

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 and moving fish 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 applied the framework to draw compared inferences on community structure when using data generated from based on: commercial catch, a simulated fixed-site sampling survey design and the true (simulated) underlying populations. In doing so 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~~

*Corresponding author

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

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. In application to a mixed fishery exploiting four different populations w We found different spatial patterns were evident and that the effectiveness of the spatial closure reduced when data were aggregated across larger spatial areas. ; and then ii) We then simulated an area closure based on areas defined from the different data sources at a range of temporal and spatial resolutions. Aggregation across time periods has less of a negative impact on the closure success than over space. and w While not as effective as when based on on the true population, closures based on high catch rates observed in commercial data were still able to reduce fishing on a protected species.

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. From our application w We conclude 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, bycatch avoidance

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

9 fisheries for the biological and economic sustainability (Ulrich et al., 2011; Bat-
10 sleer et al., 2015).

11
12 There is increasing interest in technical solutions such as gear and spatial clo-
13 sures as measures to reduce unwanted catch [which is often discarded](#) (Kennelly
14 and Broadhurst, 2002; Catchpole and Reville, 2008; Bellido et al., 2011; Cos-
15 grove et al., 2019). ~~A-and~~ adaptive spatial management strategies have been
16 proposed as a way of reducing over-quota discards (Holmes et al., 2011; Little
17 et al., 2015; Dunn et al., 2014). However, if fisheries are to reduce unwanted
18 catch through spatial avoidance, an in-depth understanding of spatiotemporal
19 fishery dynamics is required.

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

33
34
35 Identifying appropriate spatial scales for fisheries closures has been a high-
36 lighted as crucial to their success (Costello et al., 2010; Dunn et al., 2016).
37 Inference on fisheries spatial dynamics is hampered where spatial information
38 is coarse due to low resolution reporting of fisheries catch which is aggregated
39 across larger gridded areas (Branch et al., 2005). Further, if data does not allow

40 identification of spatial features it may lead to poorly sited closures which are
41 ineffectual or have unintended consequences. For example, increased benthic
42 impact on previously unexploited areas from the cod closure in the North Sea
43 were observed without the intended effect of reducing cod exploitation (Rijns-
44 dorp et al., 2001; Dinmore et al., 2003)).

45
46 More refined spatiotemporal information has since become available through
47 the combination of logbook and Vessel Monitoring System (VMS) data (Lee
48 et al., 2010; Bastardie et al., 2010; Gerritsen et al., 2012; Mateo et al., 2017)
49 and more real-time spatial management has been possible (e.g. Holmes et al.,
50 2011). However, fishers establish favoured fishing grounds through an explore-
51 exploit strategy (Rijnsdorp et al., 2011; Bailey et al., 2019) where they search
52 for areas with high catches and then use experience to return to areas where
53 they’ve experienced high catch in the past. This leads to an inherently biased
54 sampling where target species are over-represented in the catch as fishers exploit
55 areas of high abundance. There is a need to understand the influence of these
56 biases on any spatial management measures which are implemented based on
57 inference from commercial landings or catch data.

58
59 To understand the effect of spatiotemporal aggregation of data and fishery
60 targeting on our perception of spatial abundance of different fish populations we
61 ask two fundamental questions regarding inference derived from observational
62 data:

- 63 1. Do different source of sampling-derived fisheries data reflect the underly-
64 ing community structure?
- 65 2. How does data aggregation and data source impact on the success of spa-
66 tial fisheries management measures?

67 To answer these questions we i) develop a simulation model where popula-
68 tion dynamics are highly-resolved in space and time, using a Gaussian spatial

69 process to define suitable habitat for different populations. As the precise lo-
70 cations of the fish are known directly rather than inferred from sampling or
71 commercial catch, we can use the population model to validate how inference
72 from fisheries-dependent and fisheries independent sampling relates to the real
73 community structure in a way we could not with real data. We ii) compare, at
74 different spatial and temporal aggregations, the real (simulated) population dis-
75 tributions to samples from fisheries-dependent and fisheries independent catches
76 to test if these are a true reflection of the relative density of the populations.
77 We then iii) simulate a fishery closure to protect a species based on different
78 spatial and temporal data aggregations.

79

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

82 2. Materials and Methods

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

90

91 Population dynamics for any number of species, as chosen by the user oper-
92 ate on a daily time-step (with recruitment occurring only during defined seasons
93 for each population), while population movement occurs on a weekly time-step,
94 with the fishing module operating on a tow-by-tow basis (i.e. multiple events a
95 day).

96

97 *2.1. Population dynamics*

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

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

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

113

114 Mortality $Z_{c,d}$ can be decomposed to natural mortality, $M_{c,d}$, and fishing
 115 mortality, $F_{c,d}$, where both $M_{c,d}$ and $F_{c,d}$ are instantaneous rates with $M_{c,d}$
 116 fixed and $F_{c,d}$ calculated by solving the Baranov catch equation (Hilborn and
 117 Walters, 1992) for $F_{c,d}$:

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

118 where $C_{c,d}$ is the summed catch from the fishing model across all fleets and ves-
 119 sels 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.

125

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 relation-
ship, or a stochastic Ricker stock recruitment relationship. The Beverton-Holt
relationship is defined as (Beverton and Holt, 1957):

$$\bar{R}_{c,d} = \frac{(\alpha \cdot S_{c,d})}{(\beta + S_{c,d})} \quad (3)$$

$$R_{c,d} \sim \log N[(\log(\bar{R}_{c,d}), \sigma^2)]$$

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:

$$\bar{R}_{c,d} = B_{c,d} \cdot e^{(\alpha - \beta \cdot B_{c,d})} \quad (4)$$

$$R_{c,d} \sim \log N[(\log(\bar{R}_{c,d}), \log(\sigma^2))]$$

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 adja-
cent cells, and random (diffusive) movement, governed by a stochastic process
where movement between adjacent cells is described by a set of probabilities

143 which are affected by the suitability of habitat, temperature in a cell and the
144 thermal tolerance of a population to that temperature.

145

146 The combined process results in a population structure and movement pat-
147 tern unique to each population, with population movement occurring on a
148 weekly basis. The decision to model population movement on a weekly timescale
149 was to reflect that fish tend to aggregate in species specific locations that have
150 been observed to last around one to two weeks (Poos and Rijnsdorp, 2007b).
151 Therefore this process approximated the demographic shifts in fish populations
152 throughout a year with seasonal spawning patterns (Figure S7).

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

174 the GRFs), temperature tolerance and distance from current cell:

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

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

179

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

185

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

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

190 Where $Tol_{c,p,wk}$ is the tolerance of population p for cell c in week wk , $T_{c,wk}$ is
 191 the temperature in the cell given the week and μ_p and σ_p the mean and stan-
 192 dard deviation of the population temperature tolerance. The variables, their
 193 meaning and units for population movement is provided in Table 2.

