

Working title: Highly resolved spatiotemporal simulations for exploring mixed fishery dynamics

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

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

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

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

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

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

Abstract

To understand how data resolution impacts inference on mixed fisheries interactions, we developed a highly resolved spatiotemporal event-based simulation model incorporating: i) delay-difference population dynamics, ii) population movement using Gaussian Random Fields to simulate patchy, heterogeneously distributed populations, and iii) fishery dynamics for multiple fleet characteristics based on species targeting under an explore-exploit strategy. This is implemented via a mix of correlated random walk movement (for exploration) and learned behaviour (for exploitation) phases of the fisheries.

Fifty years of sub-daily fishing was simulated and used to draw inference on the underlying community structures. We compared inferences based on: commercial catch, a simulated fixed-site sampling survey design and the true underlying community. We i) establish the potential limitations of fishery-dependent data in providing a robust picture of spatiotemporal distributions; and then ii) simulated an area closure based on areas defined from the different data sources at a range of temporal and spatial resolutions.

Our framework allows users to explore the assumptions in modelling observational data and evaluate the underlying dynamics of such approaches at a fine

*Corresponding author

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

spatial and temporal scale. We conclude from our example framework application that commercial data, while containing bias, provide a useful tool for managing catches in mixed fisheries if applied at the correct spatiotemporal scale. [NEED A LITTLE MORE DETAIL OF THE RESULTS HERE - 2 MORE SENTENCES ON KEY TAKE-HOME RESULTS]

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. As fishers do not have full control over what species they select in ‘mixed fisheries’ this can result in catch of low quota or protected species. This leads to discarding of over-quota catch if it is a species for which they have no quota, limiting control over fishing mortality (Alverson et al., 1994; Crowder et al., 1998; Rijnsdorp et al., 2007) and the ability to manage fisheries for the biological and economic sustainability (Ulrich et al., 2011; Batsleer et al., 2015).

There is increasing interest in technical solutions such as gear and spatial closures as measures to reduce unwanted catch (Kennelly and Broadhurst, 2002; Catchpole and Revill, 2008; Bellido et al., 2011; Cosgrove et al., 2019) and adaptive spatial management strategies have been proposed as a way of reducing over-quota discards (Holmes et al., 2011; Little et al., 2014; Dunn et al., 2014). However, if fisheries are to reduce unwanted catch through spatial avoidance, an in-depth understanding of spatiotemporal fishery dynamics is required. Implementation of spatial measures is hampered by a lack of knowledge of fish and fishery spatiotemporal dynamics and understanding of the scale at which processes become important for management.

22 Understanding the correct scale for spatial measures is also crucial as it
23 enables implementation of effective solutions which minimise economic impact
24 (Dunn et al., 2016). For example, the problem can be to identify a scale that
25 promotes species avoidance for vulnerable or low quota species while allowing
26 continuance of sustainable fisheries for available quota species. Identifying the
27 correct spatial scale remains a challenge because data on fish location at high
28 temporal and spatial resolutions is expensive and difficult to collect and proxies
29 are usually inferred from scientific surveys or commercial catches with limited
30 spatial and temporal resolution.

31

32 Identifying appropriate spatial scales for fisheries closures has been a high-
33 lighted as crucial to their success (Costello et al., 2010; Dunn et al., 2016).
34 Inference is hampered where spatial information is coarse due to low resolu-
35 tion reporting of fisheries catch which is aggregated across larger gridded areas
36 (Branch et al., 2005). Further, if data does not allow identification of spatial
37 features it may lead to poorly sited closures which are ineffectual or have un-
38 intended consequences. For example, increased benthic impact on previously
39 unexploited areas from the cod closure in the North Sea were observed without
40 the intended effect of reducing cod exploitation (Rijnsdorp et al., 2001; Dinmore
41 et al., 2003)).

42

43 More refined spatiotemporal information has since become available through
44 the combination of logbook and Vessel Monitoring System (VMS) data (Lee
45 et al., 2010; Bastardie et al., 2010; Gerritsen et al., 2012; Mateo et al., 2016) and
46 more real-time spatial management has been possible (e.g. Holmes et al., 2011).
47 However, fishers establish favoured fishing grounds through an explore-exploit
48 strategy (Bailey et al., 2018) where they search for areas with high catches and
49 then use experience to return to areas where they’ve experienced high catch in
50 the past. This leads to an inherently biased sampling where target species are
51 over-represented in the catch as fishers exploit areas of high abundance.

52

53 To understand the effect of spatiotemporal aggregation of data and fishery
54 targeting we ask two fundamental questions regarding inference derived from
55 observational data:

- 56 1. How does sampling-derived fisheries data reflects the underlying commu-
57 nity structure?
- 58 2. How does data aggregation and source impact on spatial fisheries man-
59 agement measures?

60 To answer these questions we i) develop a simulation model where popula-
61 tion dynamics are highly-resolved in space and time by use of a Gaussian spatial
62 process to define suitable habitat for different populations. Precise locations of
63 the fish being known directly rather than inferred from sampling or commercial
64 catch, we can use the population model to validate how inference from fisheries-
65 dependent and fisheries independent sampling relates to the real community
66 structure in a way we could not with real data. We ii) compare, at different
67 spatial and temporal aggregations, the real (simulated) population distributions
68 to samples from fisheries-dependent and fisheries independent catches to test if
69 these are a true reflection of the relative density of the populations. We then
70 iii) simulate a fishery closure to protect a species based on different spatial and
71 temporal data aggregations.

72
73 We use these evaluations to draw inference on the utility of commercial data
74 in supporting management decisions.

75 2. Materials and Methods

76 An event-based simulation model of a hypothetical fishery was developed as
77 a software package (*MixFishSim*). The modular approach enabled efficient com-
78 putation by allowing for sub-modules implemented on time-scales appropriate
79 to capture the characteristic of the different processes (Figure 1). The following
80 sub-modules were included to capture the full system: 1) Population dynamics,

81 2) Recruitment dynamics, 3) Population movement, 4) fishery dynamics.

82

83 Population dynamics operate on a daily time-step, while population move-
84 ment occurs on a weekly time-step, with the fishing module operating on a
85 tow-by-tow basis (i.e. multiple events a day).

86 2.1. Population dynamics

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

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

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

102

103 Mortality $Z_{c,d}$ can be decomposed to natural mortality, $M_{c,d}$, and fishing
104 mortality, $F_{c,d}$, where both $M_{c,d}$ and $F_{c,d}$ are instantaneous rates with $M_{c,d}$

fixed and $F_{c,d}$ calculated by solving the Baranov catch equation (Hilborn and Walters, 1992) for $F_{c,d}$:

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

where $C_{c,d}$ is the summed catch from the fishing model across all fleets and vessels in cell c for the population during the day d , and $B_{c,d}$ the daily biomass for the population in the cell. Here, catch and fishing mortality are the sum of those across all fleets and vessels, where $F_{fl,v,c,d,p} = E_{fl,v,c,d} \cdot Q_{fl,p} \cdot D_{c,d,p}$ with fl , v and p the fleet, vessel and population respectively and E and Q fishing effort and catchability of the gear, and D is the density of the population at the location fished.

2.2. Recruitment dynamics

Recruitment is modelled through a function relating to adult biomass. In *MixFishSim*, it can be either as a stochastic Beverton-Holt stock-recruit form (Beverton and Holt, 1957):

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

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):

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

where α is the maximum productivity per spawner and β the density dependent reduction in productivity as the SSB increases.

