mixture of correlated random walk (solid lines) and experience-based (dashed lines), and that the field is wrapped on a torus so that opposite sides of the spatial domain are considered spatially close; (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.

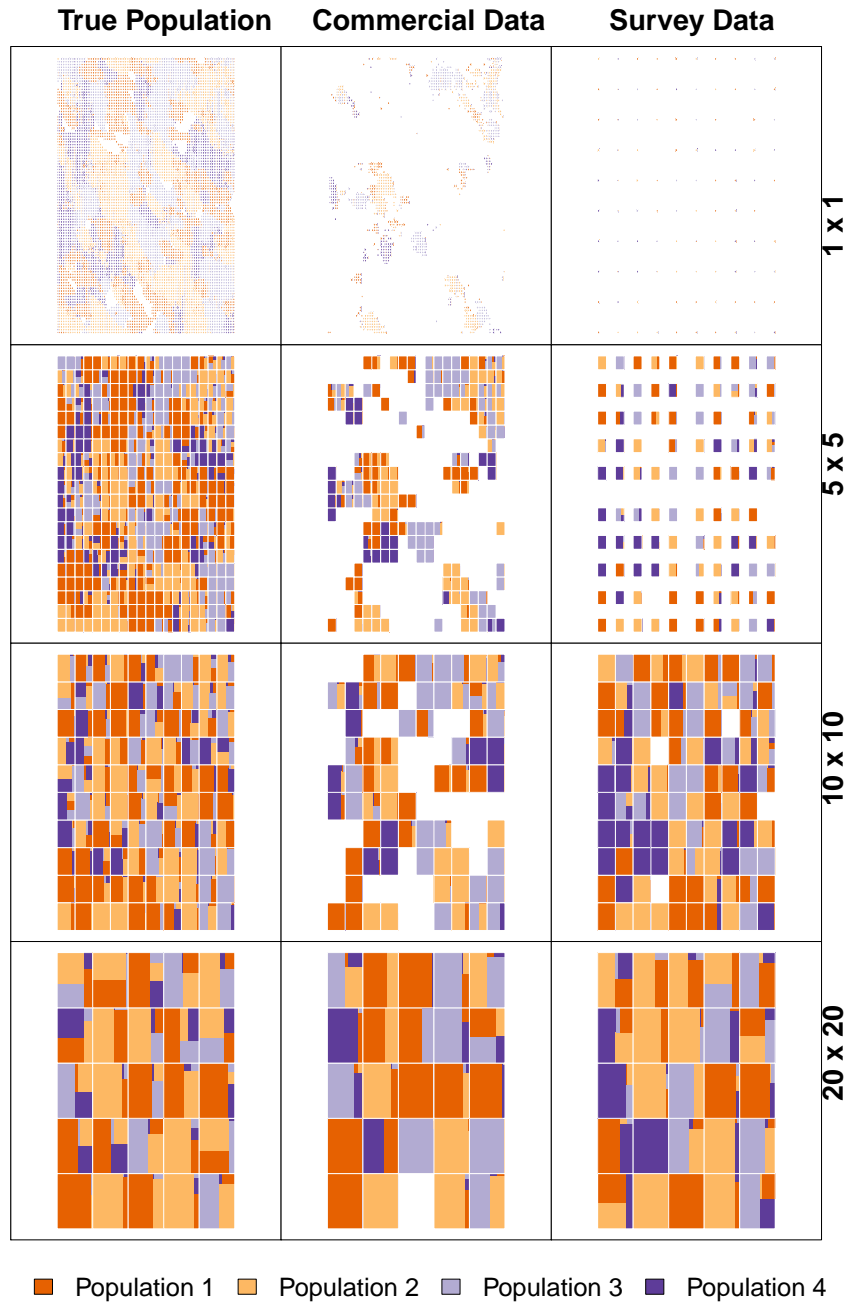


Figure 5: [Colour] Data aggregation at different spatial resolutions over a ten year period. The figure shows catch composition at each spatial unit as visualised using Gerritsen (2014) mapplots R package.



Figure 6: [Colour]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.

