

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 a simulated fixed-site sampling design commonly used for fisheries monitoring purposes and the true underlying population structures input to the simulation. We i) use the results to establish the potential and limitations of fishery-dependent data in providing a robust picture of spatiotemporal distributions; and ii) simulate an area closure based on areas defined from the different data sources at a range of 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 and 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 one or more quota. This may lead to overexploitation of fish populations (Ulrich et al., 2011; Batsleer et al., 2015). Discarding

8 of fish in excess of quota limits the ability to maintain fishing mortality within
9 sustainable limits (Alverson et al., 1994; Crowder et al., 1998; Rijnsdorp et al.,
10 2007) and the ability to manage for the biological and economic sustainability
11 of fisheries. As such, there is increasing interest in technical solutions such as
12 gear and spatial closures as measures to reduce unwanted catch (Kennelly and
13 Broadhurst, 2002; Catchpole and Revill, 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). Implemen-
17 tation of avoidance measures is, however, restricted by lack of knowledge of fish
18 and fishery spatiotemporal dynamics and understanding of the scale at which
19 processes become important for management. Understanding the correct scale
20 for spatial measures is crucial for implementation at a resolution that ensures ef-
21 fective management (Dunn et al., 2016) while minimising economic impact. For
22 example, a scale that promotes species avoidance for vulnerable or low quota
23 species while allowing continuance of sustainable fisheries for available quota
24 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). Such information is, however, derived from an inherently biased
35 sampling programme, targeted fishing, where fishers establish favoured fishing
36 grounds first through an explore-exploit strategy Bailey et al. (2018) and then
37 use experience to return to areas of high catch.

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

39 We ask two fundamental questions regarding spatiotemporal inference de-
40 rived from observational data:

- 41 1. How does sampling-derived data reflects the underlying population struc-
42 tures?
- 43 2. How does data aggregation and source impact on monitoring spatial fish-
44 eries management measures ?

45 To answer these questions we i) develop a simulation model where popu-
46 lation dynamics are highly-resolved in space and time . Being known directly
47 rather than inferred from sampling or commercial catch, we can use the pop-
48 ulation model to evaluate how inference from fisheries-dependent and fisheries
49 independent sampling relates to the real population structure. We ii) compare,
50 at different spatial and temporal aggregations, the simulated population distri-
51 butions to samples from fisheries-dependent and fisheries independent catches
52 to test if these are a true reflection of the relative density of the populations. We
53 then iii) simulate a fishery closure to protect a species based on different spatial
54 and temporal data aggregations. We use these evaluations to draw inference on
55 the utility of commercial data in supporting management decisions.

56
57 [We find..]

58 2. Materials and Methods

59 A simulation model that is modular and discrete-event based was developed.
60 This approach enables efficient computation by allowing for sub-modules imple-
61 mented on time-scales appropriate to capture the characteristic of the different
62 processes (Figure 1). The following sub-modules were included to capture the
63 full system: 1) Population dynamics, 2) Recruitment dynamics, 3) Population
64 movement, 4) fishery dynamics.

65

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 validation of the data aggregation, rather than effectiveness of the closures themselves - so its a continuation of the same question in my eyes

66 Population dynamics (fishing and natural mortality, growth) operate on a
67 daily time-step, while population movement occurs on a weekly time-step. Re-
68 cruitment takes place periodically each year for a set time duration specified for
69 each population, while the fishing module operates on a tow-by-tow basis (i.e.
70 multiple events a day).

71 In the model system population movement is driven by random (diffusive)
72 and directed (advective) processes and we incorporate characterisation of a num-
73 ber of different fishing fleet dynamics exploiting four fish populations with dif-
74 ferent spatial and population demographics. The following describes the imple-
75 mentation of each of the sub-modules.



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

76 *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 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 c is incremented each day d as follows (the full parameter list is detailed in Table 1):

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

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

82

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 $F_{c,d}$:

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

83 where $C_{c,d}$ is the summed catch from the fishing model across all fleets and
 84 vessels in cell c for the population during the day d , and $B_{c,d}$ the daily biomass
 85 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 either as a stochastic Beverton-Holt stock-recruit form (Beverton and Holt, 1957):

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

Where α is the maximum recruitment rate, β the spawning stock biomass (SSB) required to produce half the maximum stock size, S current stock size and σ^2 the variability in the recruitment due to stochastic processes, 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 our example application the Beverton-Holt form of stock recruit relationship was used for all populations though either functional form can be chosen.