125 2.3. Population movement dynamics

126 Population movement is a combination of random (diffusive) movement,
 127 governed by a stochastic process where movement between adjacent cells is
 128 described by a set of probabilities, and directed (advective) movement where
 129 at certain times of year the population moves towards spawning grounds by
 130 increasing the probabilities of moving into the spawning grounds from adjacent
 131 cells. We characterise a set of different fishing fleet dynamics exploiting four
 132 fish populations with different spatial and population demographics.

133
 134 To simulate fish population distribution in space and time a Gaussian spa-
 135 tial process was employed to model habitat suitability for each of the popula-
 136 tions on a 2d grid. We first defined a Gaussian random field process, $\{S(c) :$
 137 $c \in \mathbb{R}^2\}$, where for any set of cells c_1, \dots, c_n , the joint distribution of $S =$
 138 $\{S(c_1), \dots, S(c_n)\}$ is multivariate Gaussian with a *Matérn* covariance structure,
 139 where the correlation strength weakens with distance. This enables us to model
 140 the spatial autocorrelation observed in animal populations where density is more
 141 similar in nearby locations (Tobler, 1970; F. Dormann et al., 2007) and we
 142 change the parameters to implement different spatial structures for the differ-
 143 ent populations using the *RandomFields* R package (Schlatter et al., 2015). We
 144 define a stationary habitat field and combine with a temporally dynamic ther-
 145 mal tolerance field to imitate two key drivers of population dynamics. Each
 146 population was initialised at a single location, and subsequently moved accord-
 147 ing to a probabilistic distribution based on habitat suitability (represented by
 148 the normalised values from the GRFs), temperature and distance from current
 149 cell:

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

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

153 week wk (see below).

154

155 During pre-defined weeks of the year the habitat suitability is modified with
156 user-defined spawning habitat locations, resulting in each population having
157 concentrated areas where spawning takes place. In the simulations the popu-
158 lations move towards these cells in the weeks prior to spawning, resulting in
159 directional movement towards the spawning grounds.

160

161 An advection-diffusion process controls population movement, with a time-
162 varying temperature covariate used to change the interaction between time and
163 suitable habitat on a weekly time-step. Each population p was assigned a ther-
164 mal tolerance with mean, μ_p and variance, σ_p^2 so that each cell and population
165 temperature suitability is defined that:

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

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

169

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

177 2.4. Fleet dynamics

178 Fleet dynamics can be broadly categorised into three components: fleet tar-
179 geting - that determined the fleet catch efficiency and preference towards a
180 particular species; trip-level decisions, that determines the initial location to

181 be fished at the beginning of a trip; and within-trip decisions, that determines
 182 movement from one fishing spot to another within a trip. Together, these ele-
 183 ments implement an explore-exploit type strategy for individual vessels to max-
 184 imise their catch from an unknown resource distribution (Bailey et al., 2018).
 185 The decision to use an individual based model for fishing vessels was taken
 186 because fishers are heterogeneous in their location choice behaviour due to dif-
 187 ferent objectives, risk preference and targeting preference (Van Putten et al.,
 188 2012). Therefore in the simulations fleet dynamics reflect individual experiences
 189 rather than pre-defined group dynamics.

190 *2.4.1. Fleet targeting*

191 Each fleet of n vessels was characterised by both a general efficiency, Q_{fl} ,
 192 and a population specific efficiency, $Q_{fl,p}$. Thus, the product of these param-
 193 eters $[Q_{fl} \cdot Q_{fl,p}]$ affects the overall catch rates for the fleet and the preferential
 194 targeting of one population over another. This, in combination with the param-
 195 eter choice for the step-function defined below (as well as some randomness from
 196 the exploratory fishing process) determined the preference of fishing locations
 197 for the fleet.

198 *2.4.2. Trip-level decisions*

199 Several studies (e.g. Hutton et al., 2004; Tidd et al., 2012; Girardin et al.,
 200 2015) have confirmed past activity and past catch rates are strong predictors of
 201 fishing location choice. For this reason, the fleet dynamics sub-model included a
 202 learning component, where a vessel's initial fishing location in a trip was based
 203 on selecting from previously successful fishing locations. This was achieved by
 204 calculating an expected revenue based on the catches from locations fished in
 205 the preceding trip as well as the same month periods in previous years and the
 206 travel costs from the port to the fishing grounds, and choosing randomly from
 207 the top 75 % of fishing events as defined by the expected profit, that has a
 208 seasonal component.

209 2.4.3. *Within-trip decisions*

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

223
 224 For our implementation of a random walk directional change is based on a
 225 negatively correlated circular distribution where a favourable fishing ground is
 226 likely to be “fished back over” by the vessel returning in the direction it came
 227 from. The step length (i.e. the distance travelled from the current to the next
 228 fishing location) is determined by relating recent fishing success, measured as
 229 the summed value of fish caught (revenue, Rev);

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

230 where L_p is landings of a population p , and Pr_p price of a population. All
 231 species prices were kept the same across fleets and seasons. Here, when fishing
 232 is successful vessels remain in a similar location and continue to exploit the local
 233 fishing grounds. When unsuccessful, they move some distance away from the
 234 current fishing location. The movement distance retains some degree of stochas-
 235 ticity, that can be controlled separately, but is determined by the relationship:

236

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

237 Where β_1 , β_2 and β_3 are parameters determining the shape of the step function
 238 in its relation to revenue, so that, a step from (x1,y1) to (x2, y2) is defined by:

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

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

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

239 where L is the step length, k the concentration parameter from the von Mises
 240 distribution that we correlate with the revenue so that $k = (Rev + 1/RefRev) *$
 241 max_k , where max_k is the maximum concentration value, k , and $RefRev$ is
 242 parametrised as for β_3 in the step length function.

243 2.4.4. Local population depletion

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

253 2.5. Fisheries independent survey

254 A fisheries-independent survey is simulated where fishing on a regular grid
 255 begins each year at the same time for a given number of stations (a fixed station
 256 survey design). Catches of the populations at each station are recorded but not
 257 removed from the population (catches are assumed to have negligible impact

on population dynamics). 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.

2.6. Software: R-package development

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

3. Parameterisation

We parameterise *MixFishSim* to investigate the influence of data aggregation on spatial inference.

3.1. Population models

We parametrised the simulation model for four example populations with different demographics, growth rates, natural mortality and recruitment parameters (Table 4). Habitat preference (Figure S1) and temperature tolerances (Figures S3, S4) were defined to be unique to each population resulting in differently weekly distribution patterns (Figures S5-S7). In addition, each of the populations was assumed to have two defined spawning areas that result in the populations moving towards these areas in pre-defined weeks (Figure S2) with population-specific movement rates (Table 4).

3.2. Fleet parametrisation

The fleets were parametrised to reflect five different characteristic fisheries with unique exploitation dynamics (Table 5). By setting different catchability parameters ($Q_{fl,p}$) we create different targeting preferences between the fleets and hence spatial dynamics. The learned random walk process implies that

284 within a fleet different vessels have different spatial distributions based on indi-
 285 vidual experience. The step function was parametrised dynamically within the
 286 simulations as the maximum revenue obtainable was not known beforehand.
 287 This was implemented so that vessels take smaller steps when fishing at a loca-
 288 tion that yields landings value in the top 90th percentile of the value experienced
 289 in that year so far (as defined per fleet in Table 5).

290
 291 With increasing probability throughout the simulation, fishing locations were
 292 chosen based on experience of profitable catches built up in the same month from
 293 previous years and from the previous trip. 'Profitable' in this context was de-
 294 fined as the locations where the top 70 % of expected profit would be found
 295 given revenue from previous trips and cost of movement to the new fishing lo-
 296 cation. This probability was based on a logistic sigmoid function with a lower
 297 asymptote of 0 and upper asymptote of 0.95, and a growth rate that ensures
 298 the upper asymptote (where decisions are mainly based on past knowledge) is
 299 reached approximately halfway through the simulation.

