

MixFishSim: highly resolved spatiotemporal simulations for exploring mixed fishery dynamics

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

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

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

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

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

Abstract

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

If fisheries are to avoid unwanted catch a good understanding of spatiotemporal fishery dynamics is required. However, traditional scientific advice is limited by a lack of highly resolved knowledge of population distributions, population movement and how fishers interact with different fish populations. This reflects the fact that data on fish location at high temporal and spatial resolutions is expensive and difficult to collect. Proxies inferred from either scientific surveys or commercial catch data are often used to model distributions, often with sparse data at limited spatial and temporal resolution.

To understand how data resolution impacts inference on mixed fisheries interactions, we develop a highly resolved spatiotemporal simulation model incorporating: i) delay-difference population dynamics, ii) population movement

*Corresponding author

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

using Gaussian Random Fields to simulate patchy, heterogeneously distributed populations, and iii) fishery dynamics for multiple fleet characteristics based on species targeting via a mix of correlated random walk movement (for exploration) and learned behaviour (for exploitation) phases of the fisheries.

We simulate 50 years of fishing and use the results from the fisheries catch to draw inference on the underlying population structures. We compare this inference to i) a simulated fixed-site sampling design commonly used for fisheries monitoring purposes, and ii) the true underlying population structures input to the simulation. We use the results to establish the potential and limitations of fishery-dependent data in providing a robust picture of spatiotemporal distributions. Finally, we simulate an area closure based on areas defined from the known ("real-population") distribution, commercial catch data and survey data at different temporal and spatial resolutions and assess their effectiveness on reducing catches of a fish population.

We conclude from our simulations that commercial data, while containing bias, provides a useful tool for managing catches in mixed fisheries if applied at the correct spatiotemporal scale.

[333 words]

Keywords: Some, keywords, here. Max 6

2010 MSC: 00-01, 99-00

1. Introduction

Fishers exploit a variety of fish populations that are heterogeneously distributed in space and time with varying knowledge of species distributions using species non-selective fishing gear. In doing so fisheries catch an assemblage of species and may discard over-quota catch when managed by single species quotas and fishers exhaust or more quota, may lead to overexploitation of fish

7 populations (Ulrich et al., 2011; Batsleer et al., 2015). This discarding of fish in
8 excess of quota hampers the ability to limit fishing mortality to within sustain-
9 able limits (Alverson et al., 1994; Crowder et al., 1998; Rijnsdorp et al., 2007)
10 and the ability to manage for the biological and economic sustainability of fish-
11 eries. As such, there is increasing interest in technical solutions such as gear and
12 spatial closures as ways of reducing unwanted catch (Kennelly and Broadhurst,
13 2002; Catchpole and Reville, 2008; Bellido et al., 2011).

14

15 Changes to spatial fishing patterns have been proposed as a method to reduce
16 discards (Holmes et al., 2011; Little et al., 2014; Dunn et al., 2014). However,
17 implementation of avoidance measures is hampered by lack of knowledge of fish
18 and fishery spatiotemporal dynamics and understanding of the scale at which
19 processes are important for management. Understanding the correct scale for
20 spatial measures is crucial in order to implement measures at a resolution that
21 ensures effective management (Dunn et al., 2016) while minimising economic
22 impact. For example, a scale that promotes species avoidance for vulnerable or
23 low quota species while allowing continuance of sustainable fisheries for avail-
24 able quota species.

25

26 Identifying an appropriate scale has been a challenge in the past that has
27 led to ineffectual measures with unintended consequences such as limited impact
28 towards the management objective or increased benthic impact on previously
29 unexploited areas (e.g. the cod closure in the North Sea (Rijnsdorp et al., 2001;
30 Dinmore et al., 2003)). More refined spatial information has since become avail-
31 able through the combination of logbook and Vessel Monitoring System (VMS)
32 data (Lee et al., 2010; Bastardie et al., 2010; Gerritsen et al., 2012; Mateo et al.,
33 2016) and more real-time spatial management has been possible (e.g. Holmes
34 et al., 2011). However, such information is derived from an inherently biased
35 sampling programme, targeted fishing.

36

37 In order to understand the consequences of using VMS-linked landings to

This comes as a surprise: I thought this was going to be about discards. Agree, have removed this to avoid confusion

draw inference on the underlying population structure we develop a simulation model where population dynamics are highly-resolved in space and time. Being known directly rather than inferred from sampling or commercial catch, we can use the population model to evaluate how inference from fisheries-dependent and fisheries independent sampling relates to the real population structure. In our model system population movement is driven by random (diffusive) and directed (advective) processes and we incorporate characterisation of a number of different fishing fleet dynamics exploiting four fish populations with different spatial and population demographics.

Using our model we simulate 50 years of exploitation of the fish populations. We use the results

1. to understand how sampling-derived data reflects the underlying population structures. We compare at different spatial and temporal aggregations of the simulated population distributions to:
 - (a) the inferred population from a stratified fixed-site sampling survey design commonly used for fisheries monitoring purposes, otherwise known as a fisheries-independent survey,
 - (b) the inferred population from our fishery-dependent model which includes fishery-induced sampling dynamics.
2. to understand the impact of data aggregation and data source on spatial fisheries management measures we simulate a fishery closure to protect a species based on different spatial and temporal data aggregations:
 - (a) as if the real spatial population structure were known,
 - (b) the fishery-independent inferred population structure
 - (c) the fishery-dependent inferred population structure

We evaluate the theoretical "benefit" to the population of the closure(s), the effect on the other three populations and fishery catch.

If the paper has two goals this should be clear from the start, but may be better over 2 MSsI would like to keep both parts, but have made clearer in how its set out. The closure scenarios form valida-

68 2. Materials and Methods

69 A modular event-based simulation model was developed with sub-modules
70 implemented on independent time-scales appropriate to capture the character-
71 istic of the different processes (Figure 1). The following sub-modules were in-
72 cluded to capture the full system: 1) Population dynamics, 2) Recruitment
73 dynamics, 3) Population movement, 4) fishery dynamics.

