

MixFishSim: highly resolved spatiotemporal simulations for exploring mixed fishery dynamics

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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

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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

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1. Introduction

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

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

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

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 $F_{c,d}$:

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

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

93 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
 94 fl , v and p the fleet, vessel and population respectively and E and Q fishing
 95 effort and catchability.

97 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):

$$\bar{R}_{c,d} = \frac{(\alpha * B_{c,d})}{(\beta + B_{c,d})}$$

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

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):

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

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

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

101 2.3. Population movement dynamics

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

107
 108 For habitat we first defined a Gaussian random field process, $\{S(c) : c \in$
 109 $\mathbb{R}^2\}$, 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:

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

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:

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

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 assigned? 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 SUPPLEMENTARY).
174

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),

$$Rev = \sum_{p=1}^P L_p \cdot Pr_p \quad (3)$$

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:

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

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:

$$(x2, y2) = x1 + StepL \cdot \cos\left(\frac{\pi \cdot Br}{180}\right),$$

$$y1 + StepL \cdot \sin\left(\frac{\pi \cdot Br}{180}\right)$$

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

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

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

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

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

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

3.3. Survey settings

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

3.4. Simulation settings

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

Move some of the supplementary 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 similar patterns, though there are unsampled gaps in the
305 commercial data from a lack of fishing activity (particularly in the lower left
306 part of the sampling domain). The survey data at this spatial resolution shows
307 very sparse information about the spatial distributions of the populations. The
308 slightly aggregated data on a 5 x 5 grid shows similar patterns, and while los-
309 ing some of the spatial detail there remains good consistency between the 'real
310 population' and the commercial data. Survey data starts to pick out some of
311 the similar patterns as the other data sources, but lacks coverage. The spatial
312 catch information on a 10 x 10 and 20 x 20 grid loses a significant amount of
313 information about the spatial resolutions for all data sources, and some differ-
314 ences between the survey, commercial and 'real population' data emerge.

315

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

319

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

are present, and the biases in the survey sampling from over representation of the spatial distribution.

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

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

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

For the commercial data, the most effective closure scenario was based on 1 x 1 data at a monthly temporal resolution. This results in $\sim 10\%$ reduction in F for species 1. This was the only closure scenario to have positive effect

363 according to Figure 5, though looking at the trend in Figure 4 this looks more
364 related to the continued increased in F trend, as other scenarios had an initial
365 effect. Interestingly the monthly data scenario was more effective than weekly
366 data, which I'd posit is due to the increase amount of data available from the
367 commercial sampling across a month compared to a week.i Commercial data
368 used at an annual timestep was ineffective in bringing fishing mortality down
369 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 timeframe, which is the scenario that gave the worst
374 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 6. Conclusions