301 3.3. Survey settings

302 The survey simulation was set up with a fixed gridded station design with
 303 100 stations fished each year, starting on day 92 and ending on day 112 (5
 304 stations per day) with same catchability parameters for all populations ($Q_p =$
 305 1). This approximates a real world survey design with limited seasonal and
 306 spatial coverage.

307 3.4. Example research question

308 To illustrate the capabilities of *MixFishSim*, we investigate the influence of
 309 the temporal and spatial resolution of different data sources on the reduction in
 310 catches of a population given spatial closures. To do so, we set up a simulation
 311 to run for 50 years based on a 100×100 square grid (undetermined units), with
 312 five fleets of 20 vessels each and four fish populations. Fishing takes place four

313 times a day per vessel and five days a week, while population movement is every
314 week.

315

316 *How does sampling-derived fisheries data reflect the underlying population*
317 *structure?*

318

319 To answer this question we compare different spatial and temporal aggrega-
320 tions of the real population distributions to:

- 321 a) **fisheries-independent data:** the inferred population from a fixed-site
322 sampling survey design as commonly used for fisheries monitoring pur-
323 poses;
- 324 b) **fisheries-dependent data:** the inferred population from our fleet model
325 that includes fishery-induced sampling dynamics.

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

330

331 The following steps are undertaken to determine closures:

- 332 1. Extract data source (real population, commercial or survey),
- 333 2. Aggregate according to desired spatial and temporal resolution,
- 334 3. Interpolate across entire area at desired resolution using simple bivariate
335 interpolation using the *interp* function from the R package *akima* (Akima,
336 2006). This is intended to represent a naive spatial model of catch rates,
337 without knowledge of the spatial population dynamics.
- 338 4. Close area covering top 5 % of catch rates

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

- 340 • **data types:** commercial logbook data, survey data and real population,
- 341 • **temporal resolutions:** weekly, monthly and yearly closures,
- 342 • **spatial resolutions:** 1 x 1 grid, 5 x 5 grid, 10 x 10 grid and 20 x 20 grid,
- 343 • **closure basis:** highest 5 % of catch rates for the protected species

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

346 4. Results

347 4.1. Emergent simulation dynamics

348 Individual habitat preferences and thermal tolerances result in different spa-
 349 tial habitat use for each population (Figure 2) and consequently different sea-
 350 sonal exploitation patterns (Fishing mortality in Figure 3).

It can be seen from a single vessels movements during a trip that the ves-
 sel exploits three different fishing grounds, each of them multiple times (Figure
 4(A)), while across several trips fishing grounds that are further apart are fished
 (Figure 4 (B)). These different locations relate to areas where the highest rev-
 enue were experienced, as shown by Figure 5, where several vessels tracks are
 overlaid on the revenue field, i.e.

$$\sum_{c=1}^c \sum_{s=1}^s B_{s,c} \cdot Q_{s,c}$$

351 Vessels from the same fleet (and therefore targeting preference) may exploit
 352 some shared and some different fishing grounds depending on their own personal
 353 experience during the exploratory phase of the fishery (Figure 4 (C)). This
 354 results from the randomness in the correlated random walk step function, with
 355 distance moved during the exploitation phase and the direction stochastically
 356 related to the revenue experienced on the fishing ground (Figure 4 (D)).

357 *4.2. How does sampling-derived fisheries data reflect the underlying population*
 358 *structure?*

359 The aggregated catch composition from each of the data sources over a ten-
 360 year period (which shows average seasonal patterns) at different spatial resolu-
 361 tions highlights different patterns in perceived community structure depending
 362 on the data source and aggregation level (Figure 6). The finer spatial grid for
 363 the real population (top left) and commercial data (top middle) show visually
 364 similar patterns, though there are large unsampled areas in the commercial data
 365 from a lack of fishing activity (particularly in the lower left part of the sam-
 366 pling domain). The survey data at this spatial resolution displays very sparse
 367 information about the spatial distributions of the populations. The slightly ag-
 368 gregated data on a 5 x 5 grid shows similar patterns and, while losing some of
 369 the spatial detail, there remains good consistency between the real population
 370 and the commercial data. Survey data starts to pick out some of the similar
 371 patterns as the other data sources, but lacks spatiotemporal coverage. The spa-
 372 tial catch information on a 10 x 10 and 20 x 20 grid lose a significant amount
 373 of information about the spatial resolutions for all data sources, and some dif-
 374 ferences between the survey, commercial and real population data emerge.

375
 376 Different perceptions of the proportion of each stock in an area are seen when
 377 we aggregate the data over a smaller geographical region at different timescales,
 378 with weekly (top), monthly (middle) and yearly (bottom) catch compositions
 379 from across an aggregated 20 x 20 area (Figure 7). In the real population, the
 380 monthly aggregation captures the major patterns of composition seen in the
 381 weekly data with the percentage of different species in the catch having simi-
 382 lar mean and standard deviations. In the weekly data species 1 = 9.36 (3.99),
 383 species 2 = 83.2 (5.60), species 3 = 3.57 (1.23), species 4 = 3.91 (1.59); in the
 384 monthly data species 1 = 9.23 (3.87), species 2 = 83.3 (5.52), species 3 = 3.62
 385 (1.15), species 4 = 3.86 (1.52). While means were similar some of the variation
 386 was lost when aggregated to an annual level; species 1 = 9.90 (0.173), species 2
 387 = 82.2 (0.308), species 3 = 3.82 (0.119), species 4 = 4.03 (0.0502).

388

389 The commercial data on a weekly basis shows some of the same patterns
390 as the real population, though the species 1 (in red) is less well represented
391 and some weeks are missing catches from the area. Here, weekly and monthly
392 compositions were nearly identical, with monthly composition of species 1 =
393 0.0472 (0.0139), species 2 = 94.4 (1.47), species 3 = 3.12 (1.47), species 4 =
394 2.40 (0.444). Again, yearly values head a similar mean but smaller standard
395 deviation.

396

397 The survey data was only available on an annual basis, and showed again
398 a slightly different composition; species 1 = 0.372 (0.00473), species 2 = 87.7
399 (0.193), species 3 = 0.729 (0.0200), species 4 = 11.2 (0.172).

400 *4.3. How does data aggregation and source impact on spatial fisheries manage-*
401 *ment measures?*

402 We implemented a spatial closure using the different data sources and spatial
403 and temporal aggregations as outlined in the protocol in Section 3.4. We used
404 this to assess the efficacy of a closure in reducing fishing mortality on species 3,
405 given availability of data and its use at different resolutions in order to evaluate
406 the trade-offs in data sources.

407 The trend in fishing mortality for each species show that in most cases the
408 fishery closure was successful in reducing fishing mortality on the species of in-
409 terest (species 3; Figure 8), though interestingly the largest reductions in fishing
410 mortality happened immediately after the closures, following which the fisheries
411 “adapted” to the closures and fishing mortality increased again somewhat. The
412 exception to the success was the closures implemented based on the coarsest
413 spatial (20 x 20) and temporal resolution (yearly) that was ineffective with all
414 data sources. As expected, closures based on the “known” population distribu-
415 tion were most effective, with differing degrees of success using the commercial
416 data. Fishing mortality rates on the other species changed in different propor-
417 tions, depending on whether the displaced fishing effort moved to areas where

418 the populations were found in greater or lesser density.