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.

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

[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]

Not clear how habitat/GRF affect local abundances, only have $B_{y,d}$ Have included cell reference, c to make spatial link explicit

102 is multivariate Gaussian with a *Matérn* covariance structure, where the corre-
 103 lation strength weakens with distance. This enables us to model the spatial
 104 autocorrelation observed in animal populations where density is more similar
 105 in nearby locations (Tobler, 1970; F. Dormann et al., 2007) and we change the
 106 parameters to implement different spatial structures for the populations.

107

The habitat for each of the populations was generated with the *RFSimulate* function of the *RandomFields* R package (Schlatter et al., 2015). Each population 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:

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

108 Where d_{IJ} is the euclidean distance between cell I and cell J , λ is a given rate
 109 of decay, $Hab_{J,p}^2$ is the squared index of habitat suitability for cell J and popu-
 110 lation p , with $Tol_{J,p,wk}$ the temperature tolerance for cell J by population p in
 111 week wk (see below).

112

113 During pre-defined weeks of the year the habitat quality is modified with
 114 user-defined spawning habitat locations, resulting in each population having
 115 concentrated areas where spawning takes place. In the simulations the popu-
 116 lations moved towards these cells in the weeks prior to spawning, resulting in
 117 directional movement towards the spawning grounds.

118

An advection-diffusion process controlled population movement, with a time-varying temperature covariate used to change the interaction between time and suitable habitat on a weekly time-step. Each population p was assigned a thermal tolerance with mean, μ_p and variance, σ_p^2 so that each cell and popula-

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

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

tion temperature suitability is defined that:

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

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

The final process resulted in population structures and movement patterns unique to each species, with population movement occurring on a weekly basis. The decision to model population movement on a weekly timescale was to reflect that fish tend to aggregate in species specific locations and range within a week is fairly limited [REF!!]. Therefore this process approximated the demographic shifts in fish populations throughout a year with seasonal spawning patterns (e.g. Figure S5).

2.4. Fleet dynamics

The fleet dynamics can be broadly categorised into three components; fleet targeting - which determined the fleet catch efficiency and preference towards a particular species; trip-level decisions, which determined the initial location to be fished at the beginning of a trip; and within-trip decisions, determining movement from one fishing spot to another within a trip. Together, these elements implement an explore-exploit type strategy for individual vessels to maximise their catch from an unknown resource distribution (Bailey et al. (2018)). The decision to use an individual based model for fishing vessels was taken because fishers as a group tend to show heterogeneity and individual rather than group dynamics. Thus this was the fleet dynamics is the productive of individual experiences rather than pre-ordained 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, $Q_{fl,p}$. Thus, the product of these parameters $[Q_{fl} \cdot Q_{fl,p}]$ affects the overall catch rates for the fleet and the preferential

146 targeting of one population over another. This, in combination with the param-
147 eter choice for the step-function defined below (as well as some randomness from
148 the exploratory fishing process) determined the preference of fishing locations
149 for the fleet. All species prices were kept the same across fleets and seasons.

150 2.4.2. *Trip-level decisions*

151 Several studies (e.g. Hutton et al., 2004; Tidd et al., 2012; Girardin et al.,
152 2015) have confirmed past activity and past catch rates are strong predictors of
153 fishing location choice. For this reason, the fleet dynamics sub-model included a
154 learning component, where a vessel's initial fishing location in a trip was based
155 on selecting from previously successful fishing locations. This was achieved by
156 calculating an expected revenue based on the catches from locations fished in
157 the preceding trip as well as the same month periods in previous years and the
158 travel costs from the port to the fishing grounds, and choosing randomly from
159 the top 75 % of fishing events as defined by the expected profit.

160 2.4.3. *Within-trip decisions*

161 Fishing locations within a trip are initially determined by a modified ran-
162 dom walk process. As the simulation progresses the within-trip decision become
163 gradually more influenced by experience gained from past fishing locations (as
164 per the initial trip-level location choice), moving location choice towards areas
165 of higher perceived profit. A random walk was chosen for the exploratory fishing
166 process as it is the simplest assumption commonly used in ecology to describe
167 optimal animal search strategy for exploiting homogeneously distributed prey
168 about which there is uncertain knowledge (Viswanathan et al., 1999). In a ran-
169 dom walk, movement is a stochastic process through a series of steps. These
170 steps have a length, and a direction that can either be equal in length or take
171 some other functional form. The direction of the random walk was also cor-
172 related (known as 'persistence') providing some overall directional movement
173 (Codling et al., 2008).