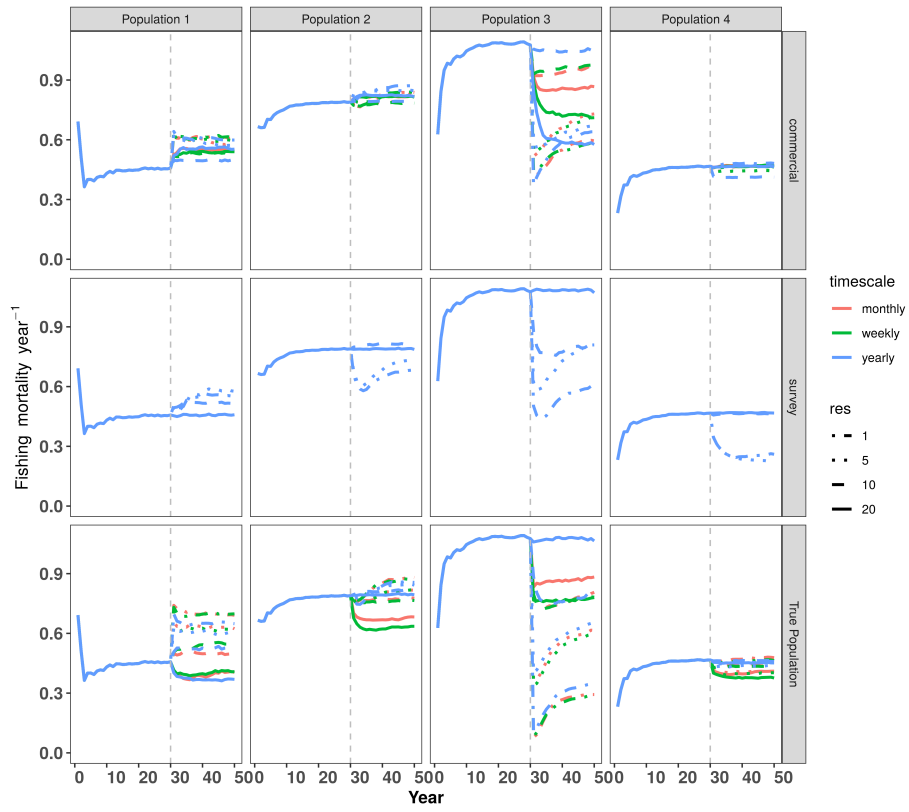


Figure 7: [Colour]Comparison of closure scenarios effect on fishing mortality trends. Line colour denotes timescale, while linestyle denotes spatial resolution. The vertical dashed line indicates the onset of the spatial closures.



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.

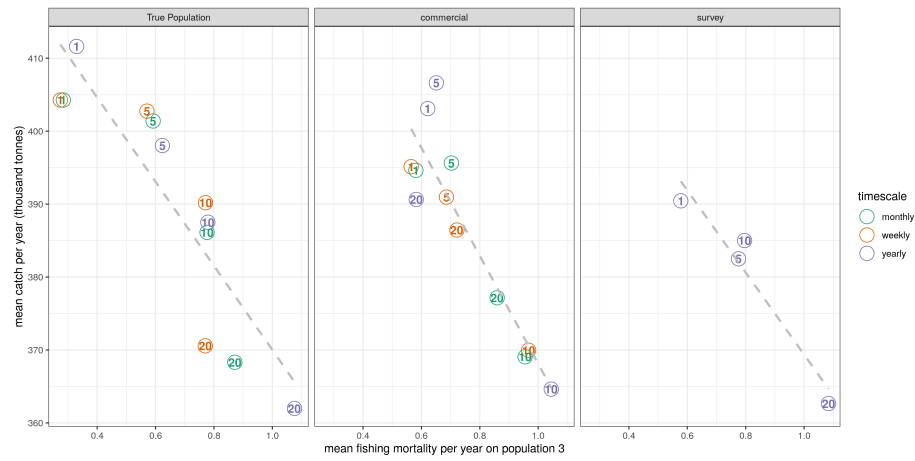


Figure 10: [Colour]Effectiveness of closure with regards to reducing fishing mortality on protected population (further left on x-axis is best) and maintaining high catches in the fishery (highest on y-axis is best). The numbers indicate the spatial resolution of the data, while grey lines indicate the direction of the trade-off between reducing fishing mortality and overall catches.