419

420 A regression tree (using the R package REEMtree (Sela and Simonoff, 2012))
421 highlights that the factor most contributing to differences in fishing mortality
422 before and after the closure was the population (72 % showing that the closures
423 were effective for population 3), followed by data resolution (21 %), data type
424 (7 %) with the least important factor the timescale (< 1 %). In general the finer
425 the spatial resolution of the data used the greater reduction in fishing mortality
426 for population 3 after the closures (Figure 9). The notable outliers are the com-
427 mercial data at the coarsest spatial resolution (20 x 20) at a yearly and weekly
428 timescale, where closures were nearly as effective as the fine-scale resolution. In
429 this case the closures were sufficiently large to protect a core area of the habitat
430 for the population, but this was achieved in a fairly crude manner by closing
431 a large area - including area where the species was not found (Figure 10) that
432 may have consequences in terms of restricting the fishery in a much larger area
433 than necessary.

434

435 5. Discussion

436 Our study presents a new highly resolved fisheries simulation framework,
437 evaluates the importance of data scaling and considers potential bias introduced
438 through data aggregation when using fisheries data to infer spatiotemporal dy-
439 namics of fish populations. Understanding how fishers exploit multiple hetero-
440 geneously distributed fish populations with different catch limits or conservation
441 status requires detailed understanding of the overlap of resources; this is difficult
442 to achieve using conventional modelling approaches due to species targeting in
443 fisheries resulting in preferential sampling (Martínez-Minaya et al., 2018). Of-
444 ten data are aggregated or extrapolated which requires assumptions about the
445 spatial and temporal scale of processes. Our study explores the assumptions
446 behind such aggregation and preferential sampling to identify potential impacts

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

454 5.1. *Simulation dynamics*

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

460
461 Our approach is unique in that it captures fine scale population and fish-
462 ery dynamics and their interaction in a way not usually possible with real data
463 and thus not usually considered in fisheries simulations. While other simulation
464 frameworks seek to model individual vessel dynamics based on inferred dynam-
465 ics from VMS and logbook records (Bastardie et al., 2010), or as a system to
466 identify measures to meet particular management goals (Bailey et al., 2018), our
467 framework allows users to explore the assumptions in modelling observational
468 data and evaluate the underlying dynamics of such approaches at a fine spatial
469 and temporal scale. This offers the advantage that larger scale fishery patterns
470 are emergent properties of the system and results can be compared to those
471 obtained under a statistical modelling framework.

472
473 Typically, simulation models that treat fish as individuals are focussed on
474 exploring the inter- and intra- specific interactions among fish populations (e.g.
475 OSMOSE Shin et al. (2004)) in order to understand how they vary over space
476 and time. Our focus was on understanding the strengths and limitations of

477 inference from catch data obtained through commercial fishing activity with
 478 fleets exploiting multiple fish populations and realising catch distributions that
 479 may differ from the underlying populations. As such, we favoured a minimum
 480 realistic model of the fish populations (Plagányi et al., 2014) taking account of
 481 environmental but not demographic stochasticity, while incorporating detailed
 482 fishing dynamics that take account of different drivers in a mechanistic way.

483
 484 Demographic stochasticity arises due to individual-level variability in time to
 485 reproduction and death. This form of stochasticity is often modelled by drawing
 486 random time intervals from a given distribution (Gillespie, 1977). The impact
 487 of demographic stochasticity depends on the population size, with the effects
 488 expected to decrease with increasing population size (Lande et al., 2010). This
 489 contrasts with environmental stochasticity, which affects all population sizes
 490 and is present at the population level in our model by variability in recruitment.

491
 492 We take account of heterogeneity in fleet dynamics due to different prefer-
 493 ences and drivers similarly to other approaches (Fulton et al., 2011), but at an
 494 individual vessel rather than fleet level. We do not explicitly define fleets as
 495 rational profit maximisers at the outset, but consider there are several stages
 496 to development of the fishery; information gathering through search where the
 497 resource location is not known, followed by individual learnt behaviour of prof-
 498 itable locations. This provides a realistic model of how fishing patterns are
 499 established and maintained to exploit an uncertain resource through an explore-
 500 exploit strategy (Mangel and Clark, 1983; Bailey et al., 2018).

501 *5.2. How does sampling-derived fisheries data reflect the underlying population* 502 *structure?*

503 Our results demonstrate the importance of considering data scale and resolu-
 504 tion when using observational data to support management measures. We find
 505 that understanding of the community composition dynamics will depend on the
 506 level of data aggregation and its important to consider the scale of processes;

507 including population movement rates, habitat uniformity and fishing targeting
508 practices if potential biases in data are to be understood and taken into account
509 (Figures X,Y,Z).

510

511 Our simulation shows that, despite biases introduced through the fishing
512 process, the commercially derived data could still inform on the key spatial
513 patterns in the community structures where the fisheries occurred, which was
514 spatially limited due to the “hotspots” of commercially valuable species being
515 fished. Similarly, despite the even spatial coverage the survey was able to cap-
516 ture some of the same spatial patterns as the real population, but missed others
517 due to gaps between survey stations limiting spatial and temporal coverage
518 (Figures X,Y,Z). This provides a challenge when modelling unsampled areas in
519 inferring species distribution maps, though these limitations may be overcome
520 by understanding the relationship between the species and habitat covariates
521 where these are known at unsampled locations (Robinson et al., 2011).

522

523 *5.3. How does data aggregation and source impact on spatial fisheries manage-* 524 *ment measures?*

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

529

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

537 1. This is likely due to the biases in commercial sampling, with the fisheries
538 not targeting the areas where species 1 are present and the survey sampling
539 areas where species 1 is more abundant than on average. This indicates that
540 fixed closures, at the right resolution, when based on commercially derived data
541 have the potential to reduced fishing mortality. The likely cost of poor spatial
542 and temporal resolution is associated with reduced effectiveness and potentially
543 closing fishing opportunities for other fisheries.

544

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

554

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

560 5.4. *Model assumptions and caveats*

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

565

566 Fish populations in our simulations move in pre-defined timescales and ac-
 567 cording to fixed habitat preferences and temperature gradients (Figures S1, S3).
 568 Our assumptions in parameterising the model (movement rates, temperature
 569 tolerances) will have a direct impact on our conclusions on the relative impor-
 570 tance of spatial and temporal processes. These assumptions could be explored
 571 in a future study by varying the parameters and assessing the robustness of our
 572 conclusions. For our example application we have chosen movement rates to re-
 573 flect aggregation periods observed in past studies (Poos and Rijnsdorp, 2007b).

574
 575 In addition, we have assumed that fishing vessels are not restricted by quota
 576 and therefore discarding of species for which vessels have no quota or that are
 577 unwanted is not taken into account. This is likely to be a significant source of
 578 bias in any inference using commercial data and should also be explored. For
 579 example, *MixFishSim* could be altered to allow for spatiotemporal appraisal of
 580 the impact of discarding on fisher behaviour and underlying populations via in-
 581 clusion as discarding behaviour, or through move-on rules or cessation of fishing
 582 activity when quota is exhausted.

584 5.5. Future applications of *MixFishSim*

585 We consider that the increased availability of high resolution catch and lo-
 586 cational information from commercial fisheries will require it to be a key source
 587 of data for ensuring management is implemented at the right scale in future.
 588 For example, identifying hot-spots for bycatch reduction or identifying spatial
 589 overlaps in mixed fisheries (Dolder et al., 2018; Gardner et al., 2008; Little et al.,
 590 2014; Dedman et al., 2015; Ward et al., 2015). Our simulation model has the
 591 potential to test some of the assumptions behind the modelling approaches in
 592 identifying such hotspots and indeed behind spatiotemporal modelling in gen-
 593 eral (e.g. comparing GAMs, GLMMs, Random Forests and geostatistical mod-
 594 els under different data generation processes as exemplified by Stock et al. (2019)).