74
75 Population dynamics (fishing and natural mortality, growth) operate on a
76 daily time-step, while population movement occurs on a weekly time-step. Re-
77 cruitment takes place periodically each year for a set time duration specified for
78 each population, while the fishing module operates on a tow-by-tow basis (i.e.
79 multiple events a day). The simulation framework is implemented in the sta-
80 tistical software package R (R Core Team, 2017) and available as an R package
81 from the authors github site (www.github.com/pdolder/MixFishSim).

82



Figure 1: Overview Schematic of simulation model. The 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.

83 *2.1. Population dynamics*

The basic population level processes are simulated using a modified two-stage Deriso-Schnute delay difference model (Deriso, 1980; Schnute, 1985; Dichmont et al., 2003) occurring at a daily time-step. A daily time-step was chosen as to discretise continuous population processes on a biologically relevant and computationally tractable timescale. Under the population dynamics module population biomass growth and depletion for pre-recruits and recruited fish are modelled separately as a function of previous recruited biomass, intrinsic population growth and recruitment. Biomass for each cell is incremented each day as follows (the full parameter list is detailed in Table 1):

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

84 where ρ is Brody's coefficient, shown to be approximately equal to e^{-K} when
 85 K is the growth rate from a von Bertalanffy logistic growth model (Schnute,
 86 1985). Wt_{R-1} is the weight of fish prior to recruitment, while Wt_R is the re-
 87 cruited weight. α_d represents the proportion of fish recruited during that day
 88 for the year, while $R_{c,\tilde{y}}$ is the annual recruits in cell c for year y .

89

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 $F_{c,d}$:

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

90 where $C_{c,d}$ is the summed catch from the fishing model across all fleets and
 91 vessels in cell c for the population during the day d , and $B_{c,d}$ the daily biomass
 92 for the population in the cell. Here, catch and fishing mortality are the sum of

those across all fleets and vessels, where $F_{fl,v,c,d,p} = E_{fl,v,c,d} \cdot Q_{fl,p} \cdot B_{c,d,p}$ with fl , v and p the fleet, vessel and population respectively and E and Q fishing effort and catchability.

2.2. Recruitment dynamics

Recruitment is modelled through a function relating the mature biomass to recruits at time of recruitment. In *MixFishSim*, it can be modelled either as a stochastic Beverton-Holt stock-recruit form (Beverton and Holt, 1957):

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

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

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

where α is the maximum productivity per spawner and β the density dependent reduction in productivity as the SSB increases. In this study, the Beverton-Holt form of stock recruit relationship was used for all populations.

2.3. Population movement dynamics

To simulate fish population distribution in space and time a Gaussian spatial process was employed to model habitat suitability for each of the populations on a 2d grid. An advection-diffusion process controlled population movement, with a time-varying temperature covariate used to change the spatial bounds of suitable habitat on a weekly time-step.

For habitat we first defined a Gaussian random field process, $\{S(c) : c \in \mathbb{R}^2\}$, where for any set of cells c_1, \dots, c_n , the joint distribution of $S =$

[link F to effort and catchability - as I think we have F as an emergent property of the fleets rather than something we solve for (I could be wrong though!) - catch for a vessel is a product of catchability and biomass, i.e. $C = qB$, but this catch is summed to solve for F . So its both really]

What have a temperature covariate? Could just use time- Was intended as some biological meaning - species thermal tolerances load onto the temperature effect - so could be different per species

Not clear how

110 $\{S(c_1), \dots S(c_n)\}$ is multivariate Gaussian. The distribution is specified by its
 111 mean function, $\mu(c) = E[S(c)]$ and its covariance function, $\gamma(c, c') = Cov\{S(c), S(c')$
 112 (Diggle and Ribeiro, 2007).

113
 114 The covariance structure affects the smoothness of the surfaces which the
 115 process generates; we used the *Matérn* covariance structure, where the corre-
 116 lation strength weakens with distance. This enables us to model the spatial
 117 autocorrelation observed in animal populations where density is more similar
 118 in nearby locations (Tobler, 1970; F. Dormann et al., 2007) and we change the
 119 parameters to implement different spatial structures for the populations. The
 120 *Matérn* correlation is a two-parameter family where:

$$121 \quad \rho(u) = \{2^{\kappa-1}\Gamma\kappa\}^{-1}(u/\phi)^\kappa K_\kappa(u/\phi)$$

122 $K_\kappa(\cdot)$ is a modified Bessel function of order κ , $\phi > 0$ is a scale parameter with
 123 the dimensions of distance, and $\kappa > 0$, called the order, is a shape parameter
 124 which determines the smoothness of the underlying process (Figure S16).

125

The habitat for each of the populations was generated with the *RFSimulate*
 function of the *RandomFields* R package (Schlatter et al., 2015). Each popu-
 lation was initialised at a single location, and subsequently moved according
 to a probabilistic distribution based on habitat suitability (represented by the
 normalised values from the GRFs), temperature and distance from current cell:

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

126 Where d_{IJ} is the euclidean distance between cell I and cell J , λ is a given rate
 127 of decay, $Hab_{J,p}^2$ is the squared index of habitat suitability for cell J and popu-
 128 lation p , with $Tol_{J,p,wk}$ the temperature tolerance for cell J by population p in
 129 week wk .

130

131 During pre-defined weeks of the year the habitat quality is modified with

Introduce the gamma function, and why this covariance structure? Why correlate values in the random field? to allow populations to have different aggregation densities: have tried to clarify

132 user-defined spawning habitat locations, resulting in each population having
133 concentrated areas where spawning takes place. In the simulations the popu-
134 lations moved towards these cells in the weeks prior to spawning, resulting in
135 directional movement towards the spawning grounds.