684 References

- 685 Akima, H., Gebhardt, A., 2016. akima: Interpolation of Irregularly and Regularly
686 Space data. R package version 0.6-2.
- 687 Alverson, D.L., Freeberg, M., Pope, J., Murawski, S., 1994. A Global Assessment
688 of Fisheries By-catch and Discards: A Summary Overview. Technical
689 Report 339.
- 690 Bailey, R.M., Carrella, E., Axtell, R., Burgess, M.G., Cabral, R.B., Drexler, M.,
691 Dorsett, C., Madsen, J.K., Merkl, A., Saul, S., 2019. A computational approach
692 to managing coupled human–environmental systems: the POSEIDON
693 model of ocean fisheries. *Sustainability Science* 14, 259–275.
- 694 Bastardie, F., Nielsen, J.R., Ulrich, C., Egekvist, J., Degel, H., 2010. Detailed
695 mapping of fishing effort and landings by coupling fishing logbooks
696 with satellite-recorded vessel geo-location. *Fisheries Research* 106, 41–53.
- 697 Batsleer, J., Hamon, K.G., Overzee, H.M.J., Rijnsdorp, A.D., Poos, J.J., 2015.
698 High-grading and over-quota discarding in mixed fisheries. *Reviews in Fish
699 Biology and Fisheries* 25, 715–736.
- 700 Bellido, J.M., Santos, M.B., Pennino, M.G., Valeiras, X., Pierce, G.J., 2011.
701 Fishery discards and bycatch: Solutions for an ecosystem approach to fisheries
702 management? *Hydrobiologia* 670, 317–333.
- 703 Beverton, R.J., Holt, S.J., 1957. On the Dynamics of Exploited Fish Populations.
704 HM Stationary Office, London.
- 705 Boonstra, W.J., Hentati-Sundberg, J., 2016. Classifying fishers’ behaviour. An
706 invitation to fishing styles. *Fish and Fisheries* 17, 78–100.
- 707 Branch, T.A., Hilborn, R., Bogazzi, E., 2005. Escaping the tyranny of the grid:
708 A more realistic way of defining fishing opportunities. *Canadian Journal of
709 Fisheries and Aquatic Sciences* 62, 631–642.

710 Catchpole, T.L., Reville, A.S., 2008. Gear technology in Nephrops trawl fisheries.
711 Reviews in Fish Biology and Fisheries 18, 17–31.

712 Codling, E.A., Plank, M.J., Benhamou, S., Interface, J.R.S., 2008. Random
713 walk models in biology. Journal of the Royal Society, Interface / the Royal
714 Society 5, 813–34.

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

718 Costello, C., Rassweiler, A., Siegel, D., De Leo, G., Micheli, F., Rosenberg, A.,
719 2010. The value of spatial information in MPA network design. Proceedings
720 of the National Academy of Sciences of the United States of America 107,
721 18294–18299.

722 Cotter, A.J., Pilling, G.M., 2007. Landings, logbooks and observer surveys:
723 Improving the protocols for sampling commercial fisheries. Fish and Fisheries
724 8, 123–152.

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

727 Dedman, S., Officer, R., Brophy, D., Clarke, M., Reid, D.G., 2015. Modelling
728 abundance hotspots for data-poor Irish Sea rays. Ecological Modelling 312,
729 77–90.

730 Deriso, R.B., 1980. Harvesting Strategies and Parameter Estimation for an Age-
731 Structured Model. Canadian Journal of Fisheries and Aquatic Sciences 37,
732 268–282. [arXiv:1410.7455v3](#).

733 Dichmont, C.M., Punt, A.E., Deng, A., Dell, Q., Venables, W., 2003. Applica-
734 tion of a weekly delay-difference model to commercial catch and effort data
735 for tiger prawns in Australia ’ s Northern Prawn Fishery. Fisheries Research
736 65, 335–350.

737 Dinmore, T.A., Duplisea, D.E., Rackham, B.D., Maxwell, D.L., Jennings, S.,
738 2003. Impact of a large-scale area closure on patterns of fishing disturbance
739 and the consequences for benthic communities. *ICES Journal of Marine Sci-*
740 *ence* 60, 371–380.