Other novel applications of our framework could be: testing different survey designs given multiple species and data generating assumptions (Xu et al., 2015); commercial index standardisation methods and approaches and understanding of appropriate scales and data aggregations and non-proportionality in catch rate and abundance (Harley et al., 2001; Maunder and Punt, 2004); exploring assumptions about the distribution of natural mortality and fishing mortality throughout the year and importance of capturing in-year dynamics in estimating stock status (Liu and Heino, 2013); at sea sampling scheme designs to deliver unbiased estimates of population parameters (Cotter and Pilling, 2007; Kimura and Somerton, 2006); adaptive management (Walters, 2007; Dunn et al., 2016); testing the ability of commonly employed fleet dynamics models such as Random Utility Models to capture fine scale dynamics and understand their importance (Girardin et al., 2016); and as a detailed operating model in a management strategy evaluation (Mahévas and Pelletier, 2004).

6. Conclusions

MixFishSim provides a detailed simulation framework to explore the interaction of multiple fisheries exploiting different fish populations. The framework enables users to evaluate assumptions in modelling commercially derived data through comparison to the true underlying dynamics at a fine spatial and temporal scale. Understanding these dynamics, the limitations of the data and any potential biases that may be introduced when making inference on spatiotemporal interactions will enable users to identify weaknesses in modelling approaches and identify where data collection is needed to strengthen inference.

Our application shows that inference on community dynamics may change depending on the scale of data aggregation. There is an important balance in ensuring that the data are sufficiently spatially and temporally disaggregated that the main features of the data are captured, yet maintaining enough data

625 coverage that the features can be distinguished. We found in our application
626 that there was greater spatial heterogeneity than temporal heterogeneity and
627 that when using aggregated data to define spatial closures coarser temporal reso-
628 lution (months instead of weeks) could still achieve the same results in reducing
629 exploitation rates of a vulnerable species at the highest temporal resolution
630 data. Conversely, reducing the spatial resolution had a negative effect on the
631 effectiveness of the measures (though importantly, there was still some benefit
632 even with coarse spatial resolution).

633

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

639

640 *MixFishSim* has numerous potential additional applications as it enables
641 the user to apply methods to a fisheries system where there is detailed under-
642 standing of underlying spatiotemporal dynamics. This enables identification of
643 weaknesses or limitations which would not be possible otherwise. In future, we
644 recommend use of the framework to test hypothesis that are otherwise unable
645 to be analysed using real world data due to limitations of data collection. That
646 way the knowledge gained through simulation can inform the future design of
647 management measures.

648 **Abbreviations**

649 Detail any unusual ones used.

650 **Acknowledgements**

651 those providing help during the research..

652 **Funding**

653 This work was supported by the MARES doctoral training program (MARES_14_15)
654 and the Centre for Environment, Fisheries and Aquaculture Science seedcorn
655 program (DP227AC).

656 **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}
$S_{c,d}$	is the stock size in cell c for day d	d^{-1}
α	the maximum recruitment rate	kg
β	the stock size 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	pop	pop	-	pop 4	pop
	2/4	1/3			2/3
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. Results show the fishing mortality before the closure (f.before) and after the closure (f.after) and the percentage change in f (f.change). The results are ordered by most effective scenario first, least effective last.)

scenario	metric	pop	f.before	f.after	f.change	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: Proportions of each species at different levels of temporal aggregation

data_type	timescale	spp1	sd_spp1	spp2	sd_spp2	spp3	sd_spp3	spp4	sd_spp4
commercial	monthly	0.047	0.014	94.435	1.470	3.122	1.468	2.396	0.444
commercial	weekly	0.047	0.016	94.426	1.514	3.117	1.563	2.411	0.498
commercial	yearly	0.051	0.001	94.388	0.205	3.021	0.175	2.539	0.046
real_pop	monthly	9.225	3.872	83.287	5.522	3.624	1.151	3.864	1.519
real_pop	weekly	9.358	3.992	83.165	5.596	3.567	1.233	3.910	1.592
real_pop	yearly	9.899	0.173	82.250	0.308	3.821	0.119	4.031	0.050
survey	yearly	0.372	0.005	87.667	0.193	0.729	0.020	11.232	0.172



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

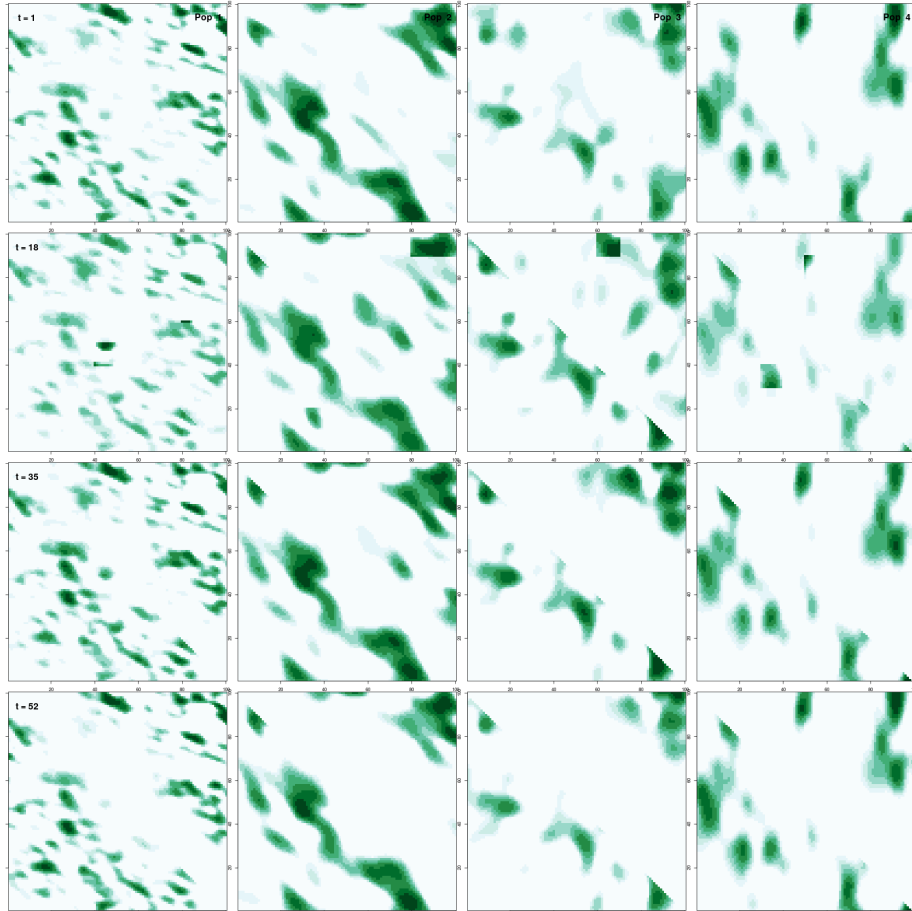


Figure 2: Simulated spatial dynamics - the four populations abundance ($\log+1$) at four time steps.