194

195 ~~The final combined process results in a population structure and movement~~
 196 ~~pattern unique to each population, with population movement occurring on a~~
 197 ~~weekly basis. The decision to model population movement on a weekly timescale~~
 198 ~~was to reflect that fish tend to aggregate in species specific locations that have~~
 199 ~~been observed to last around one to two weeks (Poos et al 2007). Therefore this~~

process approximated the demographic shifts in fish populations throughout a year with seasonal spawning patterns (Figure S7).

2.4. Fleet dynamics

Fleet dynamics were can be broadly categorised into three components. *Fleet targeting* determined determines the fleet catch efficiency and preference towards a particular population; *trip-level decisions* determined that determines the initial location to be fished at the beginning of a trip; and *within-trip decisions* determined fishing locations, that determines movement from one fishing spot to another within a trip. This results in an explore-exploit strategy was implemented in the model that combined these three components for individual vessels to maximise their catch from an unknown resource distribution (Bailey et al., 2019). The decision to use an individual based model for fishing vessels was taken because fishers are heterogeneous in their location choice behaviour due to different objectives, risk preference and targeting preference (Van Putten et al., 2012; Boonstra and Hentati-Sundberg, 2016). Therefore fleet dynamics are emergent from individual dynamics rather than pre-defined group dynamics.

2.4.1. Fleet targeting

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

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

Several studies (for a review see Girardin et al., 2017) have confirmed past activity and past catch rates are strong predictors of fishing location choice. For this reason, the fleet dynamics sub-model included a learning component, where a vessel's initial fishing location in a trip was based on selecting from

229 previously successful fishing locations. This was achieved by calculating an
 230 expected revenue based on the catches from locations fished in the preceding
 231 trip as well as the same month periods in previous years and the travel costs
 232 from the port to the fishing grounds. Then a vessel chooses randomly from the
 233 top 70 % of fishing events (defined as the ‘threshold’) in terms of expected profit
 234 within that season.

235 *2.4.3. Decision about where to fish within a trip*

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

249

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

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

256 where $L_{c,d,p}$ is landings of a population p , and Pr_p price of a population. All

257 population prices were kept the same across fleets and seasons. Here, when
 258 fishing is successful vessels remain in a similar location and continue to exploit
 259 the local fishing grounds. When unsuccessful, they move some distance away
 260 from the current fishing location. The movement distance retains some degree
 261 of stochasticity, that can be controlled separately, but is determined by the
 262 relationship:

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

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

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

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

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

266 where Le is the step length, Br_t is the bearing at time t , k the concentration
 267 parameter from the von Mises distribution that we correlate with the revenue so
 268 that $k = (Rev + 1/RefRev) \cdot max_k$, where max_k is the maximum concentration
 269 value, k , and $RefRev$ is parametrised as for β_3 in the step length function.
 270 Details of the variables, meaning and units for fleet dynamics are provided in
 271 Table 3.

272 2.4.4. Local population depletion

273 Where several fishing vessels exploit the same fish population competition is
 274 known to play an important role in local distribution of fishing effort (Gillis and
 275 Peterman, 1998). If several vessels are fishing on the same patch of fish, local
 276 depletion and interference competition will affect fishing location choice of the
 277 fleet as a whole (Rijnsdorp, 2000; Poos and Rijnsdorp, 2007a). To account for
 278 this behaviour, the fishing sub-model operates spatially on a daily time-step so
 279 that for future days the biomass available to the fishery is reduced in the areas

280 fished. The cumulative effect is to make heavily fished areas less attractive as a
281 future fishing location choice as reduced catch rates will be experienced.

282 2.5. Fisheries independent survey

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

290

291 2.6. Software: R-package development

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

295

296 3. Model calibration

297 We calibrate *MixFishSim* to investigate the influence of data aggregation on
298 spatial inference.

299 3.1. Population models

300 We calibrated the simulation model for four example populations with dif-
301 ferent demographics, growth rates, natural mortality and recruitment (Table 4).
302 Habitat preference (Figure S3) and temperature (Figures S5, with temperature
303 tolerance S6) defined to be unique to each population resulting in differently
304 weekly distribution patterns (Figures S7-S9). In addition, each of the pop-
305 ulations was assumed to have two defined spawning areas that result in the
306 populations moving towards these areas in pre-defined weeks (Figure S4) with

307 population-specific movement rates (Table 4). The population demographics
 308 were defined to broadly represent three mobile low-medium value groundfish
 309 species and one high value species with low mobility, with the dynamics hypo-
 310 thetical but as you might expect to find in a typical demersal fishery.

311 3.2. Fleet calibration

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

322

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

332

333 3.3. Survey settings

334 The survey simulation was set up with a fixed gridded station design with
 335 100 stations fished each year, starting on day 92 and ending on day 112 (5

stations per day) with same catchability parameter ($Q_p = 1$) for all populations p . 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 100×100 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:

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

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

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

376 We implemented a series of spatial closures targeted at reducing fishing mor-
 377 tality on population 3, given the different data sources and spatial and temporal
 378 resolutions above. We use the effectiveness of these closures in reducing fishing
 379 mortality as a way of evaluating the trade-offs in data sources and resolution.
 380 Survey closures were on an annual basis only, as this was the most temporally
 381 resolved survey data available. We evaluated the factors contributing to the suc-
 382 cess of the closures through a regression tree (using the R package REEMtree
 383 (Sela and Simonoff, 2011)) to identify the factor most contributing to differences
 384 in fishing mortality before and after the closure.

385 4. Results

386 4.1. Emergent simulation dynamics

387 Individual habitat preferences and thermal tolerances result in different spa-
 388 tial habitat use for each population (Figure S1) and consequently different sea-
 389 sonal exploitation patterns (Figure S2).

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 2(A)), while across several trips fishing grounds that are further apart are fished (Figure 2 (B)). These different locations relate to areas where the highest revenue were experienced, as shown by Figure 2 (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 2 (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 2 (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 3). 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.

411 The spatial catch information on a 10 x 10 and 20 x 20 grid lose a signifi-
412 cant amount of information about the spatial resolutions for all data sources,
413 and some differences between the survey, commercial and true population data
414 emerge.

415

416 Different perceptions of the proportion of each stock in an area are seen when
417 we aggregate the data at different timescales, with weekly (top), monthly (mid-
418 dle) and yearly (bottom) catch compositions from across an aggregated 20 x 20
419 area showing different patterns (Figure 4). In the true population, the monthly
420 aggregation captures the major patterns of composition seen in the weekly data
421 with the percentage of different populations in the catch having similar mean
422 and standard deviations (Table 7). In the weekly and monthly data population
423 2 dominates. However, some of the variation was lost when aggregated to an
424 annual level, as indicated from the lower standard deviations (Table 7).

425

426 The commercial data on a weekly basis shows some of the same patterns as
427 the true population, though the population 1 (in red) is less well represented
428 and some weeks are missing catches from the area. Here, weekly and monthly
429 compositions were nearly identical (Figure 4; Table 7). Again, yearly values
430 head a similar mean but smaller standard deviation.

431

432 The survey data was only available on an annual basis, and showed again
433 a slightly different composition from the true population and the commercial
434 data; in particular a greater proportion of population 4 (Figure 4).

435 4.3. How does data aggregation and source impact on spatial fisheries manage- 436 ment measures?