136
The temperature field was defined on a gradient from a South-Westerly to
North-Easterly direction, with temperature in each cell changing gradually on
a week-by-week basis so that initially high temperature areas cycled to lower
temperatures and low temperature areas *vice versa*. Each population p was
assigned a thermal tolerance with mean, μ_p and variance, σ_p^2 so that each cell
and population temperature suitability is defined that:

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

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

140

141 The final process resulted in independent populations structure and move-
142 ment patterns, with population movement occurring on a weekly basis. This
143 process approximated the demographic shifts in fish populations throughout a
144 year with seasonal spawning patterns (e.g. Figure S5).

145 2.4. Fleet dynamics

146 The fleet dynamics can be broadly categorised into three components; fleet
147 targeting - which determined the fleet catch efficiency and preference towards a
148 particular species; trip-level decisions, which determined the initial location to
149 be fished at the beginning of a trip; and within-trip decisions, determining move-
150 ment from one fishing spot to another within a trip. Together, these element
151 implement an explore-exploit type strategy for individual vessels to maximise
152 their catch from an unknown resource distribution (Bailey et al. (2018)).

What does it mean concisely?
Areas are as-
signed? Yes,
the areas are
pre-defined - I
have amended
to reflect and
tried to clarify

153 *2.4.1. Fleet targeting*

154 Each fleet of n vessels was characterised by both a general efficiency, Q_{fl} ,
155 and a population specific efficiency, $Q_{fl,p}$. Thus, the product of these parameters $[Q_{fl} \cdot Q_{fl,p}]$ affects the overall catch rates for the fleet and the preferential
156 targeting of one population over another. This, in combination with the parameter choice for the step-function defined below (as well as some randomness from
157 the exploratory fishing process) determined the preference of fishing locations
158 for the fleet. All species prices were kept the same across fleets and seasons.
159
160

161 *2.4.2. Trip-level decisions*

162 Several studies (e.g. Hutton et al., 2004; Tidd et al., 2012; Girardin et al.,
163 2015) have confirmed past activity and past catch rates are strong predictors of
164 fishing location choice. For this reason, the fleet dynamics sub-model included a
165 learning component, where a vessel's initial fishing location in a trip was based
166 on selecting from previously successful fishing locations. This was achieved by
167 calculating an expected revenue based on the catches from locations fished in
168 the preceding trip as well as the same month periods in previous years and the
169 travel costs from the port to the fishing grounds, and choosing randomly from
170 the top 75 % of fishing events as defined by the expected profit. Simulation
171 testing indicated that this learning increased the mean value of catches for the
172 vessels, over just relying on the correlated random walk function as described
173 for the 'within trip' decisions below (MIGHT NEED TO INCLUDE IN SUP-
174 PLEMENTARY).

Correlated random walk of what

175 *2.4.3. Within-trip decisions*

176 Fishing locations within a trip are initially determined by a modified random walk process. As the simulation progresses the within-trip decision become
177 gradually more influenced by experience gained from past fishing locations (as
178 per the initial trip-level location choice), moving location choice towards areas
179 of higher perceived profit. A random walk was chosen for the exploratory fishing
180 process as it is the simplest assumption commonly used in ecology to describe
181

182 optimal animal search strategy for exploiting homogeneously distributed prey
183 about which there is uncertain knowledge (Viswanathan et al., 1999). In a ran-
184 dom walk, movement is a stochastic process through a series of steps. These
185 steps have a length, and a direction that can either be equal in length or take
186 some other functional form. The direction of the random walk was also cor-
187 related (known as ‘persistence’) providing some overall directional movement
188 (Codling et al., 2008) .

189

190 We use a *Lévy flight* which is a particular form of random walk charac-
191 terised by a heavy-tailed distribution of step-length. The Lévy flight has re-
192 ceived a lot of attention in ecological theory in recent years as having shown to
193 have very similar characteristics as those observed by animals in nature, and
194 being a near optimum searching strategy for predators pursuing patchily dis-
195 tributed prey (Viswanathan et al., 1999; Bartumeus et al., 2005; Sims et al.,
196 2008). Bertrand et al. (2007) showed that Peruvian anchovy fishermen have a
197 stochastic search pattern similar to that observed with a lévy flight. However,
198 it remains a subject of debate (e.g. see Edwards et al., 2011; Reynolds, 2015),
199 with the contention that search patterns may be more simply characterised as
200 random walks (Sakiyama and Gunji, 2013) with specific patterns related to the
201 characteristics of the prey field (Sims et al., 2012).

202

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

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

where L_p is landings of a population p , and Pr_p price of a population. 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, which can be controlled separately, but is determined by the relationship:

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

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 (x1,y1) to (x2, y2) is defined by:

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

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

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

So step length increases with increasingly gross revenue? No, the opposite

where k the concentration parameter from the von Mises distribution which we correlate with the revenue so that $k = (Rev + 1/RefRev) * max_k$, where max_k is the maximum concentration value, k , and $RefRev$ is parametrised as for β_3 in the step length function. A realised example of the step length and turning angle relationships to revenue can be seen at Figure S15.

2.4.4. Local population depletion

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

218 2.5. Fisheries independent survey

219 A fisheries-independent survey is simulated where fishing on a regular grid
220 begins each year at the same time for a given number of stations (a fixed station
221 survey design). Catches of the populations at each station are recorded but not
222 removed from the population. This provides a fishery independent snapshot
223 of the populations at a regular spatial intervals each year, similar to scientific
224 surveys undertaken by fisheries research agencies.

225 3. Calculation

226 3.1. Population parametrisation

227 We parametrised the simulation model for four populations with different
228 population demographics; growth rates, natural mortality and recruitment func-
229 tions (Table 4). Habitat preference (Figure S1) and temperature tolerances
230 (Figures S3, S4) were unique to each population resulting in differently weekly
231 distribution patterns (Figures S5-S7). In addition, each of the populations has
232 two defined spawning areas which result in the populations moving towards
233 these areas in pre-defined weeks (Figure S2) with population-specific movement
234 rates (Table 4). The realised movement of the populations for a number of
235 weeks is shown in Figure S9 while the realised daily fishing mortality are shown
236 in Figure S10.