174

175 We use a *Lévy flight* which is a particular form of random walk charac-
 176 terised by a heavy-tailed distribution of step-length. The Lévy flight has re-
 177 ceived a lot of attention in ecological theory in recent years as having shown to
 178 have very similar characteristics as those observed by animals in nature, and
 179 being a near optimum searching strategy for predators pursuing patchily dis-
 180 tributed prey (Viswanathan et al., 1999; Bartumeus et al., 2005; Sims et al.,
 181 2008). Bertrand et al. (2007) showed that Peruvian anchovy fishermen have a
 182 stochastic search pattern similar to that observed with a lévy flight. However,
 183 it remains a subject of debate (e.g. see Edwards et al., 2011; Reynolds, 2015),
 184 with the contention that search patterns may be more simply characterised as
 185 random walks (Sakiyama and Gunji, 2013) with specific patterns related to the
 186 characteristics of the prey field (Sims et al., 2012).

187

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

So step length
increases with
increasingly
gross rev-
enue? No, the
opposite

in its relation to revenue, so that, a step from $(x1, y1)$ to $(x2, y2)$ is defined by:

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

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

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 exploit 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.

2.5. Fisheries independent survey

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

211 2.6. Software

212 The simulation framework is implemented in the statistical software package
213 R (R Core Team, 2017) and available as an R package from the authors github
214 site (www.github.com/pdolder/MixFishSim).
215

216 3. Parameterisation

217 3.1. Population models

218 We parametrised the simulation model for four populations with different
219 demographics; growth rates, natural mortality and recruitment functions (Table
220 4). Habitat preference (Figure S1) and temperature tolerances (Figures S3,
221 S4) were unique to each population resulting in differently weekly distribution
222 patterns (Figures S5-S7). In addition, each of the populations has two defined
223 spawning areas which result in the populations moving towards these areas in
224 pre-defined weeks (Figure S2) with population-specific movement rates (Table
225 4). The individual habitat preferences and thermal tolerances results different
226 spatial habitat use for each population (Figure S9) and consequently different
227 seasonal exploitation patterns (Fishing mortality in Figure S10).

228 3.2. Fleet parametrisation

229 The fleets were parametrised to reflect five different characteristic fisheries
230 with unique exploitation dynamics (Table 5). By setting different catchability
231 parameters ($Q_{fl,p}$) we create different targeting preferences between the fleets
232 and hence spatial dynamics. The stochasticity in the random walk process
233 ensures that within a fleet different vessels have slightly different spatial dis-
234 tributions based on individual experience. The step function was parametrised
235 dynamically within the simulations as the maximum revenue obtainable was
236 not known beforehand. This was implemented so that vessels take smaller steps
237 when fishing at a location that yields landings value in the top 90th percentile

238 of the value experienced in that year so far (as defined per fleet in Table 5).

239

240 With increasing probability throughout the simulation, fishing locations were
241 chosen based on experience of profitable catches built up in the same month from
242 previous years and from the previous trip. 'Profitable' in this context was de-
243 fined as the locations where the top 70 % of expected profit would be found
244 given previous trips revenue and cost of movement to the new fishing location.
245 This probability was based on a logistic sigmoid function with a lower asymptote
246 of 0 and upper asymptote of 0.95, and a growth rate which ensures the upper
247 asymptote (where decisions are mainly based on past knowledge) is reached ap-
248 proximately halfway through the simulation.

249

250 It can be seen from a single vessels movements during a trip that the ves-
251 sel exploits four different fishing grounds, three of them multiple time (Figure
252 S11), while across multiple trips fishing grounds that are further apart are fished
253 (Figure S12). These different locations relate to areas where the highest rev-
254 enue were experienced, as shown by Figure S13, which shows several trips for
255 the vessel overlaid on the value field (sum of the population densities \times price).
256 Vessels from the same fleet (and therefore targeting preference) exploit similar
257 but slightly different fishing grounds depending on their own personal experi-
258 ence during the explore phase of the fishery (Figure S14), which is the result
259 of the correlated random walk step function, with distance moved during the
260 exploitation phase related to the revenue experienced on the fishing ground
261 (Figure S15).