437 ~~We implemented a spatial closure using the different data sources and spatial~~
438 ~~and temporal aggregations as outlined in the protocol in Section 3.4. We used~~
439 ~~this to assess the efficacy of a closure in reducing fishing mortality on population~~
440 ~~3, given availability of data and its use at different resolutions in order to~~

441 ~~evaluate the trade-offs in data sources.~~

442 In most cases the fishery closure was successful in reducing fishing mortality
443 on the species of interest (population 3; Figure 5). Interestingly the largest re-
444 ductions in fishing mortality happened immediately after the closures, following
445 which the fisheries “adapted” to the closures ~~by finding new areas of high abun-~~
446 ~~dance to fish. This led to~~ fishing mortality increasing again, though not to past
447 levels (Figure 5). The exception to the success was the closures implemented
448 based on the coarsest spatial (20 x 20) and temporal resolution (yearly) that
449 was ineffective (i.e. failed to reduce fishing mortality) with all data sources.
450 As expected, closures based on the “known” population distribution were most
451 effective, with differing degrees of success using the commercial data. Fishing
452 mortality rates on the other species changed in different proportions, depending
453 on whether the displaced fishing effort moved to areas where the populations
454 were found in greater or lesser density.

455

456 The factor most contributing to differences in fishing mortality before and
457 after the closure was the population (72 % showing that the closures were ef-
458 fective for population 3), followed by data resolution (21 %), data type (7 %)
459 with the least important factor the timescale (< 1 %). In general the finer the
460 spatial resolution of the data used the greater reduction in fishing mortality for
461 population 3 after the closures (Figure 6). The notable outliers are the com-
462 mercial data at the coarsest spatial resolution (20 x 20) at a yearly and weekly
463 timescale, where closures were nearly as effective as the fine-scale resolution. In
464 this case the closures were sufficiently large to protect a core area of the habitat
465 for the population, but this was achieved in a fairly crude manner by closing a
466 large area - including area where the species was not found (Figure 7) that may
467 have consequences in terms of restricting the fishery in a much larger area than
468 necessary. We found that these trade-offs existed, with high catches maintained
469 with an effective closure when the highest resolution data was used, with the
470 effect being linear when the true population distribution was known and also
471 persisting for closures based on commercial information (Figure 8).

472

473 **5. Discussion**

474 Our study presents a new highly resolved fisheries simulation framework to
 475 evaluate the importance of data scaling and considers potential bias introduced
 476 through data aggregation when using fisheries data to infer spatiotemporal dy-
 477 namics of fish populations. Understanding how fishers exploit multiple hetero-
 478 geneously distributed fish populations with different catch limits or conservation
 479 status requires detailed understanding of the overlap of resources; this is difficult
 480 to achieve using conventional modelling approaches due to species targeting in
 481 fisheries resulting in preferential sampling (Martínez-Minaya et al., 2018). Of-
 482 ten data are aggregated or extrapolated which requires assumptions about the
 483 spatial and temporal scale of processes. Our study explores the assumptions
 484 behind such aggregation and preferential sampling to identify potential impacts
 485 on management advice. With modern management approaches increasingly
 486 employing more nuanced spatiotemporal approaches to maximise productivity
 487 while taking account of both the biological and human processes operating on
 488 different time-frames (Dunn et al., 2016), understanding assumptions behind
 489 the data used - increasingly a combination of logbook and positional informa-
 490 tion from vessel monitoring systems - is vital to ensure measures are effective.

491

492 *5.1. Simulation dynamics*

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

498

499 Our approach is unique in that it captures fine scale population and fish-
 500 ery dynamics and their interaction in a way not usually possible with real data

501 and thus not usually considered in fisheries simulations. While other simulation
 502 frameworks seek to model individual vessel dynamics based on inferred dynam-
 503 ics from VMS and logbook records (Bastardie et al., 2010), or as a system to
 504 identify measures to meet particular management goals (Bailey et al., 2019),
 505 our framework allows users to explore ~~the~~ assumptions in modelling observa-
 506 tional data and ~~to~~ evaluate the underlying dynamics of such approaches at ~~a~~
 507 fine spatial and temporal scales. This offers the advantage that larger scale fish-
 508 ery patterns are emergent properties of the system and results can be compared
 509 to those obtained under a statistical modelling framework.

510

511 Typically, simulation models that treat fish as individuals are focussed on
 512 exploring the inter- and intra- specific interactions among fish populations (e.g.
 513 OSMOSE; Shin et al. (2004)) in order to understand how they vary over space
 514 and time. Our focus was on understanding the strengths and limitations of in-
 515 ference from catch data obtained through commercial fishing activity with fleets
 516 exploiting multiple fish populations. ~~This shows how-and~~ realised ~~catch~~ dis-
 517 tributions ~~that~~ may differ from the underlying populations, as identified by
 518 Gillis et al. (2008). As such, we favoured a minimum realistic model of the
 519 fish populations (Plagányi et al., 2014) taking account of environmental but not
 520 demographic stochasticity, while incorporating detailed fishing dynamics that
 521 take account of different drivers in a mechanistic way.

522

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

530

531 We take account of heterogeneity in fleet dynamics due to different prefer-

ences 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., 2019).

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 S1, 2).

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 3). 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).

562 *5.3. How does data aggregation and source impact on spatial fisheries manage-*
563 *ment measures?*

564 From our simulations spatial disaggregation was more important than the
565 temporal disaggregation of the commercial data. This reflects the fact that there
566 was greater spatial heterogeneity over the spatial domain than experienced in
567 individual locations over the course of the year (Figure S1).

568
569 The yearly data assumes the same proportion of each population caught at
570 any time of the year due to the data aggregation. This assumption introduces
571 ‘aggregation bias’ as the data may only be representative of some point (or no
572 point) in time. The monthly data shows some consistency between the real pop-
573 ulation and commercial data for population 2 - 4, though population 1 remains
574 under-represented. On an annual basis, interestingly the commercial data un-
575 der represents the first species (in red) while the survey over represents species
576 1. This is likely due to the biases in commercial sampling, with the fisheries
577 not targeting the areas where population 1 are present and the survey sampling
578 areas where population 1 is more abundant than on average. This indicates that
579 fixed closures, at the right resolution, when based on commercially derived data
580 have the potential to reduced fishing mortality. The likely cost of poor spatial
581 and temporal resolution is associated with reduced effectiveness and potentially
582 closing fishing opportunities for other fisheries (Figure 8).

583
584 Two contrasting real world approaches in this respect were the spatial clo-
585 sures to protect cod in the North Sea. In one example, large scale spatial closures
586 were implemented with little success due to effort displacement to previously
587 unfished areas (Dinmore et al., 2003), while in another small scale targeted
588 spatiotemporal closures were considered to have some effect in reducing cod
589 mortality without having to disrupt other fisheries substantially (Needle and
590 Catarino, 2011). These examples emphasise the importance of considering the
591 right scale and aggregation of data when identifying area closures and the need
592 to consider changing dynamics in the fisheries in response to such closures.