382 Abbreviations

383 Detail any unusual ones used.

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

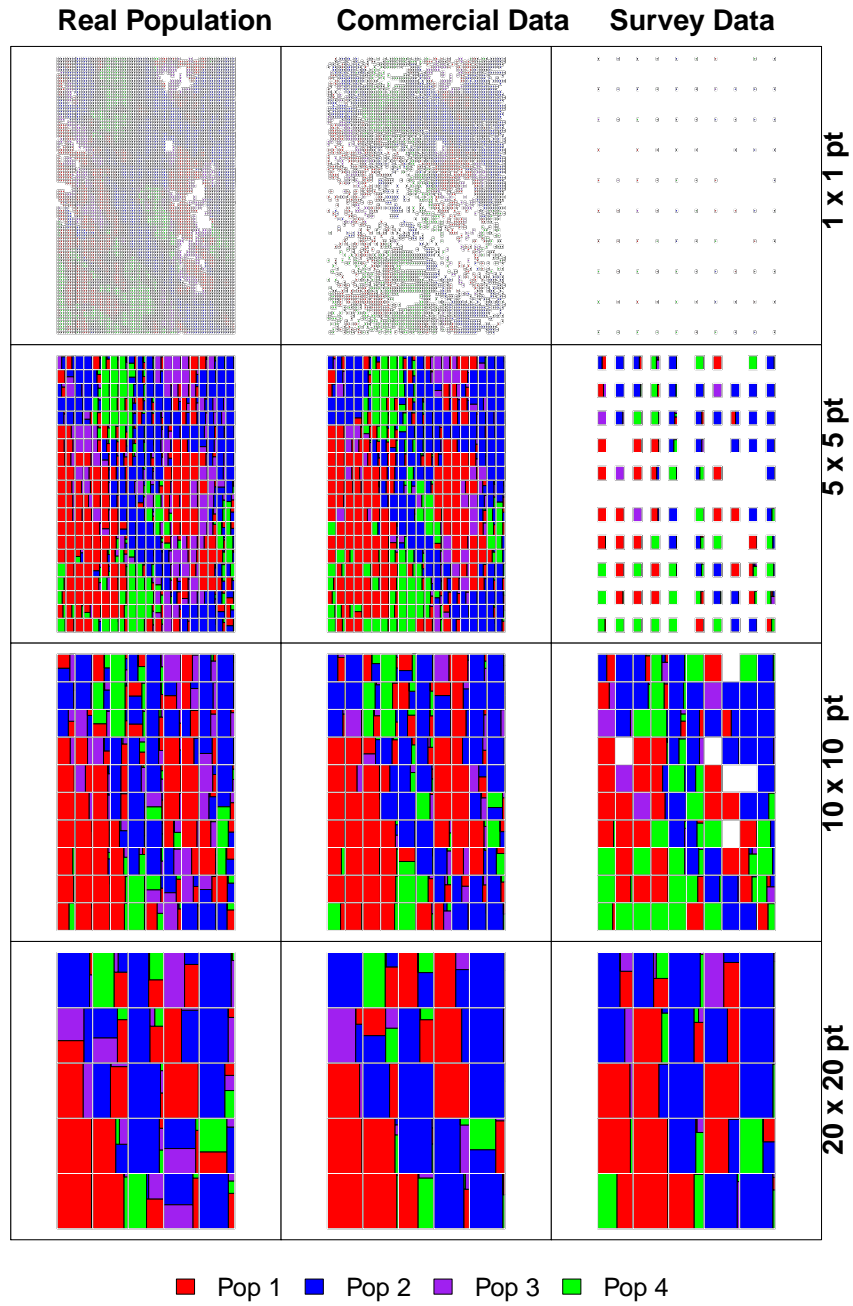


Figure 2: Data aggregation at different spatial resolutions over a ten year period