262 3.3. Survey settings

263 The survey simulation was set up with follow a fixed gridded station design
264 with 100 stations fished each year, starting on day 92 and ending on day 112 (5
265 stations per day) with same catchability parameters for all populations ($Q_p =$
266 1).

Move some of
the supplemen-
tary figures to
the manuscript

267 3.4. Example research question scenario

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

275
 276 We allow the simulation to run unrestricted for 30 years, then implement
 277 spatial closed areas for the last 20 years of the simulation based on data (either
 278 derived from the commercial catches, fisheries-independent survey or the 'real
 279 population') used at different spatial and temporal scales.

280
 281 The following steps are undertaken to determine closures:

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

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

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

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

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

294 4. Results

295 In order to answer the question of how sampling-derived data reflects the
296 underlying population structure we compare different spatial and temporal ag-
297 gregations of the simulated population distributions to:

- 298 a) **fisheries-independent data:** the inferred population from a fixed-site
299 sampling survey design as commonly used for fisheries monitoring pur-
300 poses;
- 301 b) **fisheries-dependent data:** the inferred population from our fleet model
302 which includes fishery-induced sampling dynamics.

303 The consequences of different spatial aggregations of the data are shown
304 in Figure 2, which represents the aggregation of catch from each of the data
305 sources over a ten-year period (to average seasonal patterns) at different spatial
306 resolutions.

307
308 The finer spatial grid for the real population (top left) and commercial data
309 (top middle) show visually similar patterns, though there are large unsampled
310 areas in the commercial data from a lack of fishing activity (particularly in
311 the lower left part of the sampling domain). The survey data at this spatial
312 resolution displays very sparse information about the spatial distributions of
313 the populations. The slightly aggregated data on a 5 x 5 grid shows similar
314 patterns and, while losing some of the spatial detail, there remains good con-
315 sistency between the ‘real population’ and the commercial data. Survey data
316 starts to pick out some of the similar patterns as the other data sources, but
317 lacks coverage. The spatial catch information on a 10 x 10 and 20 x 20 grid lose
318 a significant amount of information about the spatial resolutions for all data
319 sources, and some differences between the survey, commercial and ‘real popula-
320 tion’ data emerge.

321
322 Figure 3 shows the consequences of different temporal aggregations of the

323 data over a ten-year period, with weekly (top), monthly (middle) and yearly
324 (bottom) catch compositions from across an aggregated 20 x 20 area.

325

326 As can be seen by comparison to the 'real population', the monthly aggre-
327 gation captures the major patterns seen in the weekly data, albeit missing more
328 subtle differences. The yearly data results in a constant catch pattern due to the
329 aggregation process (sometimes known as an aggregation bias). The commercial
330 data on a weekly basis shows some of the same patterns as the 'real population',
331 though the first species (in red) is less well represented and some weeks are miss-
332 ing catches from the area. The monthly data shows some consistency between
333 the 'real population' and commercial data for species 2 - 4, though species 1
334 remains under-represented. On an annual basis, interestingly the commercial
335 data under represents the first species (in red) while the survey over represents
336 species 1. This is likely due to the biases in commercial sampling, with the
337 fisheries not targeting the areas where species 1 are present, and the biases in
338 the survey sampling from over representation of the spatial distribution.

339

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

349

350 For the closures based on 'real population' (bottom row), the most disaggre-
351 gated data (a weekly timescale and 1 x 1 resolution) was most effective, reducing
352 fishing mortality on species 1 (left) by ~ 60 %. Next was the monthly closures
353 ($< \sim 30$ %). The least effective were the yearly closures (blue lines) at all spatial

354 resolutions, which conversely resulted in increased fishing mortalities ($> 30\%$).