593

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

599 5.4. Model assumptions and caveats

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

604

605 Fish populations in our simulations move in pre-defined timescales and ac-
 606 cording to fixed habitat preferences and temperature gradients (Figures S3, S5).
 607 Our assumptions in calibrating the model (movement rates, temperature toler-
 608 ances) will have a direct impact on our conclusions on the relative importance
 609 of spatial and temporal processes. These assumptions could be explored in a
 610 future study by varying the parameters and assessing the robustness of our con-
 611 clusions. For our example application we have chosen movement rates to reflect
 612 aggregation periods observed in past studies (Poos and Rijnsdorp, 2007b).

613

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

622

623 5.5. Future applications of *MixFishSim*

624 We consider that the increased availability of high resolution catch and lo-
625 cational information from commercial fisheries will require it to be a key source
626 of data for ensuring management is implemented at the right scale in future.
627 For example, identifying hot-spots for bycatch reduction or identifying spatial
628 overlaps in mixed fisheries (Dolder et al., 2018; Gardner et al., 2008; Little et al.,
629 2015; Dedman et al., 2015; Ward et al., 2015). Our simulation model has the
630 potential to test some of the assumptions behind the modelling approaches in
631 identifying such hotspots and indeed behind spatiotemporal modelling in gen-
632 eral, (e.g. comparing GAMs, GLMMs, Random Forests and geostatistical mod-
633 els under different data generation processes as exemplified by Stock et al. (2019)).

634
635 Other novel applications of our framework could be: testing different sur-
636 vey designs given multiple species and data generating assumptions (Xu et al.,
637 2015); commercial index standardisation methods and approaches and under-
638 standing of appropriate scales and data aggregations and non-proportionality
639 in catch rate and abundance (Harley et al., 2001; Maunder and Punt, 2004);
640 exploring assumptions about the distribution of natural mortality and fishing
641 mortality throughout the year and importance of capturing in-year dynamics
642 in estimating stock status (Liu and Heino, 2014); at sea sampling scheme de-
643 signs to deliver unbiased estimates of population parameters (Cotter and Pilling,
644 2007; Kimura and Somerton, 2006); adaptive management (Walters, 2007; Dunn
645 et al., 2016); testing the ability of commonly employed fleet dynamics models
646 such as Random Utility Models to capture fine scale dynamics and understand
647 their importance (Girardin et al., 2017); and as a detailed operating model in a
648 management strategy evaluation (Mahévas and Pelletier, 2004).

649

650 6. Conclusions

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

659
660 Our application shows that inference on community dynamics may change
661 depending on the scale of data aggregation. There is an important balance in
662 ensuring that the data are sufficiently spatially and temporally disaggregated
663 that the main features of the data are captured, yet maintaining enough data
664 coverage that the features can be distinguished. We found in our application
665 that there was greater spatial heterogeneity than temporal heterogeneity and
666 that when using aggregated data to define spatial closures coarser temporal reso-
667 lution (months instead of weeks) could still achieve the same results in reducing
668 exploitation rates of a vulnerable species at the highest temporal resolution
669 data. Conversely, reducing the spatial resolution had a negative effect on the
670 effectiveness of the measures (though importantly, there was still some benefit
671 even with coarse spatial resolution).

672
673 While any findings are likely to be case specific, our findings emphasise the
674 need to understand population demographics, habitat use and movement rates
675 in designing any closure scenario based on observational sampling. This infor-
676 mation can then be used to set the bounds on data aggregation used in modelling
677 studies aimed at informing the management measures.

678
679 *MixFishSim* has numerous potential additional applications as it enables

680 the user to apply methods to a fisheries system where there is detailed under-
681 standing of underlying spatiotemporal dynamics. This enables identification of
682 weaknesses or limitations which would not be possible otherwise. In future, we
683 recommend use of the framework to test hypotheses that are otherwise unable
684 to be analysed using real world data due to limitations of data collection. That
685 way the knowledge gained through simulation can inform the future design of
686 management measures.

687 **Funding and Acknowledgements**

688 This work was supported by the MARES doctoral training program (MARES_14_15)
689 and the Centre for Environment, Fisheries and Aquaculture Science seedcorn
690 program (DP227AC). We thank two anonymous reviewers for their helpful com-
691 ments which greatly improved the final manuscript. The authors declare no
692 competing interests.

693 **Appendices**

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	-
$R_{c,\bar{y}}$	Annually recruited fish in cell	yr ⁻¹
ρ	Brody's growth coefficient	yr ⁻¹
Wt_R	Weight of a fully recruited fish	kg
Wt_{R-1}	Weight of a pre-recruit fish	kg
α_d	Proportion of annually recruited fish recruited during day d	-
<i>Baranov catch equation</i>		
$C_{c,d}$	Catch from cell c for day d	kg
$F_{c,d}$	Instantaneous rate of fishing mortality in cell c on day d	-
$M_{c,d}$	Instantaneous rate of natural mortality in cell c on day d	-
$B_{c,d}$	Biomass in cell c on day d	kg
Recruitment dynamics		
$\tilde{R}_{c,d}$	is the recruitment in cell c for day d	d^{-1}
$B_{c,d}$	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 landings 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)