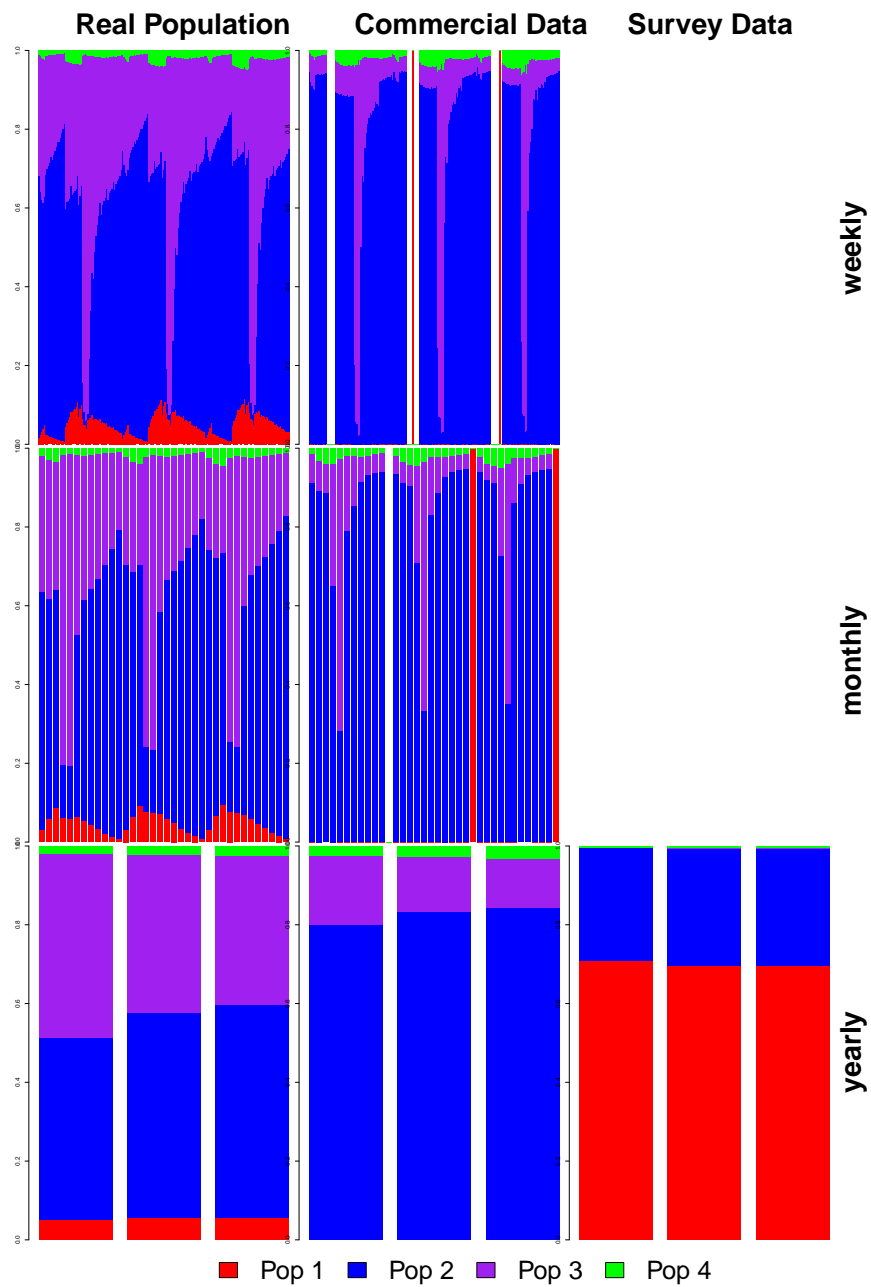


Figure 3: Data aggregation at different temporal resolutions over a three year period

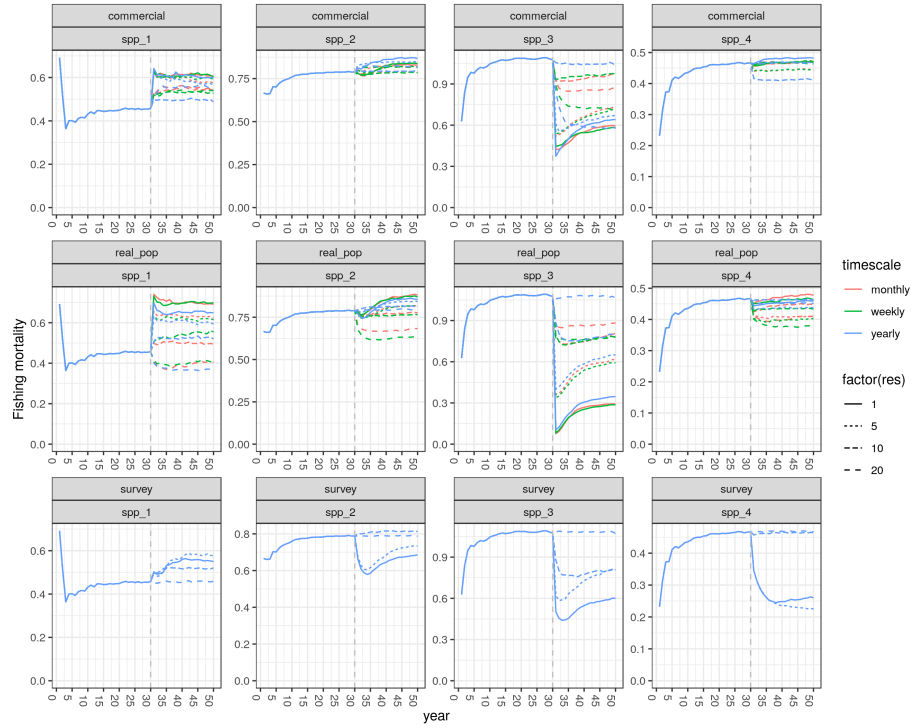


Figure 4: Comparison of closure scenarios - Fishing mortality trends. Only the scenarios based on high catch rates of population 3 are shown.