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 20×20 , 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 $\times 1$ data at a monthly temporal resolution. This results in $\sim 10\%$ reduction
363 in F for species 1. This was the only closure scenario to have positive effect
364 according to Figure 5, though looking at the trend in Figure 4 this looks more
365 related to the continued increased in F trend, as other scenarios had an initial
366 effect. Interestingly the monthly data scenario was more effective than weekly
367 data, which we posit is due to the increased data available from the commercial
368 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 comparison.
379

380 5. Discussion

381 Our study evaluates the importance of data scaling and considers potential
382 bias introduced through data aggregation when using commercial fisheries data

383 to infer spatio-temporal dynamics in fisheries. Understanding how fishers ex-
384 ploit multiple heterogeneously distributed fish populations with different catch
385 limits or conservation status requires detailed understanding of the overlap of
386 resources; this is difficult to achieve using conventional modelling approaches
387 due to species targeting in fisheries resulting in preferential sampling Martínez-
388 Minaya et al. (2018). Often data is aggregated or extrapolated which requires
389 assumptions about the spatial and temporal scale of processes. Our study ex-
390 plores the assumptions behind such aggregation and preferential sampling to
391 identify potential impacts on management advice. With modern management
392 approaches increasingly employing more nuanced spatio-temporal approaches
393 in order to maximise productivity while taking account of both the biological
394 and human processes operating on different time-frames (Dunn et al. (2016)),
395 understanding assumptions behind the data used - increasingly a combination
396 of logbook and positional information from vessel monitoring systems - is vital
397 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

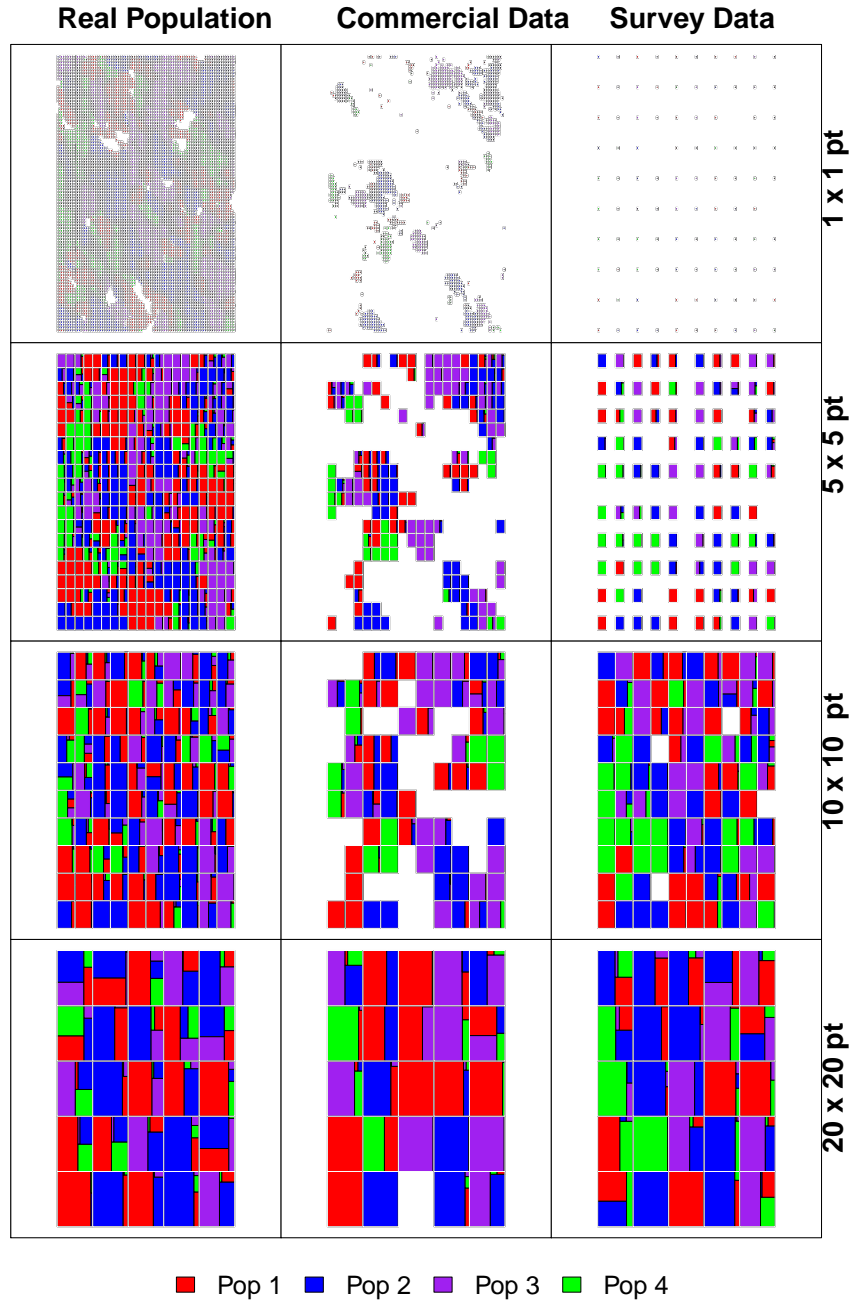


Figure 2: Data aggregation at different spatial resolutions over a ten year period