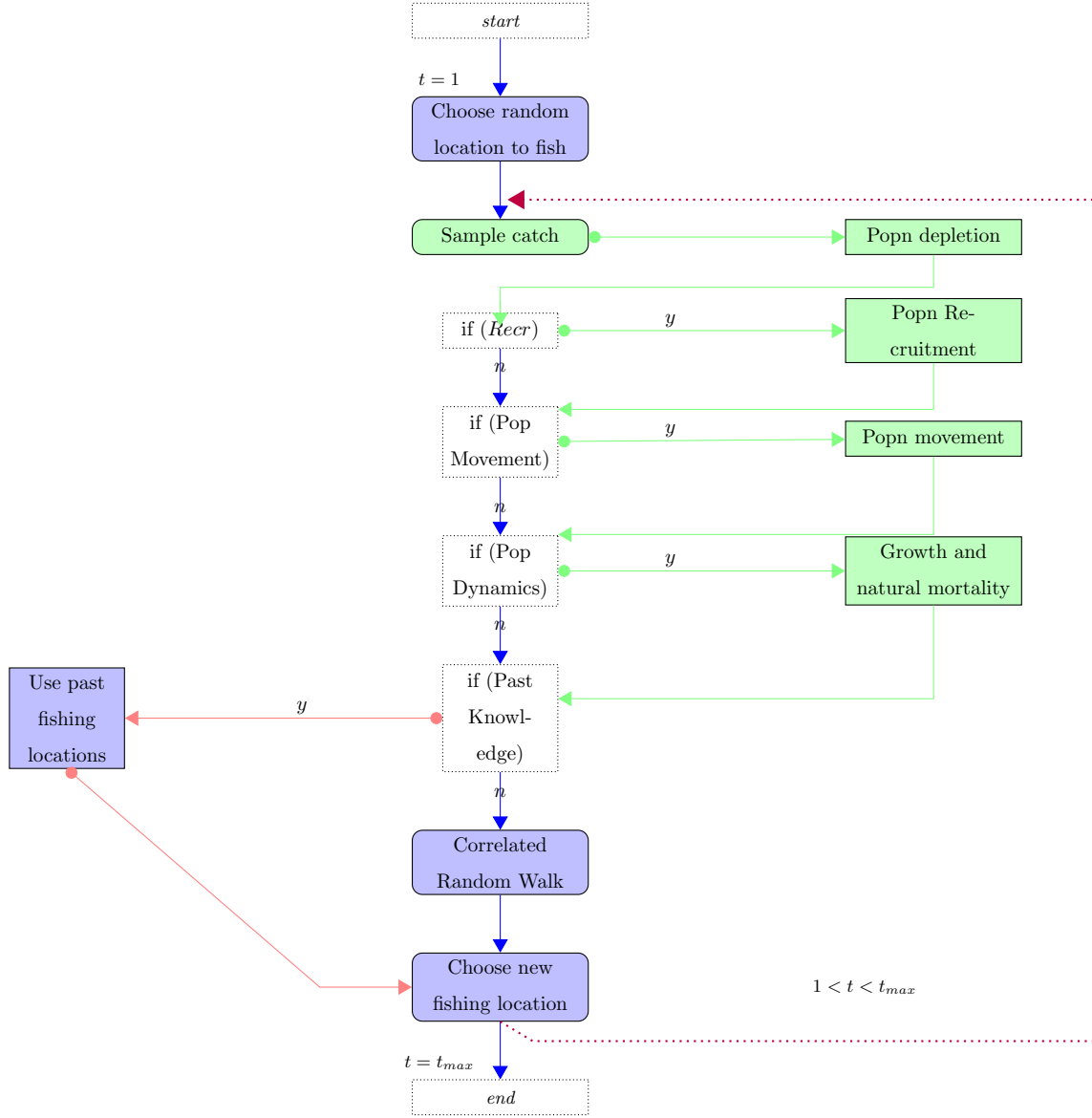


Figure 1: Schematic overview of the simulation model. Blue boxes indicate fleet dynamics processes, the green boxes population dynamics processes while the white boxes are the time steps at which processes occur; $t = \text{tow}$, t_{max} is the total number of tows; (Recr), (Pop Movement), (Pop Dynamics) 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.

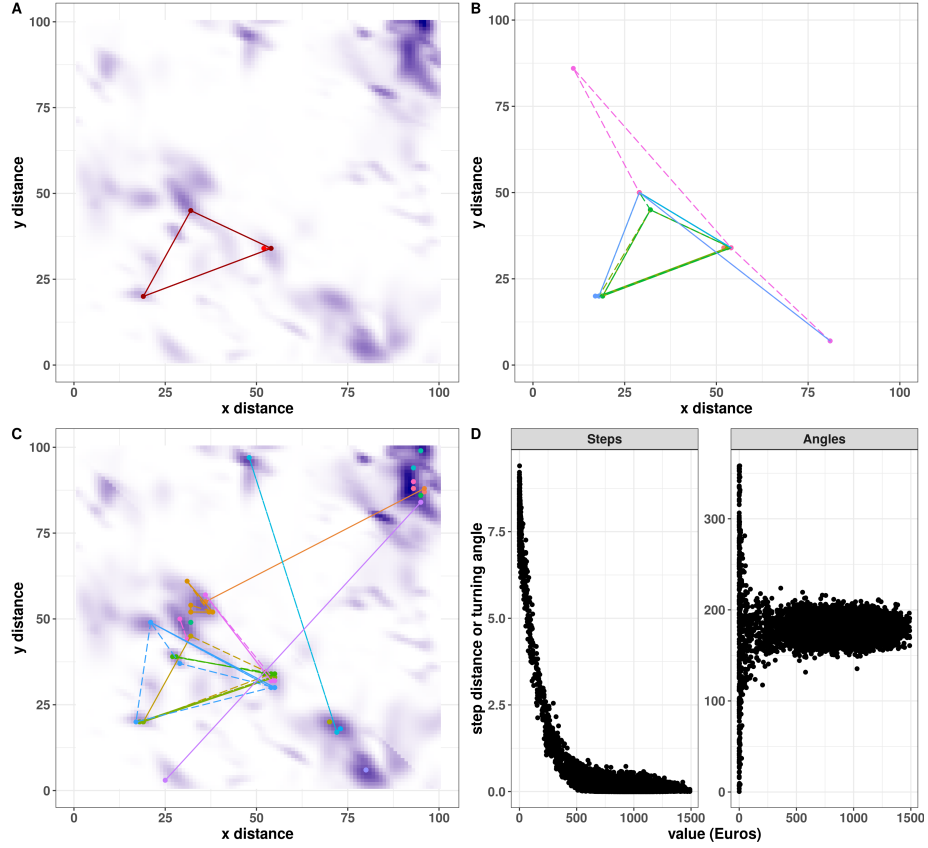


Figure 2: (A) The fishing locations (points) and movements (lines) of a single vessel during a trip overlaid on the revenue of a fishing site (landings \times price; darker purple = higher revenue); (B) the fishing locations of the vessel over several trips (value field changes over the period so not 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.