237 3.2. Fleet parametrisation

238 The fleets were parametrised to reflect five different characteristic fisheries
239 with unique exploitation dynamics (Table 5). By setting different catchability
240 parameters ($Q_{fl,p}$) we create different targeting preferences between the fleets
241 and hence spatial dynamics. The stochasticity in the random walk process
242 ensures that within a fleet different vessels have slightly different spatial dis-
243 tributions based on individual experience. The step function was parametrised
244 dynamically within the simulations as the maximum revenue obtainable was
245 not known beforehand. This was implemented so that vessels take smaller steps

246 when fishing at a location yields landings value which is in the top 90th per-
247 centile of the value experienced in that year (as defined per fleet in Table 5).

248

249 With increasing probability throughout the simulation, fishing locations were
250 chosen based on experience of profitable catches built up in the same month from
251 previous years and from the previous trip. 'Profitable' in this context was de-
252 fined as the locations where the top 70 % of expected profit would be found
253 given previous trips revenue and cost of movement to the new fishing location.
254 This probability was based on a logistic sigmoid function with a lower asymptote
255 of 0 and upper asymptote of 0.95, and a growth rate which ensures the upper
256 asymptote (where decisions are mainly based on past knowledge) is reached \sim
257 halfway through the simulation.

258

259 An example of the realised fleet movements for a single vessel during a single
260 trip are given in Figure S11, while Figure S12 shows multiple trips for a single
261 vessel, Figure S13 the vessel movements for several trips overlaid on the value
262 field (sum of the population densities \times price), Figure S14 shows fishing locations
263 for an entire fleet of 20 vessels for a single trip, and Figure S15 shows an example
264 of the step function realisation and turning angles from the correlated random
265 walk.

266 3.3. Survey settings

267 The survey simulation was set up with follow a fixed gridded station design
268 with 100 stations fished each year, starting on day 92 and ending on day 112 (5
269 stations per day) with same catchability parameters for all populations ($Q_p =$
270 1).

271 3.4. Simulation settings

272 To illustrate the capabilities on *MixFishSim*, we investigate the influence of
273 the temporal and spatial resolution of different data sources on the reduction in
274 catches of a population given spatial closures. To do so, we set up a simulation

Move some of
the supplemen-
tary figures to
the manuscript

275 to run for 50 years based on a 100×100 square grid, with five fleets of 20 vessels
276 each and four fish populations. Fishing takes place four times a day per vessel
277 and five days a week, while population movement is every week.

278
279 We allow the simulation to run unrestricted for 30 years, then implement
280 spatial closed areas for the last 20 years of the simulation based on data (either
281 derived from the commercial catches, fisheries-independent survey or the 'real
282 population') used at different spatial and temporal scales.

283
284 The following steps are undertaken to determine closures:

- 285 1. Extract data source
- 286 2. Aggregate according to desired spatial and temporal resolution
- 287 3. Interpolate across entire area at desired resolution
- 288 4. Close area covering top 5 % of catch

289 In total 56 closure scenarios were run which represent combinations of:

- 290 • **data types:** commercial logbook data, survey data and 'real population',
- 291 • **temporal resolutions:** weekly, monthly and yearly closures,
- 292 • **spatial resolutions:** 1 x 1 grid, 5 x 5 grid, 10 x 10 grid and 20 x 20 grid,
- 293 • **closure basis:** high catch rates of protected species, or high ratio of
294 protected species v secondary species.

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

297 4. Results

298 The consequences of different spatial aggregations of the data are shown
299 in Figure 2, which represents the aggregation of catch from each of the data
300 sources over a ten year period (to average seasonal patterns) at different spatial

move to start
of methods
section I think
ecological mod-
elling wants
the 'calcula-
tions' section
here. will check

Is there equi-
librium after
5 years or still
some trend in
B? I have rerun
to ensure some
steady state dy-
namics

Procedure un-
clear. Refer
to symbols in
methods sec-
tion or switch
order starting
with description
of data type
etc. Yes, will
redo

301 resolutions.

302

303 The finer spatial grid for the real population (top left) and commercial data
304 (top middle) show visually similar patterns, though there are large unsampled
305 areas in the commercial data from a lack of fishing activity (particularly in
306 the lower left part of the sampling domain). The survey data at this spatial
307 resolution shows very sparse information about the spatial distributions of the
308 populations. The slightly aggregated data on a 5 x 5 grid shows similar patterns
309 and, while losing some of the spatial detail, there remains good consistency be-
310 tween the 'real population' and the commercial data. Survey data starts to pick
311 out some of the similar patterns as the other data sources, but lacks coverage.
312 The spatial catch information on a 10 x 10 and 20 x 20 grid loses a signifi-
313 cant amount of information about the spatial resolutions for all data sources,
314 and some differences between the survey, commercial and 'real population' data
315 emerge.

316

317 Figure 3 shows the consequences of different temporal aggregations of the
318 data over a three year period, with 156 weekly (top), 36 monthly (middle) and
319 3 yearly (bottom) catch compositions from across an aggregated 20 x 20 area.

320

321 As can be seen by comparison to the 'real population', the monthly aggre-
322 gation captures the major patterns seen in the weekly data, albeit missing more
323 subtle differences. The yearly data results in a constant catch pattern due to
324 the aggregation process (sometimes known as an aggregation bias). The com-
325 mercial data on a weekly basis shows some of the same patterns as the 'real
326 population', though the first species (in red) is less well represented and some
327 weeks are missing catches from the area. The monthly data. The monthly data
328 shows some consistency between the 'real population' and commercial data for
329 species 2 - 4, though species 1 remains under-represented. On an annual ba-
330 sis, interestingly the commercial data under represents the first species (in red)
331 while the survey over represents species 1. This is likely due to the biases in

332 commercial sampling, with the fisheries not targeting the areas where species 1
333 are present, and the biases in the survey sampling from over representation of
334 the spatial distribution.