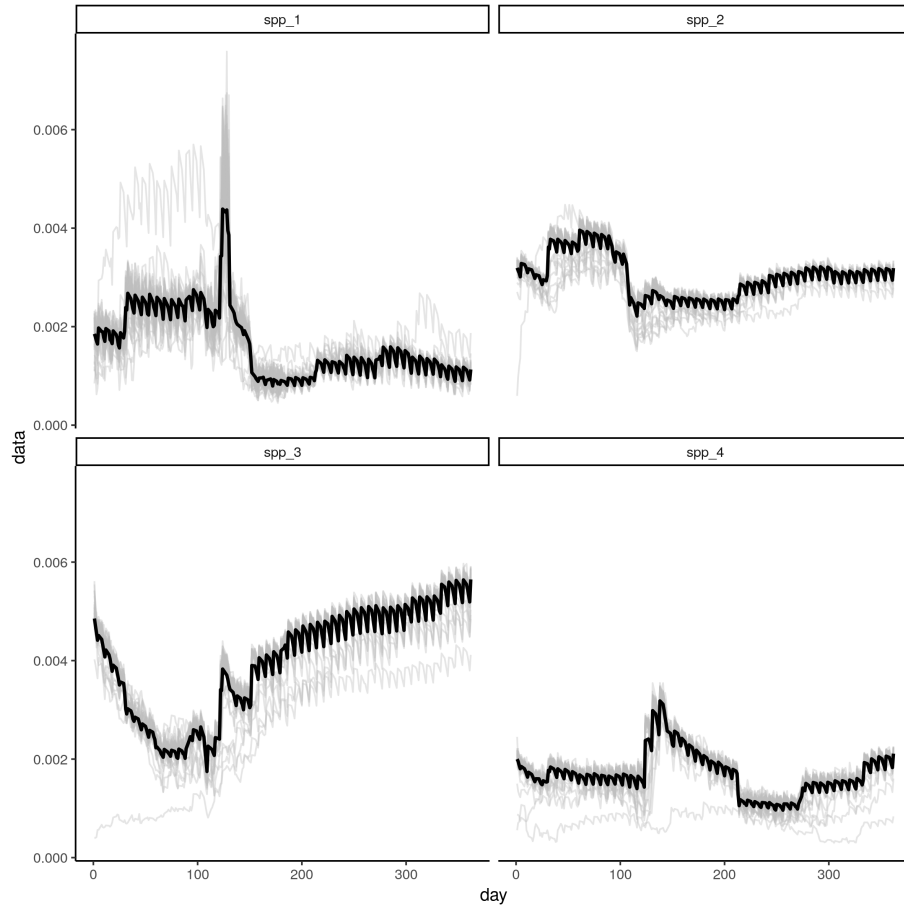


Figure 3: Fishing mortality dynamics - the daily fishing mortalities showing weekly and seasonal patterns in exploitation. Individual years and the light grey lines, the mean of all years the thick black line

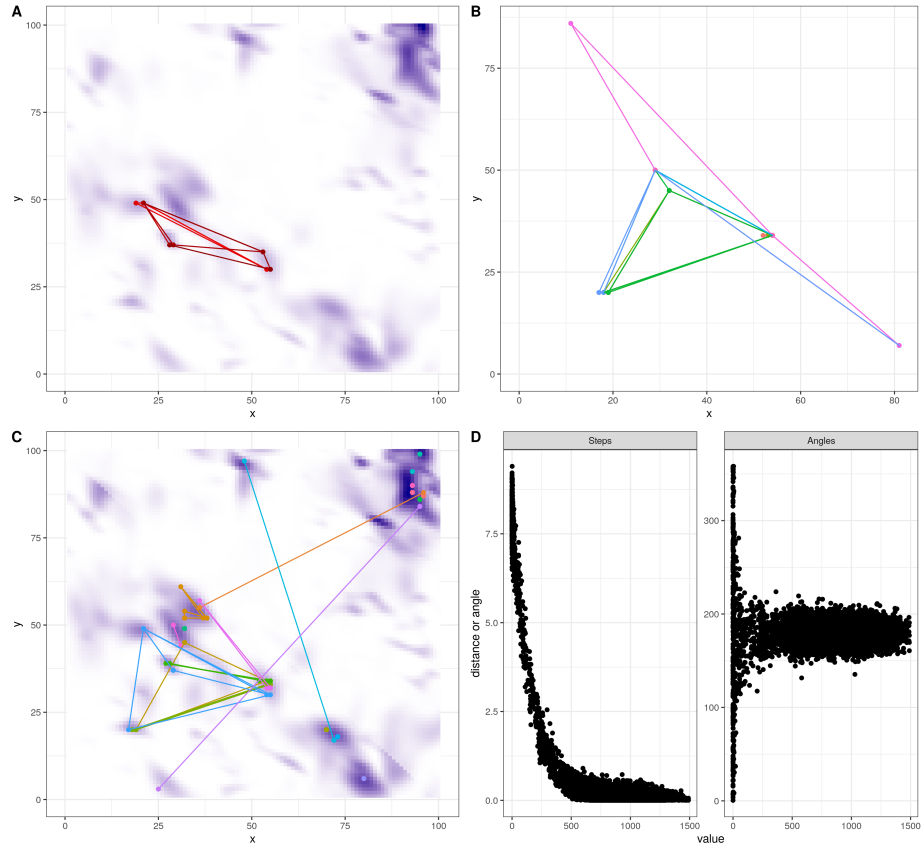


Figure 4: (A) The fishing locations (points) and movements (lines) of a single vessel during a trip overlaid on the relative value of a fishing site; (B) the fishing locations of the vessel over several trips (value field changes over the period so not shown); (C) the locations of multiple vessels from the same fleet overlaid on the value field, (D) the realised step distance and turning angles for a single vessel over the simulation

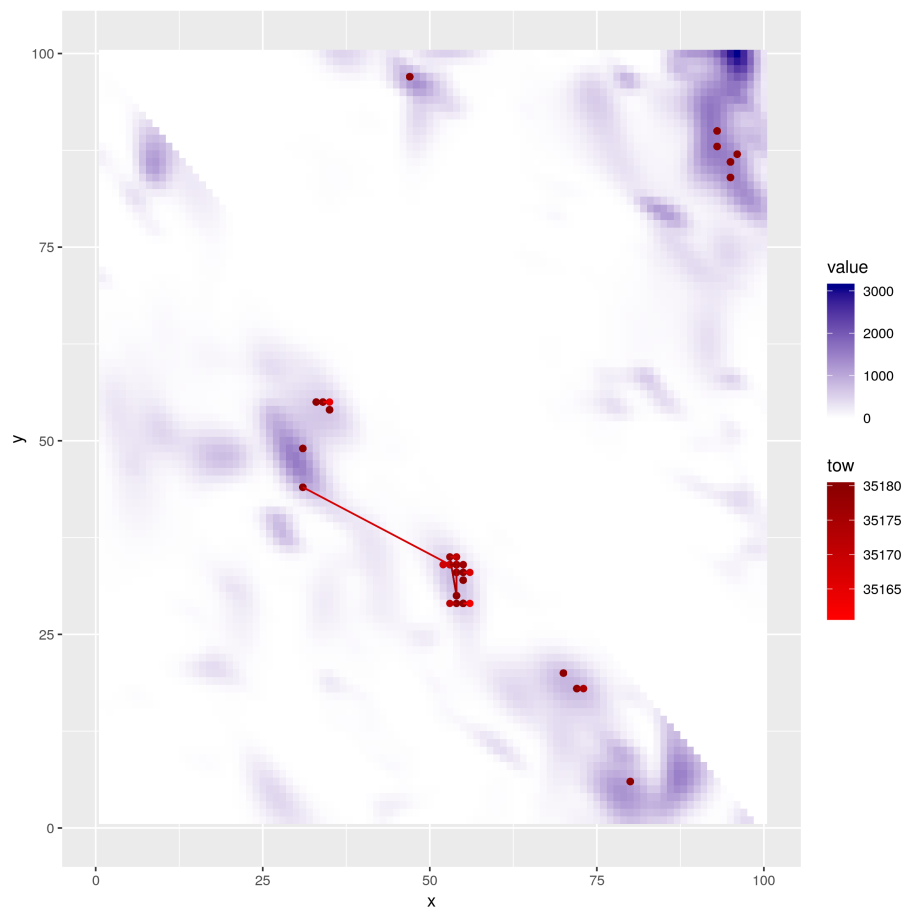


Figure 5: movement of a fleet over a single trip reference overlaid on the value field (i.e. sum of the population abundance \times catchability \times value