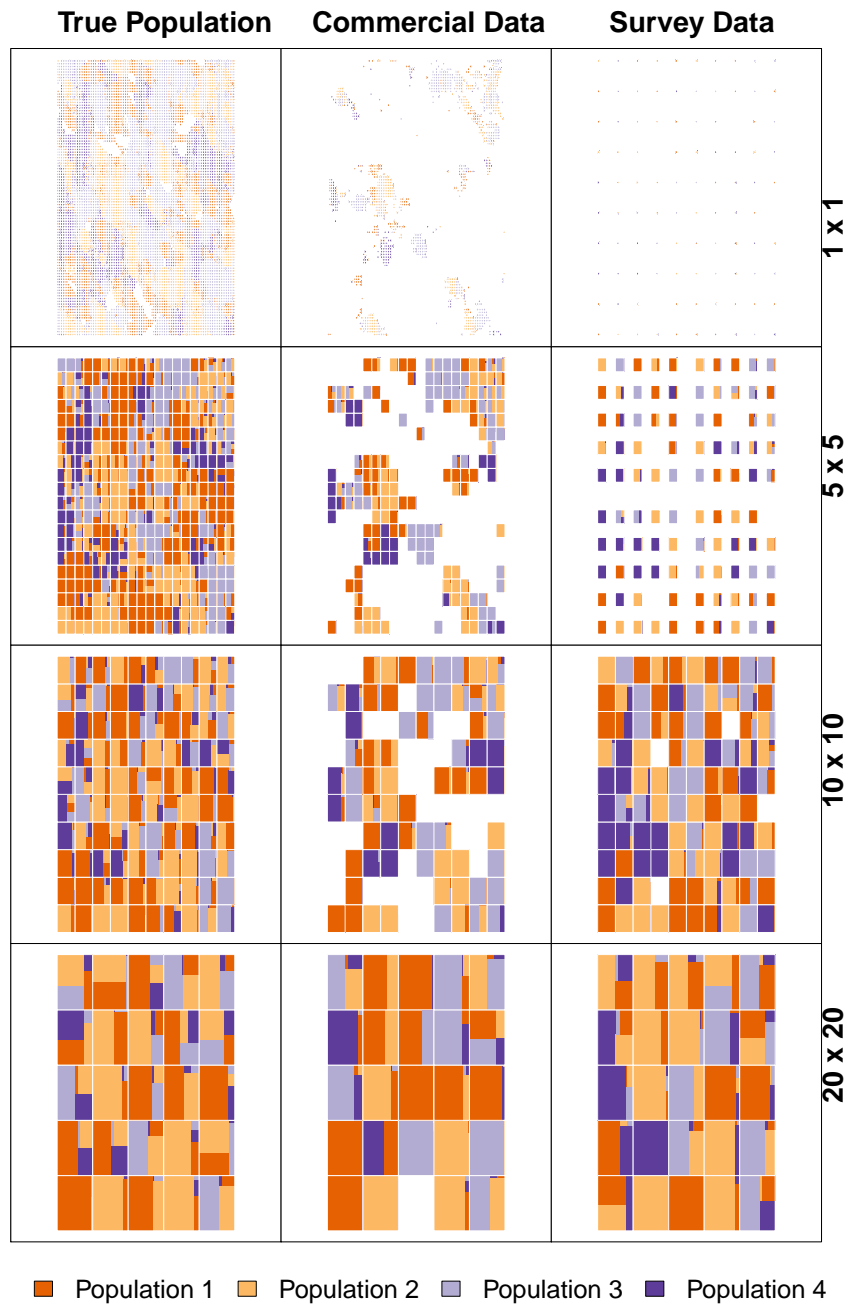


Figure 3: [Colour] Data aggregation at different spatial resolutions over a ten year period. The figure shows catch composition at each spatial unit represented by a square pie chart of the four populations. The area of each colour is proportionate to the weight of each population caught in that unit. Figure produced using the R package 'mapplots' (Gerritsen (2014)).

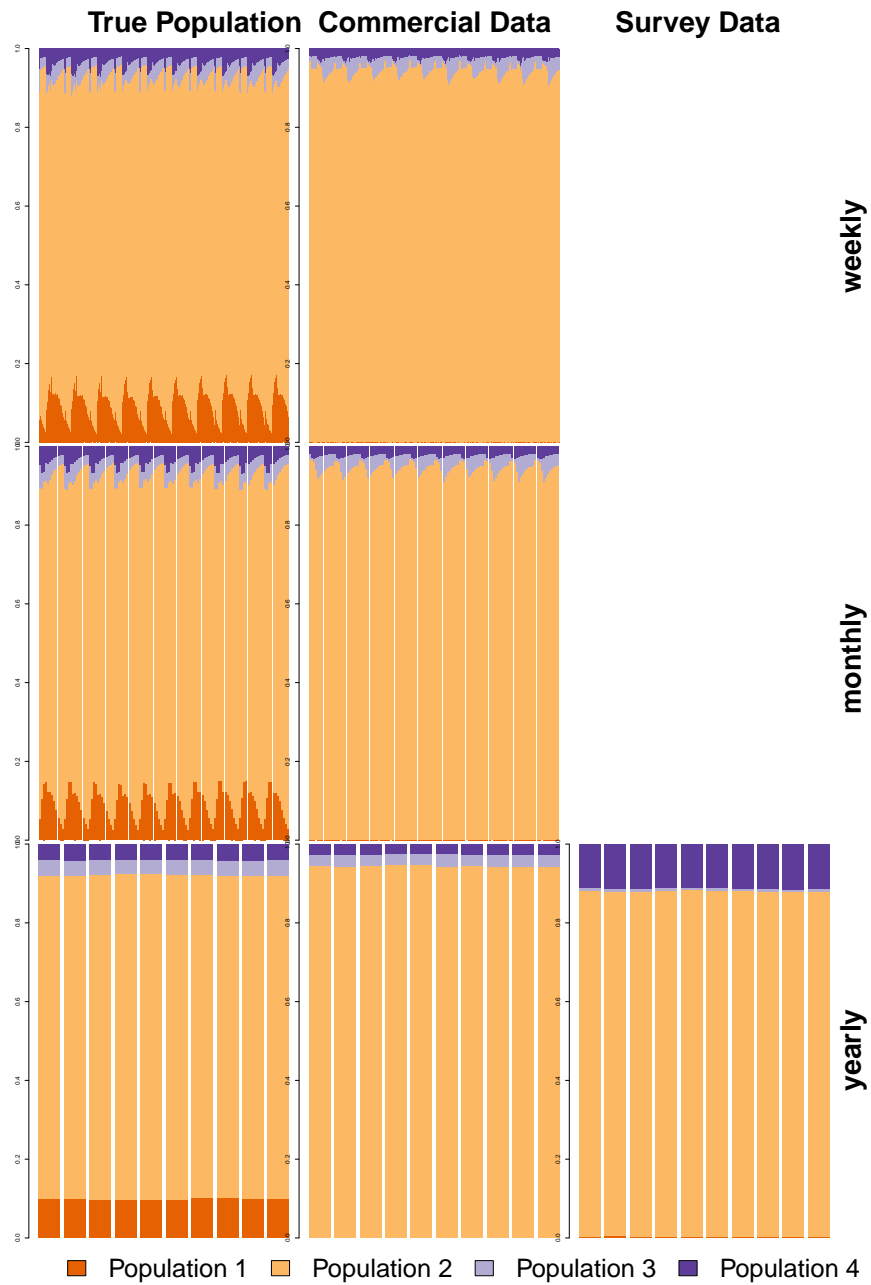


Figure 4: [Colour]Proportion of each population (y axis) for data aggregated at different temporal resolutions. Data is aggregated over a ten-year period for an area 20 x 20. Each bar represents either a week, month or year respectively.