335

336 We implemented a spatial closure using the different data sources and spatial
337 and temporal aggregations as outlined in the protocol in Section 3.4. We used
338 this to assess the efficacy of a closure in reducing fishing mortality on species 1,
339 given availability of data and its use at different resolutions in order to evaluate
340 the trade-offs in data sources. Figure 4 shows the trend in fishing mortality
341 for each species simulated (columns) given the data sources (rows), temporal
342 aggregations (colour lines) and spatial aggregations (line-styles), while Figure 5
343 shows the change in fishing mortality from before the closure (year 29) to after
344 the closure (year 50).

345

346 For the closures based on 'real population' (bottom row), the most disag-
347 gregated data (a weekly timescale and 1 x 1 resolution) was most effective,
348 reducing fishing mortality on species 1 (left) by $\sim 60\%$. Next was the monthly
349 closures ($< \sim 30\%$). The least effective were the yearly closures (blue lines)
350 at all spatial resolutions, which resulted in increased fishing mortalities (> 30
351 $\%$ - N.B. Note though, this is consistent with the increasing trends in F, which
352 is probably more related to the fact that Fs hadn't stabilised in the simulation
353 from the fishing vessels "learning" the best locations - I will rerun the sims for
354 a longer time (20 - 30 years)).

355

356 For the survey data, which can only be implemented on a yearly timescale,
357 the closures had no effect at any data resolution. The results are identical for
358 the different data resolutions except 20 x 20, which is why you can't see more
359 than 2 points. This is because of the sparsity of the sampling locations.

360

361 For the commercial data, the most effective closure scenario was based on 1
362 x 1 data at a monthly temporal resolution. This results in $\sim 10\%$ reduction in

363 F for species 1. This was the only closure scenario to have positive effect accord-
364 ing to Figure 5, though looking at the trend in Figure 4 this looks more related
365 to the continued increased in F trend, as other scenarios had an initial effect.
366 Interestingly the monthly data scenario was more effective than weekly data,
367 which I'd posit is due to the increase amount of data available from the commer-
368 cial sampling across a month compared to a week. Commercial data used at an
369 annual time-step was ineffective in bringing fishing mortality down for species 1.

370

371 Given the scenarios above, it seems clear that spatial disaggregation is more
372 important than the temporal disaggregation of the commercial data, except
373 when its used at an annual time-frame, which is the scenario that gave the
374 worst results.

375 For the other species in the simulation (population 2 - 4) there was little
376 difference in fishing mortalities across scenarios.

377 Note: The monthly commercial data scenario is the most effective of the
378 realistic scenarios, as the 'real population' can only be seen as a baseline com-
379 parison.

380 5. Discussion

381 Our study evaluates the importance of data scaling and considers potential
382 biases introduced through data aggregation when using commercial fisheries
383 data for inference on spatio-temporal dynamics in fisheries. Understanding how
384 fishers exploit multiple heterogeneously distributed fish populations with differ-
385 ent catch limits or conservation status requires detailed understanding of the
386 overlap of resources; this is difficult to achieve using conventional modelling
387 approaches due to the patchy and irregular nature of fisheries resulting in pref-
388 erential sampling Martínez-Minaya et al. (2018). Often data is aggregated or
389 extrapolated which requires assumptions about the spatial and temporal scale
390 of processes. Our study explores the assumptions behind such aggregation and
391 preferential sampling to identify potential impacts on management advice. With

392 modern management approaches increasingly employing more nuanced spatio-
393 temporal approaches in order to maximise productivity while taking account
394 of both the biological and human processes operating on different time-frames
395 Dunn et al. (2016), understanding assumptions behind the data used - increas-
396 ingly a combination of logbook and positional information from vessel monitor-
397 ing systems - is vital to ensure measures are effective.

398

399 We employ a simulation approach to model each of the population and fish-
400 ery processes in a hypothetical 'mixed fishery', allowing us to i) evaluate the
401 consequences of different aggregation assumptions on our understanding of the
402 spatio-temporal distribution of the underlying fish populations, and ii) evaluate
403 the effectiveness of a spatial closure given those assumptions. Our approach
404 captures fine scale population and fishery dynamics not usually considered (al-
405 though see Bastardie et al. (2010); Bailey et al. (2018)) which offers the ad-
406 vantage that larger scale fishery patterns are emergent properties of the system
407 rather than the result of a statistical modelling framework.

408

409 Our results show commercial data can provide at right scale and resolution
410 - depends on scale of process: pop movement etc... Important to consider how
411 fishers interact / adapt to changes with the resource and mgmt.

412

413 Closure scenarios demonstrate potential to reduce F - not as high as with
414 real pop, but good. Make link to other studies – read up on these.

415

416 The what next:

417

418 Real world spatiotemp closures rarely been able to consider these issues / de-
419 signed with these issues fully in mind - NS cod closures, plaice and trevose box...

420

421 Use of commercial data increasing - likely to become more important in
422 future. Also collaborative approach with industry, e.g. hotspot mapping, spa-

423 tiotemp advice...

424

425 Other potential uses of the model

426

427 Survey design

428

429 commercial index standardization methods

430

431 Sampling scheme design

432

433 Testing fleet dynamics models at an aggregated level

434

435 Bigger picture stuff:: LO, increasing desire for more nuanced spatiotemp

436 mgmt... Wider applicability: birds, wildlife ??

437 **6. Conclusions**

438 Study shows

439

440 This is important because

441

442 How we might apply this in future

443

444 **Abbreviations**

445 Detail any unusual ones used.

446 **Acknowledgements**

447 those providing help during the research..

448 Funding

449 This work was supported by the MARES doctoral training program; and the
450 Centre for Environment, Fisheries and Aquaculture Science seedcorn program.