741 Dolder, P.J., Thorson, J.T., Minto, C., 2018. Spatial separation of catches in
742 highly mixed fisheries. *Scientific Reports* 8.

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

746 Dunn, D.C., Maxwell, S.M., Boustany, A.M., Halpin, P.N., 2016. Dynamic
747 ocean management increases the efficiency and efficacy of fisheries manage-
748 ment. *Proceedings of the National Academy of Sciences of the United States*
749 *of America* 113, 668–673.

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

755 Fulton, E.A., Link, J.S., Kaplan, I.C., Savina-Rolland, M., Johnson, P.,
756 Ainsworth, C., Horne, P., Gorton, R., Gamble, R.J., Smith, A.D., Smith,
757 D.C., 2011. Lessons in modelling and management of marine ecosystems:
758 The Atlantis experience. *Fish and Fisheries* 12, 171–188.

759 Gardner, B., Sullivan, P.J., Morreale, S.J., Epperly, S.P., 2008. Spatial and
760 temporal statistical analysis of bycatch data: patterns of sea turtle bycatch
761 in the North Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences*
762 65, 2461–2470.

763 Gerritsen, H., 2014. mapplots: Data visualisation on maps. R package version
764 1.5. <http://CRAN.R-project.org/package=mapplots>.

765 Gerritsen, H.D., Lordan, C., Minto, C., Kraak, S.B., 2012. Spatial patterns
766 in the retained catch composition of Irish demersal otter trawlers: High-
767 resolution fisheries data as a management tool. *Fisheries Research* 129-130,
768 127–136.

769 Gillespie, D.T., 1977. Exact stochastic simulation of coupled chemical reactions.
770 *Journal of Physical Chemistry* 81, 2340–2361.

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

774 Gillis, D.M., Rijnsdorp, A.D., Poos, J.J., 2008. Behavioral inferences from
775 the statistical distribution of commercial catch: patterns of targeting in the
776 landings of the Dutch beam trawler fleet. *Canadian Journal of Fisheries and*
777 *Aquatic Sciences* 65, 27–37.

778 Girardin, R., Hamon, K.G., Pinnegar, J., Poos, J.J., Thébaud, O., Tidd, A.,
779 Vermard, Y., Marchal, P., 2017. Thirty years of fleet dynamics modelling
780 using discrete-choice models: What have we learned? *Fish and Fisheries* 18,
781 638–655.

782 Harley, S.J., Myers, R.A., Dunn, A., 2001. Is catch-per-unit-effort proportional
783 to abundance? *Canadian Journal of Fisheries and Aquatic Sciences* 58, 1760–
784 1772.

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

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

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

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

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

797 Lee, J., South, A.B., Jennings, S., 2010. Developing reliable, repeatable, and
798 accessible methods to provide high-resolution estimates of fishing-effort distri-
799 butions from vessel monitoring system (VMS) data. *ICES Journal of Marine*
800 *Science* 67, 1260–1271.

801 Little, A.S., Needle, C.L., Hilborn, R., Holland, D.S., Marshall, C.T., 2015.
802 Real-time spatial management approaches to reduce bycatch and discards:
803 Experiences from Europe and the United States. *Fish and Fisheries* 16, 576–
804 602.

805 Liu, X., Heino, M., 2014. Overlooked biological and economic implications of
806 within-season fishery dynamics. *Canadian Journal of Fisheries and Aquatic*
807 *Sciences* 71, 181–188.

808 Mahévas, S., Pelletier, D., 2004. ISIS-Fish, a generic and spatially explicit
809 simulation tool for evaluating the impact of management measures on fisheries
810 dynamics. *Ecological Modelling* 171, 65–84.

811 Mangel, M., Clark, C.W., 1983. Uncertainty, search, and information in fish-
812 eries. *ICES Journal of Marine Science* 41, 93–103.

813 Martínez-Minaya, J., Cameletti, M., Conesa, D., Pennino, M.G., 2018. Species
814 distribution modeling: a statistical review with focus in spatio-temporal is-
815 sues. *Stochastic Environmental Research and Risk Assessment* 32, 3227–3244.