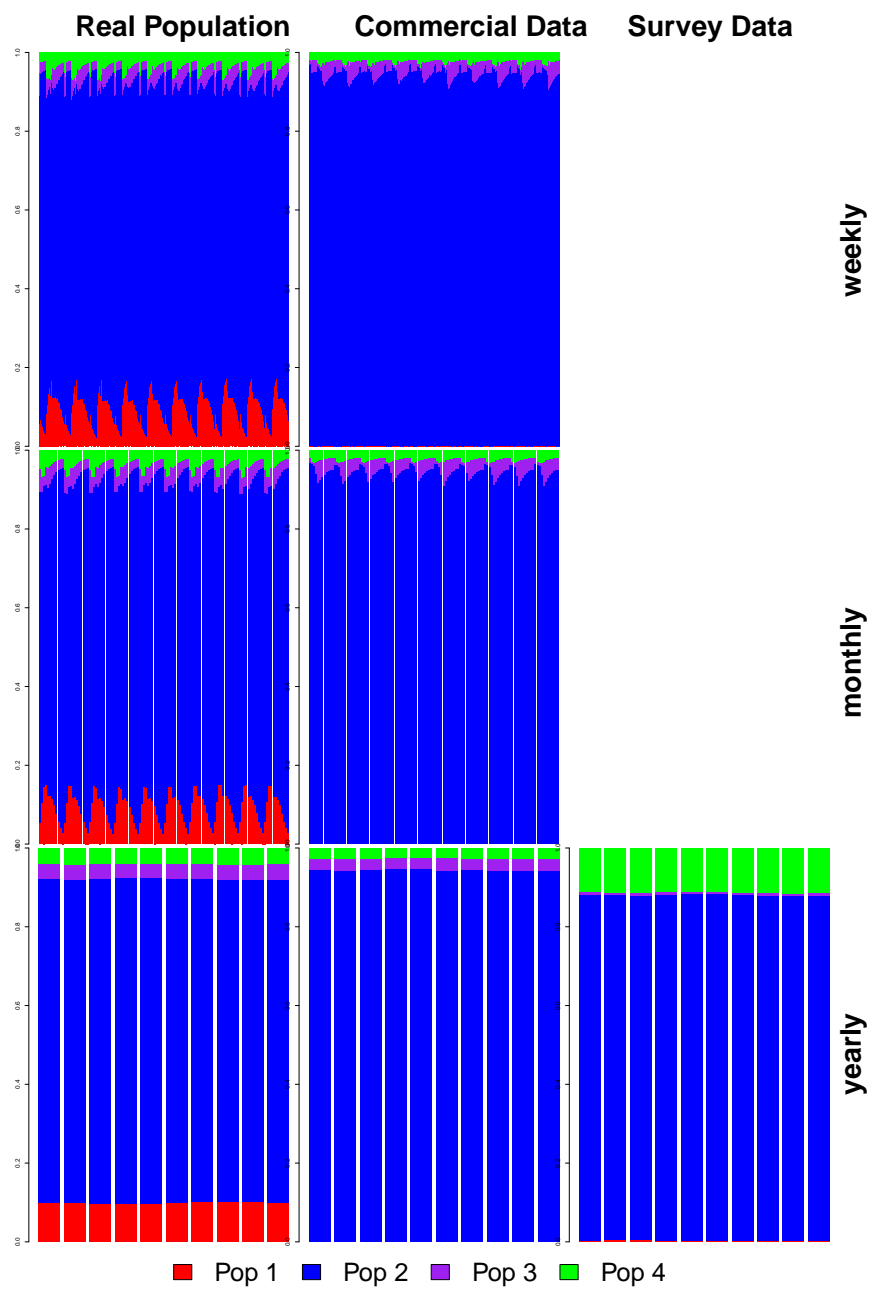


Figure 3: Data aggregation at different temporal resolutions over a ten-year period