451 Appendices

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

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

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

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

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

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

Table 4: Population dynamics and movement parameter setting

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

Table 5: Fleet dynamics parameter setting

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

Table 6: Fishing mortality effects of the closure scenarios (ordered by most effective first)

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

Table 7: Fishing mortality effects of the closure scenarios (based on highest ratio, ordered by most effective first)

scenario	metric	pop	before	after	diff	timescale	basis	data_type	resolution
6	F	spp_3	1.08	0.52	-52.27	yearly	high_ratio	commercial	1.00
48	F	spp_3	1.08	0.57	-47.06	yearly	high_ratio	commercial	20.00
50	F	spp_3	1.08	0.63	-41.53	yearly	high_ratio	survey	20.00
18	F	spp_3	1.08	0.71	-34.23	weekly	high_ratio	commercial	5.00
19	F	spp_3	1.08	0.72	-33.42	monthly	high_ratio	commercial	5.00
34	F	spp_3	1.08	0.78	-27.75	yearly	high_ratio	commercial	10.00
5	F	spp_3	1.08	0.80	-25.99	monthly	high_ratio	commercial	1.00
20	F	spp_3	1.08	0.81	-25.27	yearly	high_ratio	commercial	5.00
4	F	spp_3	1.08	0.85	-21.52	weekly	high_ratio	commercial	1.00
54	F	spp_3	1.08	0.89	-17.46	weekly	high_ratio	real_pop	20.00
55	F	spp_3	1.08	0.89	-17.46	monthly	high_ratio	real_pop	20.00
56	F	spp_3	1.08	0.89	-17.46	yearly	high_ratio	real_pop	20.00
26	F	spp_3	1.08	0.92	-14.73	weekly	high_ratio	real_pop	5.00
27	F	spp_3	1.08	0.92	-14.73	monthly	high_ratio	real_pop	5.00
28	F	spp_3	1.08	0.92	-14.73	yearly	high_ratio	real_pop	5.00
13	F	spp_3	1.08	0.96	-11.53	monthly	high_ratio	real_pop	1.00
14	F	spp_3	1.08	0.96	-11.01	yearly	high_ratio	real_pop	1.00
12	F	spp_3	1.08	0.97	-10.66	weekly	high_ratio	real_pop	1.00
32	F	spp_3	1.08	1.02	-5.94	weekly	high_ratio	commercial	10.00
22	F	spp_3	1.08	1.02	-5.64	yearly	high_ratio	survey	5.00
33	F	spp_3	1.08	1.02	-5.29	monthly	high_ratio	commercial	10.00
36	F	spp_3	1.08	1.03	-4.52	yearly	high_ratio	survey	10.00
40	F	spp_3	1.08	1.03	-4.52	weekly	high_ratio	real_pop	10.00
41	F	spp_3	1.08	1.03	-4.52	monthly	high_ratio	real_pop	10.00
42	F	spp_3	1.08	1.03	-4.52	yearly	high_ratio	real_pop	10.00
46	F	spp_3	1.08	1.04	-3.50	weekly	high_ratio	commercial	20.00
8	F	spp_3	1.08	1.06	-2.42	yearly	high_ratio	survey	1.00
47	F	spp_3	1.08	1.09	0.52	monthly	high_ratio	commercial	20.00

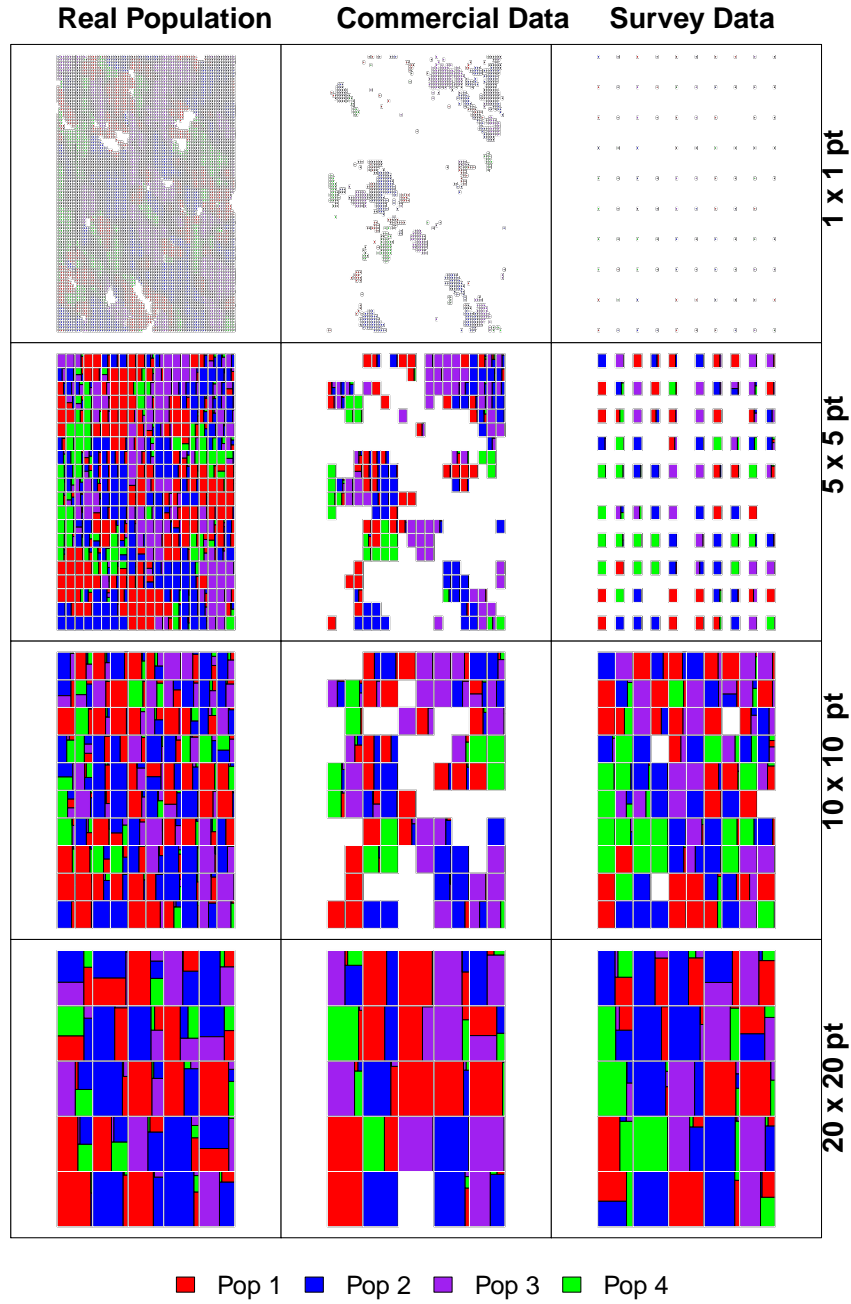


Figure 2: Data aggregation at different spatial resolutions over a ten year period