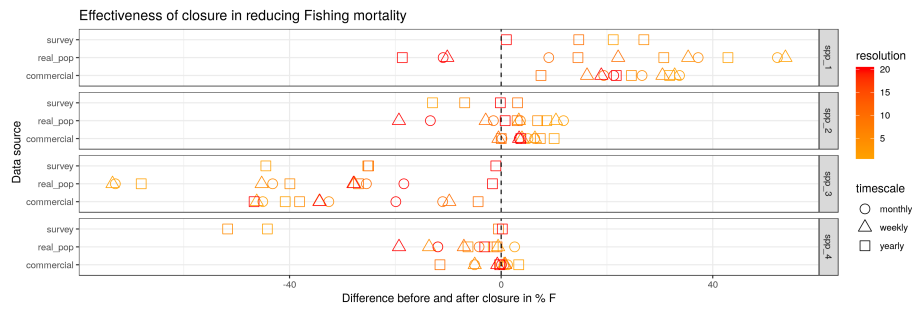


Figure 5: Comparison of closure scenarios. Points indicate the difference between the fishing mortality pre-closure (year 29) and post-closure (year 50) for population 3. Only the scenarios based on high catch rates of population 3 are shown.

References

- Alverson, D.L., Freeberg, M.H., Murawski, S.A., Pope, J., 1994. A global assessment of fisheries bycatch and discards.
- Bailey, R.M., Carrella, E., Axtell, R., Burgess, M.G., Cabral, R.B., Drexler, M., Dorsett, C., Madsen, J.K., Merkl, A., Saul, S., 2018. A computational approach to managing coupled human–environmental systems: the POSEIDON model of ocean fisheries.
- Bartumeus, F., Da Luz, M.G.E., Viswanatham, G.M., Catalan, J., 2005. Animal Search Strategies: A Quantitative Random Walk Analysis. *Ecological Society of America* 86, 3078–3087.
- Bastardie, F., Nielsen, J.R., Ulrich, C., Egekvist, J., Degel, H., 2010. Detailed mapping of fishing effort and landings by coupling fishing logbooks with satellite-recorded vessel geo-location. *Fisheries Research* 106, 41–53.
- Batsleer, J., Hamon, K.G., Overzee, H.M.J., Rijnsdorp, A.D., Poos, J.J., 2015. High-grading and over-quota discarding in mixed fisheries. *Reviews in Fish Biology and Fisheries* 25, 715–736.
- Bellido, J.M., Santos, M.B., Pennino, M.G., Valeiras, X., Pierce, G.J., 2011. Fishery discards and bycatch: Solutions for an ecosystem approach to fisheries management? *Hydrobiologia* 670, 317–333.
- Bertrand, S., Bertrand, A., Guevara-Carrasco, R., Gerlotto, F., 2007. Scale-invariant movements of fishermen: The same foraging strategy as natural predators. *Ecological Applications* 17, 331–337.
- Beverton, R.J., Holt, S.J., 1957. On the Dynamics of Exploited Fish Populations , 533.
- Catchpole, T.L., Revall, A.S., 2008. Gear technology in Nephrops trawl fisheries. *Reviews in Fish Biology and Fisheries* 18, 17–31.
- Codling, E.A., Plank, M.J., Benhamou, S., Interface, J.R.S., 2008. Random walk models in biology. *Journal of the Royal Society, Interface / the Royal Society* 5, 813–34.
- Crowder, B.L.B., Murawski, S.a., Crowder, L.B., Murawski, S.a., 1998. Fisheries Bycatch: Implications for Management. *Fisheries* 23, 8–17.
- Deriso, R.B., 1980. Harvesting Strategies and Parameter Estimation for an Age-Structured Model. *Canadian Journal of Fisheries and Aquatic Sciences* 37, 268–282. [arXiv:1410.7455v3](#).

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

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

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

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

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

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

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

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

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

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

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

453 Holmes, S.J., Bailey, N., Campbell, N., Catarino, R., Barratt, K., Gibb, A., Fernandes, P.G.,
454 2011. Using fishery-dependent data to inform the development and operation of a co-
455 management initiative to reduce cod mortality and cut discards. *ICES Journal of Marine*
456 *Science* 68, 1679–1688.

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

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

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

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

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

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

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

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

478 Ricker, W.E., 1954. Stock and recruitment. *Journal of the Fisheries Research Board of Canada*
479 11, 559 – 623.

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

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

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

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

489 Schlater, M., Malinowski, A., Menck, P.J., 2015. Analysis, Simulation and Prediction of
490 Multivariate Random Fields with Package RandomFields. *Journal of Statistical Software*
491 63, 1–25. [arXiv:1501.0228](#).

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

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

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

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

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

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

508 Viswanathan, G.M., Buldyrev, S.V., Havlin, S., Da Luz, M.G.E., Raposo, E.P., Stanley, H.E.,
509 1999. Optimizing the success of random searches. *Nature* 401, 911–914.