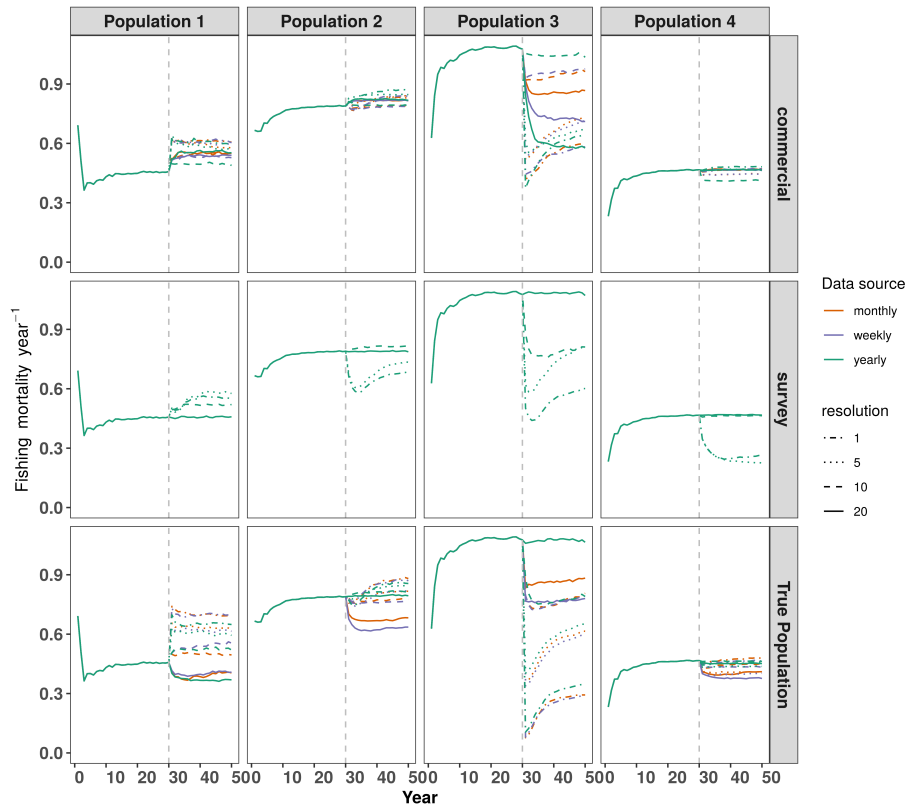


Figure 5: [Colour]Comparison of closure scenarios effect on fishing mortality trends. Line colour denotes timescale, while linestyle denotes spatial resolution. The vertical dashed line indicates the onset of the spatial closures.

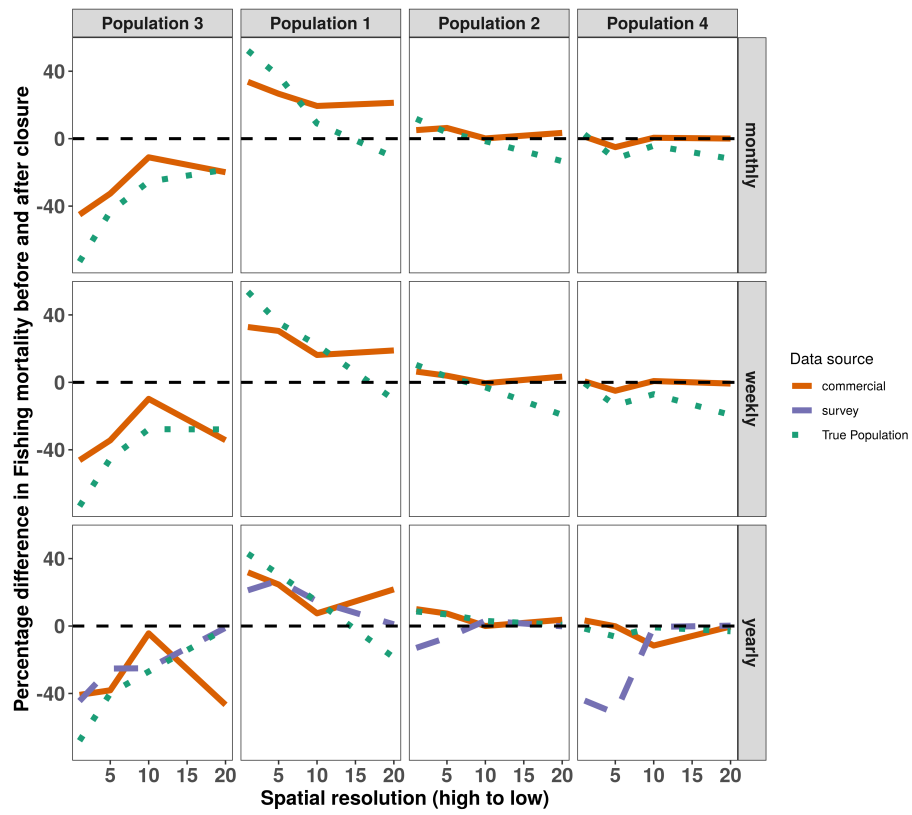


Figure 6: Comparison of closure scenario effectiveness based on different spatial and temporal resolutions.

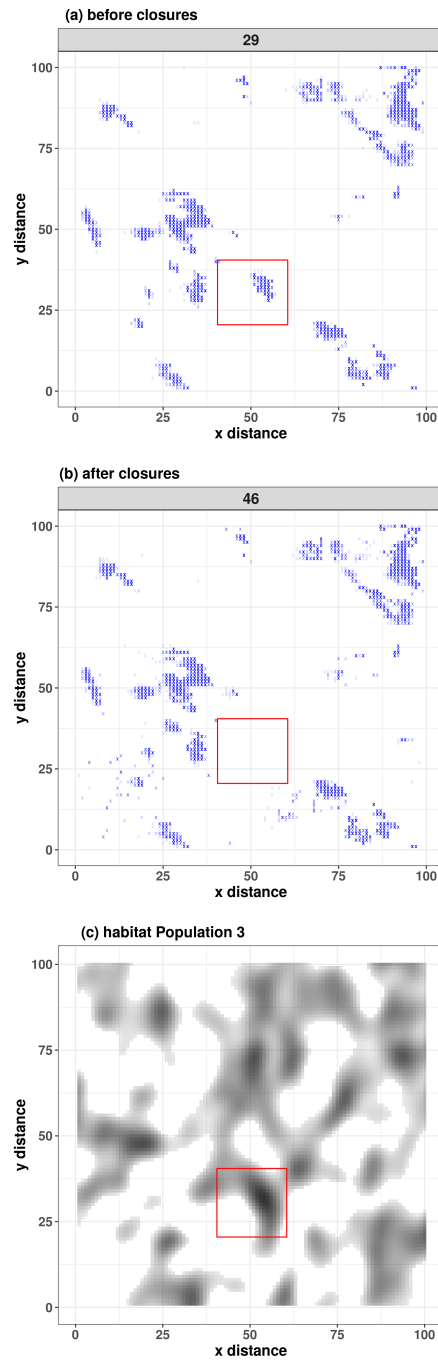


Figure 7: The location of fishing effort, (a) before the spatial closure and (b) after the spatial closure (years in panel), and (c) the suitable habitat for population 3. The site of the closure can be seen in the red box on all three panels.

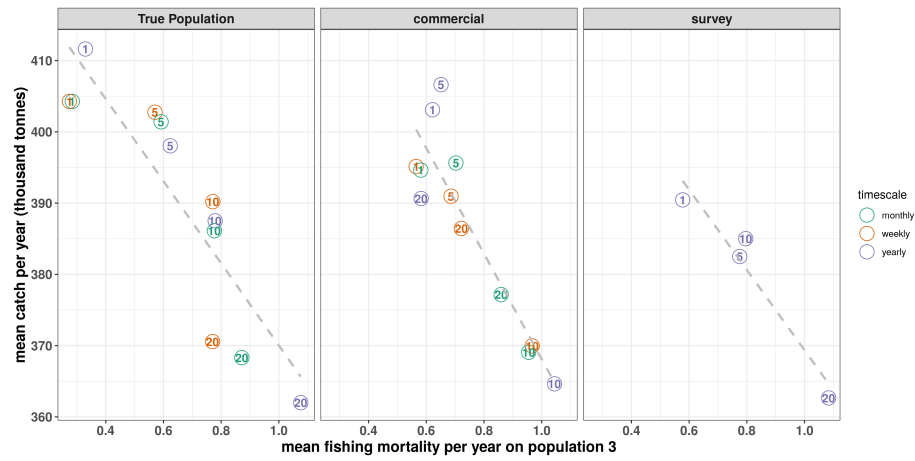


Figure 8: [Colour]Effectiveness of closure with regards to reducing fishing mortality on protected population (further left on x-axis is best) and maintaining high catches in the fishery (highest on y-axis is best). The numbers indicate the spatial resolution of the data, while grey lines indicate the direction of the trade-off between reducing fishing mortality and overall catches.