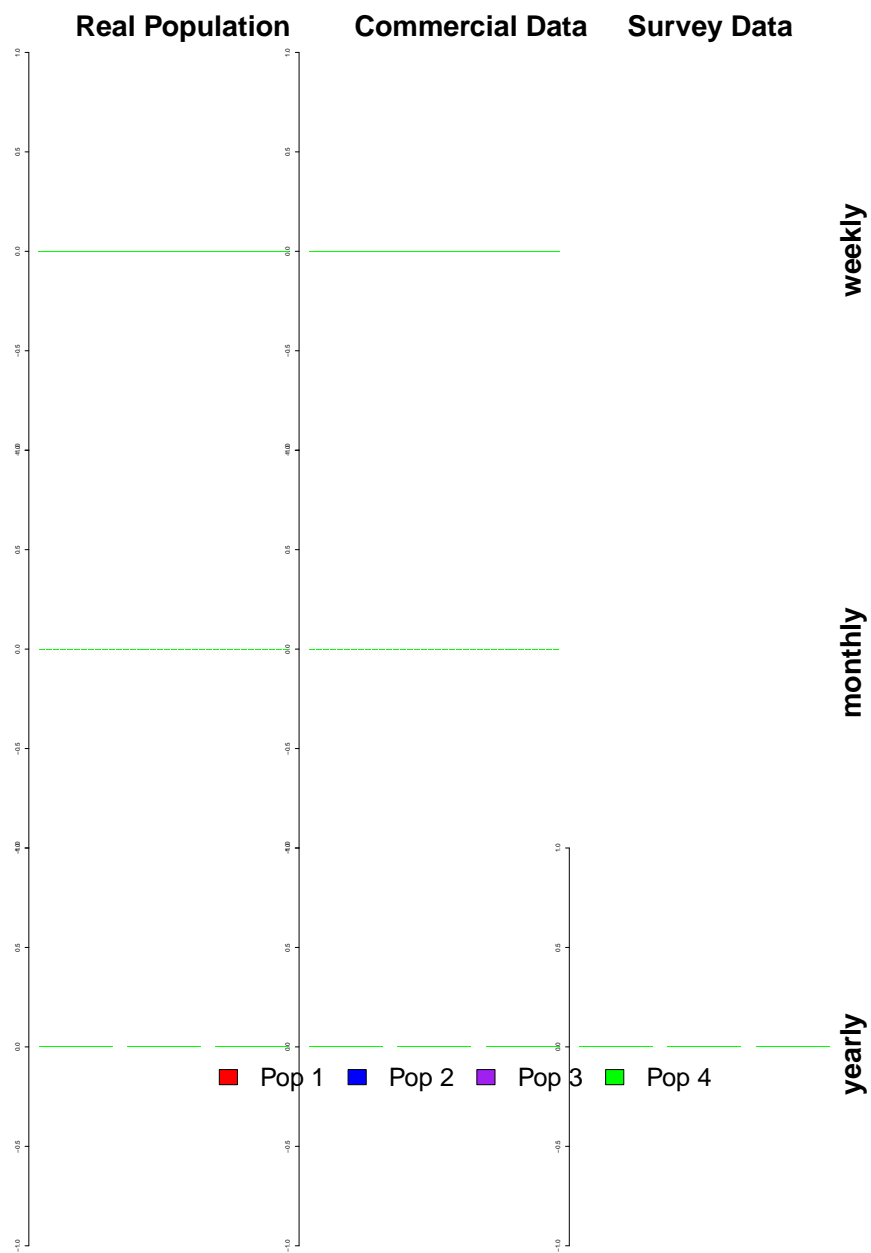


Figure 3: Data aggregation at different temporal resolutions over a three year period

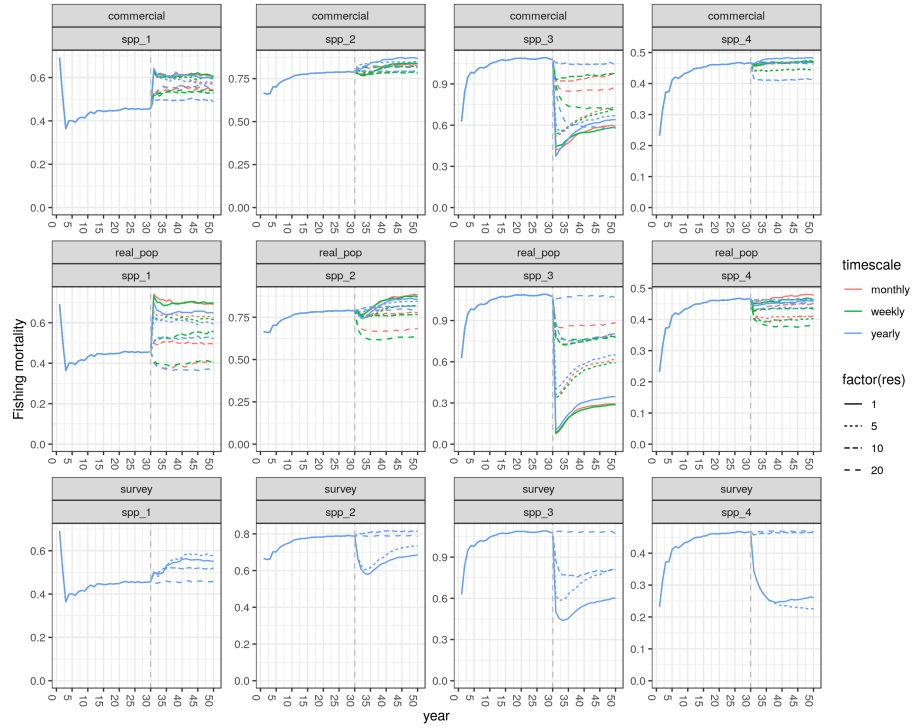


Figure 4: Comparison of closure scenarios - Fishing mortality trends. Only the scenarios based on high catch rates of population 3 are shown.