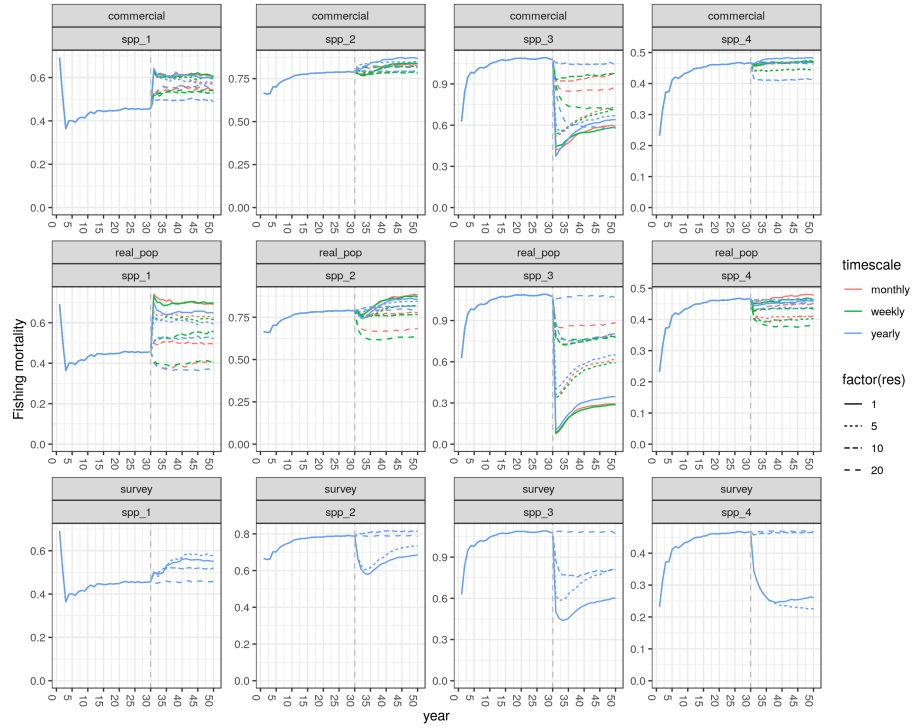


Figure 4: Comparison of closure scenarios - Fishing mortality trends. Only the scenarios based on high catch rates of population 3 are shown.

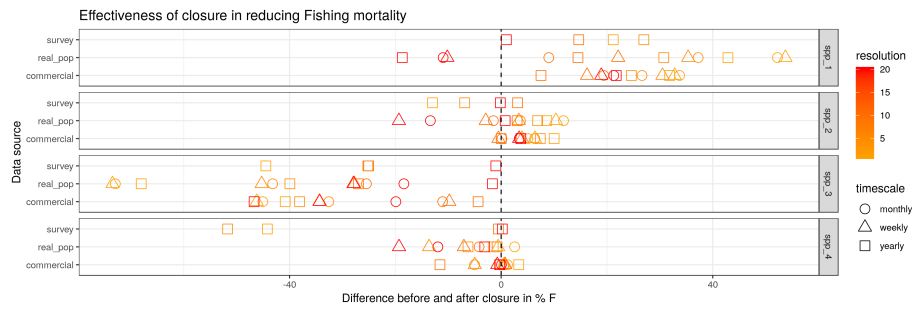


Figure 5: Comparison of closure scenarios. Points indicate the difference between the fishing mortality pre-closure (year 29) and post-closure (year 50) for population 3. Only the scenarios based on high catch rates of population 3 are shown.

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 '
485 s Northern Prawn Fishery. *Fisheries Research* 65, 335–350.

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

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

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

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

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

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

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

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

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

513 Holmes, S.J., Bailey, N., Campbell, N., Catarino, R., Barratt, K., Gibb, A., Fernandes, P.G.,
514 2011. Using fishery-dependent data to inform the development and operation of a co-
515 management initiative to reduce cod mortality and cut discards. *ICES Journal of Marine*
516 *Science* 68, 1679–1688.

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

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

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

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

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

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

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

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

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

540 Ricker, W.E., 1954. Stock and recruitment. *Journal of the Fisheries Research Board of Canada*
541 11, 559 – 623.

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

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

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

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

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

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

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

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

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

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

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

570 Viswanathan, G.M., Buldyrev, S.V., Havlin, S., Da Luz, M.G.E., Raposo, E.P., Stanley, H.E.,
571 1999. Optimizing the success of random searches. *Nature* 401, 911–914.