694 **References**

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

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

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

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

728 Costello, C., Rassweiler, A., Siegel, D., De Leo, G., Micheli, F., Rosenberg, A.,
729 2010. The value of spatial information in MPA network design. Proceedings
730 of the National Academy of Sciences of the United States of America 107,
731 18294–18299.

732 Cotter, A.J., Pilling, G.M., 2007. Landings, logbooks and observer surveys:
733 Improving the protocols for sampling commercial fisheries. Fish and Fisheries
734 8, 123–152.

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

737 Dedman, S., Officer, R., Brophy, D., Clarke, M., Reid, D.G., 2015. Modelling
738 abundance hotspots for data-poor Irish Sea rays. Ecological Modelling 312,
739 77–90.

740 Deriso, R.B., 1980. Harvesting Strategies and Parameter Estimation for an Age-
741 Structured Model. Canadian Journal of Fisheries and Aquatic Sciences 37,
742 268–282. [arXiv:1410.7455v3](#).

743 Dichmont, C.M., Punt, A.E., Deng, A., Dell, Q., Venables, W., 2003. Applica-
744 tion of a weekly delay-difference model to commercial catch and effort data
745 for tiger prawns in Australia ’ s Northern Prawn Fishery. Fisheries Research
746 65, 335–350.

747 Dinmore, T.A., Duplisea, D.E., Rackham, B.D., Maxwell, D.L., Jennings, S.,
748 2003. Impact of a large-scale area closure on patterns of fishing disturbance
749 and the consequences for benthic communities. *ICES Journal of Marine Sci-*
750 *ence* 60, 371–380.

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

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

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

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

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

769 Gardner, B., Sullivan, P.J., Morreale, S.J., Epperly, S.P., 2008. Spatial and
770 temporal statistical analysis of bycatch data: patterns of sea turtle bycatch
771 in the North Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences*
772 65, 2461–2470.

773 Gerritsen, H., 2014. mapplots: Data visualisation on maps. R package version
774 1.5. <http://CRAN.R-project.org/package=mapplots>.

775 Gerritsen, H.D., Lordan, C., Minto, C., Kraak, S.B., 2012. Spatial patterns
776 in the retained catch composition of Irish demersal otter trawlers: High-
777 resolution fisheries data as a management tool. *Fisheries Research* 129-130,
778 127–136.

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

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

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

788 Girardin, R., Hamon, K.G., Pinnegar, J., Poos, J.J., Thébaud, O., Tidd, A.,
789 Vermard, Y., Marchal, P., 2017. Thirty years of fleet dynamics modelling
790 using discrete-choice models: What have we learned? *Fish and Fisheries* 18,
791 638–655.

792 Harley, S.J., Myers, R.A., Dunn, A., 2001. Is catch-per-unit-effort proportional
793 to abundance? *Canadian Journal of Fisheries and Aquatic Sciences* 58, 1760–
794 1772.

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

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

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

- 803 Kimura, D.K., Somerton, D.A., 2006. Review of statistical aspects of survey
804 sampling for marine fisheries. *Reviews in Fisheries Science* 14, 245–283.
- 805 Lande, R., Engen, S., Saether, B.E., 2010. *Stochastic Population Dynamics in*
806 *Ecology and Conservation*.
- 807 Lee, J., South, A.B., Jennings, S., 2010. Developing reliable, repeatable, and
808 accessible methods to provide high-resolution estimates of fishing-effort distri-
809 butions from vessel monitoring system (VMS) data. *ICES Journal of Marine*
810 *Science* 67, 1260–1271.
- 811 Little, A.S., Needle, C.L., Hilborn, R., Holland, D.S., Marshall, C.T., 2015.
812 Real-time spatial management approaches to reduce bycatch and discards:
813 Experiences from Europe and the United States. *Fish and Fisheries* 16, 576–
814 602.
- 815 Liu, X., Heino, M., 2014. Overlooked biological and economic implications of
816 within-season fishery dynamics. *Canadian Journal of Fisheries and Aquatic*
817 *Sciences* 71, 181–188.
- 818 Mahévas, S., Pelletier, D., 2004. ISIS-Fish, a generic and spatially explicit
819 simulation tool for evaluating the impact of management measures on fisheries
820 dynamics. *Ecological Modelling* 171, 65–84.
- 821 Mangel, M., Clark, C.W., 1983. Uncertainty, search, and information in fish-
822 eries. *ICES Journal of Marine Science* 41, 93–103.
- 823 Martínez-Minaya, J., Cameletti, M., Conesa, D., Pennino, M.G., 2018. Species
824 distribution modeling: a statistical review with focus in spatio-temporal is-
825 sues. *Stochastic Environmental Research and Risk Assessment* 32, 3227–3244.
- 826 Mateo, M., Pawlowski, L., Robert, M., 2017. Highly mixed fisheries: Fine-scale
827 spatial patterns in retained catches of French fisheries in the Celtic Sea. *ICES*
828 *Journal of Marine Science* 74, 91–101.

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

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

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

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

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

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

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

848 Rijnsdorp, A., 2000. Competitive interactions among beam trawlers exploiting
849 local patches of flatfish in the North Sea. *ICES Journal of Marine Science* 57,
850 894–902.

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

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

857 Rijnsdorp, A.D., Poos, J.J., Quirijns, F.J., Grant, J., 2011. Spatial dimension
858 and exploitation dynamics of local fishing grounds by fishers targeting several
859 flatfish species. *Canadian Journal of Fisheries and Aquatic Sciences* 68, 1064–
860 1076.

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

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

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

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

872 Shin, Y.J., Shannon, L.J., Cury, P.M., 2004. Simulations of fishing effects on the
873 southern Benguela fish community using an individual-based model: Learning
874 from a comparison with ECOSIM. *African Journal of Marine Science* 26, 95–
875 114.

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

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

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

884 Fcube mixed-fisheries advice framework. *ICES Journal of Marine Science* 68,
885 1535–1547.

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

889 Viswanathan, G.M., Buldyrev, S.V., Havlin, S., Da Luz, M.G.E., Raposo, E.P.,
890 Stanley, H.E., 1999. Optimizing the success of random searches. *Nature* 401,
891 911–914.

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

894 Ward, E.J., Jannot, J.E., Lee, Y.W., Ono, K., Shelton, A.O., Thorson, J.T.,
895 2015. Using spatiotemporal species distribution models to identify temporally
896 evolving hotspots of species co-occurrence. *Ecological Applications* 25, 2198–
897 2209.

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