816 Mateo, M., Pawlowski, L., Robert, M., 2017. Highly mixed fisheries: Fine-scale
817 spatial patterns in retained catches of French fisheries in the Celtic Sea. *ICES*
818 *Journal of Marine Science* 74, 91–101.

819 Maunder, M.N., Punt, A.E., 2004. Standardizing catch and effort data: A
820 review of recent approaches. *Fisheries Research* 70, 141–159.

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

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

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

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

834 R Core Team, 2017. R Core Team (2017). R: A language and environment for
835 statistical computing.

836 Ricker, W.E., 1954. Stock and Recruitment. *Journal of the Fisheries Research*
837 *Board of Canada* 11, 559–623.

838 Rijnsdorp, A., 2000. Competitive interactions among beam trawlers exploiting
839 local patches of flatfish in the North Sea. *ICES Journal of Marine Science* 57,
840 894–902.

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

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

847 Rijnsdorp, A.D., Poos, J.J., Quirijns, F.J., Grant, J., 2011. Spatial dimension
848 and exploitation dynamics of local fishing grounds by fishers targeting several
849 flatfish species. *Canadian Journal of Fisheries and Aquatic Sciences* 68, 1064–
850 1076.

851 Robinson, L.M., Elith, J., Hobday, A.J., Pearson, R.G., Kendall, B.E., Poss-
852 ingham, H.P., Richardson, a.J., 2011. Pushing the limits in marine species
853 distribution modelling: Lessons from the land present challenges and oppor-
854 tunities. *Global Ecology and Biogeography* 20, 789–802.

855 Schlather, M., Malinowski, A., Menck, P.J., Oestin, M., Strokorb, K., 2015.
856 Analysis, simulation and prediction of multivariate random fields with package
857 randomfields. *Journal of Statistical Software* 63, 1–25. [arXiv:1501.0228](#).

858 Schnute, J., 1985. A genera theory for analysis of catch and effort data. *Cana-
859 dian Journal of Fisheries and Aquatic Sciences* 42, 414–429.

860 Sela, R., Simonoff, J., 2011. REEMtree: Regression Trees with Random Effects.
861 R package version 0.90.3.

862 Shin, Y.J., Shannon, L.J., Cury, P.M., 2004. Simulations of fishing effects on the
863 southern Benguela fish community using an individual-based model: Learning
864 from a comparison with ECOSIM. *African Journal of Marine Science* 26, 95–
865 114.

866 Stock, B.C., Ward, E.J., Eguchi, T., Jannot, J.E., Thorson, J.T., Feist, B.E.,
867 Semmens, B.X., 2019. Comparing predictions of fisheries bycatch using multi-
868 ple spatiotemporal species distribution model frameworks. *Canadian Journal
869 of Fisheries and Aquatic Sciences* .

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

872 Ulrich, C., Reeves, S.a., Vermard, Y., Holmes, S.J., Vanhee, W., 2011. Rec-
873 onciling single-species TACs in the North Sea demersal fisheries using the

874 Fcube mixed-fisheries advice framework. *ICES Journal of Marine Science* 68,
875 1535–1547.

876 Van Putten, I.E., Kulmala, S., Thébaud, O., Dowling, N., Hamon, K.G., Hut-
877 ton, T., Pascoe, S., 2012. Theories and behavioural drivers underlying fleet
878 dynamics models. *Fish and Fisheries* 13, 216–235.

879 Viswanathan, G.M., Buldyrev, S.V., Havlin, S., Da Luz, M.G.E., Raposo, E.P.,
880 Stanley, H.E., 1999. Optimizing the success of random searches. *Nature* 401,
881 911–914.

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

884 Ward, E.J., Jannot, J.E., Lee, Y.W., Ono, K., Shelton, A.O., Thorson, J.T.,
885 2015. Using spatiotemporal species distribution models to identify temporally
886 evolving hotspots of species co-occurrence. *Ecological Applications* 25, 2198–
887 2209.

888 Xu, B., Zhang, C., Xue, Y., Ren, Y., Chen, Y., 2015. Optimization of sampling
889 effort for a fishery-independent survey with multiple goals. *Environmental*
890 *Monitoring and Assessment* 187.