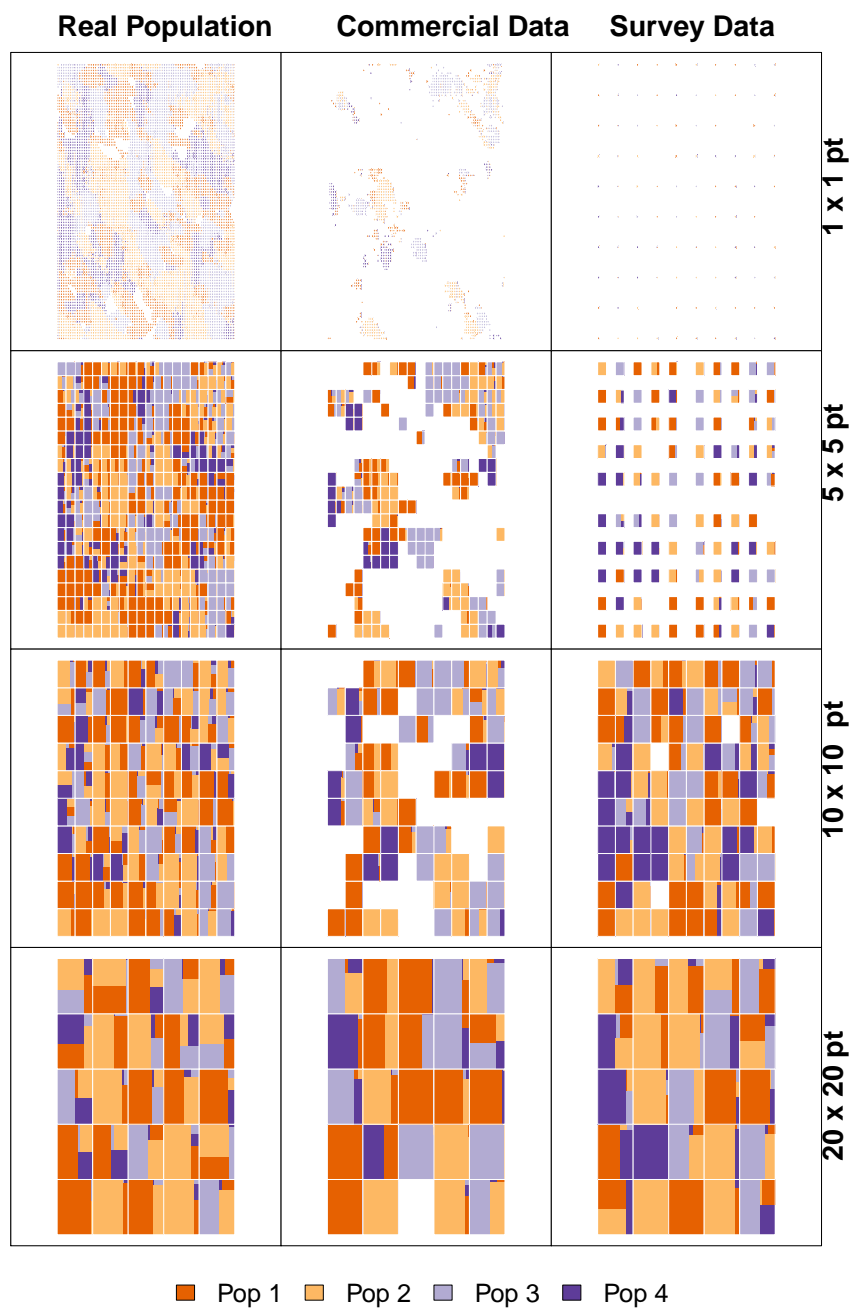


Figure 6: Data aggregation at different spatial resolutions over a ten year period

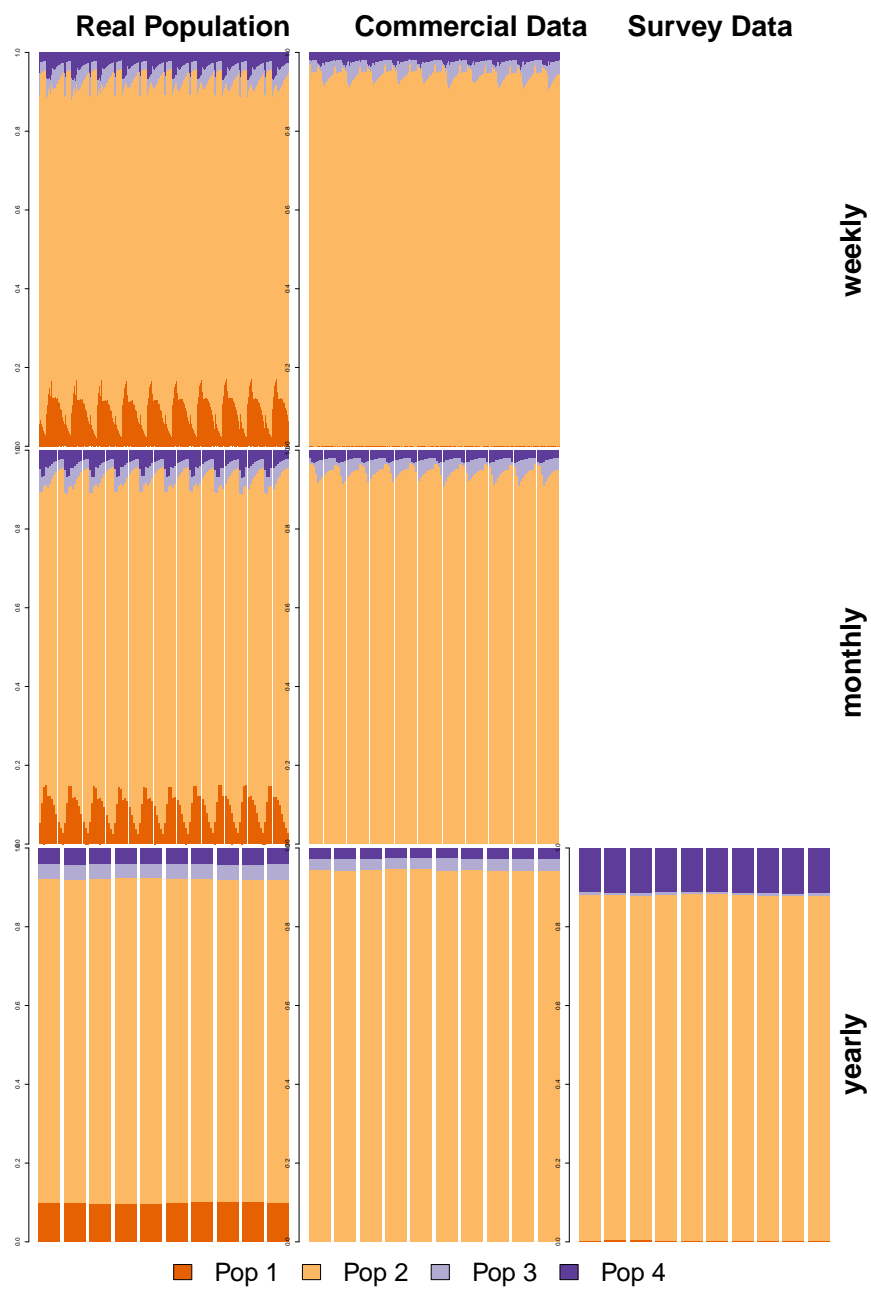


Figure 7: Data aggregation at different temporal resolutions over a ten-year period