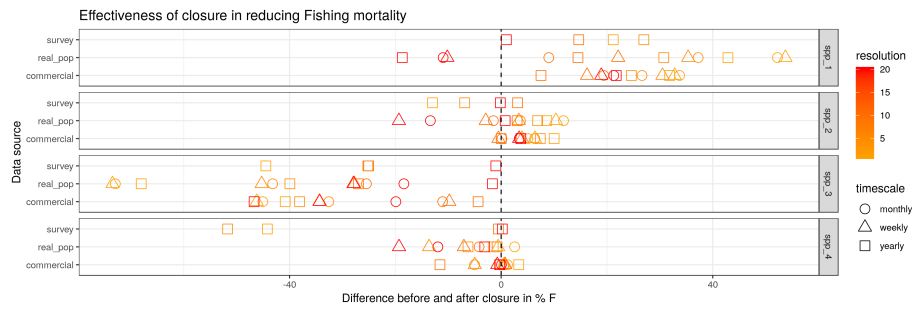


Figure 5: Comparison of closure scenarios. Points indicate the difference between the fishing mortality pre-closure (year 29) and post-closure (year 50) for population 3. Only the scenarios based on high catch rates of population 3 are shown.

452 References

- 453 Alverson, D.L., Freeberg, M.H., Murawski, S.A., Pope, J., 1994. A global assessment of
454 fisheries bycatch and discards.
- 455 Bailey, R.M., Carrella, E., Axtell, R., Burgess, M.G., Cabral, R.B., Drexler, M., Dorsett, C.,
456 Madsen, J.K., Merkl, A., Saul, S., 2018. A computational approach to managing coupled
457 human–environmental systems: the POSEIDON model of ocean fisheries.
- 458 Bartumeus, F., Da Luz, M.G.E., Viswanatham, G.M., Catalan, J., 2005. Animal Search
459 Strategies: A Quantitative Random Walk Analysis. *Ecological Society of America* 86,
460 3078–3087.
- 461 Bastardie, F., Nielsen, J.R., Ulrich, C., Egekvist, J., Degel, H., 2010. Detailed mapping
462 of fishing effort and landings by coupling fishing logbooks with satellite-recorded vessel
463 geo-location. *Fisheries Research* 106, 41–53.
- 464 Batsleer, J., Hamon, K.G., Overzee, H.M.J., Rijnsdorp, A.D., Poos, J.J., 2015. High-grading
465 and over-quota discarding in mixed fisheries. *Reviews in Fish Biology and Fisheries* 25,
466 715–736.
- 467 Bellido, J.M., Santos, M.B., Pennino, M.G., Valeiras, X., Pierce, G.J., 2011. Fishery discards
468 and bycatch: Solutions for an ecosystem approach to fisheries management? *Hydrobiologia*
469 670, 317–333.
- 470 Bertrand, S., Bertrand, A., Guevara-Carrasco, R., Gerlotto, F., 2007. Scale-invariant move-
471 ments of fishermen: The same foraging strategy as natural predators. *Ecological Applica-*
472 *tions* 17, 331–337.
- 473 Beverton, R.J., Holt, S.J., 1957. On the Dynamics of Exploited Fish Populations , 533.
- 474 Catchpole, T.L., Revill, A.S., 2008. Gear technology in Nephrops trawl fisheries. *Reviews in*
475 *Fish Biology and Fisheries* 18, 17–31.
- 476 Codling, E.A., Plank, M.J., Benhamou, S., Interface, J.R.S., 2008. Random walk models in
477 biology. *Journal of the Royal Society, Interface / the Royal Society* 5, 813–34.
- 478 Crowder, B.L.B., Murawski, S.a., Crowder, L.B., Murawski, S.a., 1998. Fisheries Bycatch:
479 Implications for Management. *Fisheries* 23, 8–17.
- 480 Deriso, R.B., 1980. Harvesting Strategies and Parameter Estimation for an Age-Structured
481 Model. *Canadian Journal of Fisheries and Aquatic Sciences* 37, 268–282. **arXiv:1410.**
482 **7455v3.**

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

486 Diggle, P.J., Ribeiro, P.J., 2007. *Model-based Geostatistics* (Springer Series in Statistics).
487 volume 1.

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

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

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

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

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

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

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

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

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

515 Holmes, S.J., Bailey, N., Campbell, N., Catarino, R., Barratt, K., Gibb, A., Fernandes, P.G.,
516 2011. Using fishery-dependent data to inform the development and operation of a co-
517 management initiative to reduce cod mortality and cut discards. *ICES Journal of Marine*
518 *Science* 68, 1679–1688.

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

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

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

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

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

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

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

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

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

542 Ricker, W.E., 1954. Stock and recruitment. *Journal of the Fisheries Research Board of Canada*
543 11, 559 – 623.

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

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

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

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

553 Schlater, M., Malinowski, A., Menck, P.J., 2015. Analysis, Simulation and Prediction of
554 Multivariate Random Fields with Package RandomFields. *Journal of Statistical Software*
555 63, 1–25. [arXiv:1501.0228](#).

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

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

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

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

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

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

572 Viswanathan, G.M., Buldyrev, S.V., Havlin, S., Da Luz, M.G.E., Raposo, E.P., Stanley, H.E.,
573 1999. Optimizing the success of random searches. *Nature* 401, 911–914.