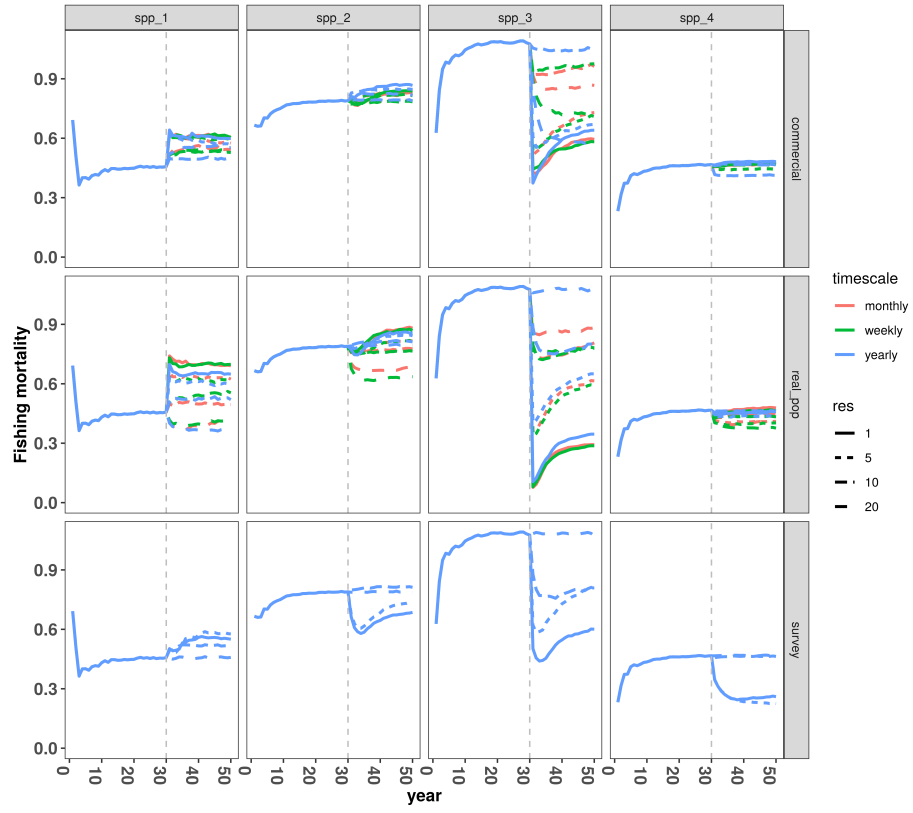


Figure 8: Comparison of closure scenarios effect on fishing mortality trends. Line colour denotes the timescale, while linestyle denotes the spatial resolution.

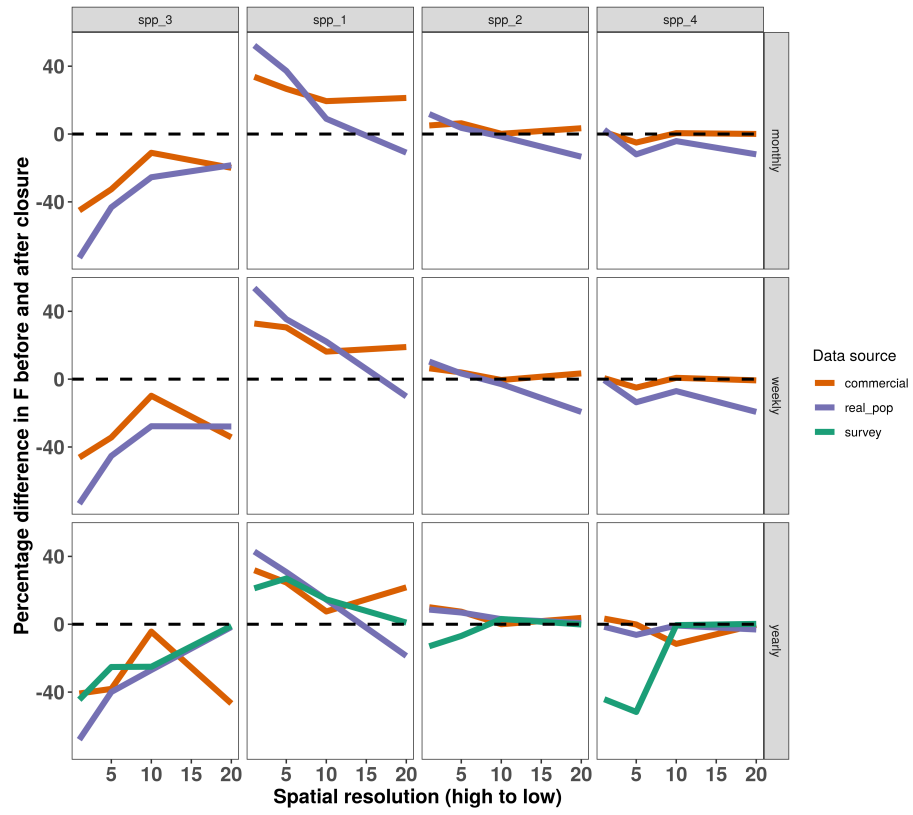


Figure 9: Comparison of closure scenario effectiveness based on different spatial and temporal resolutions.

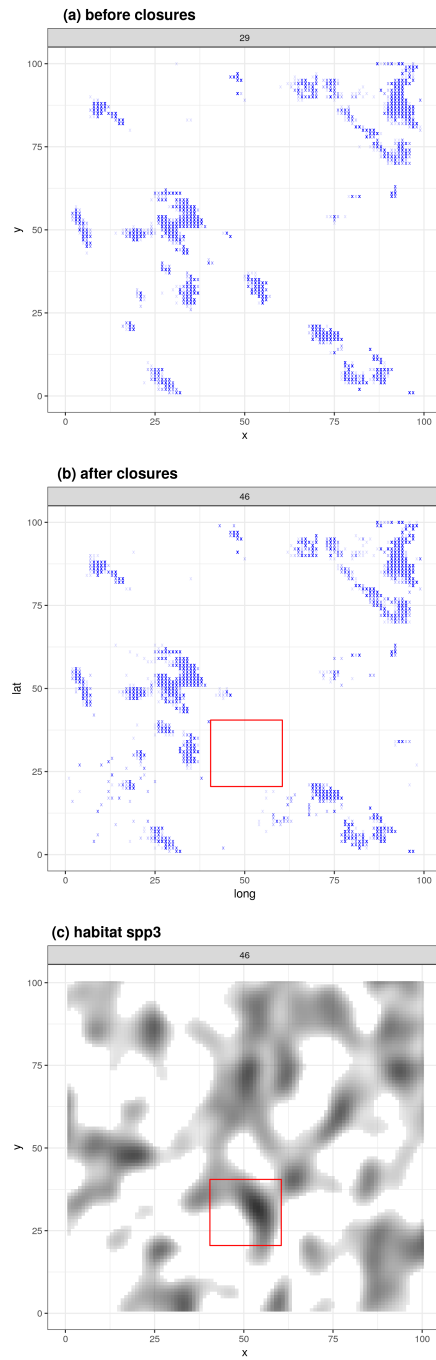


Figure 10: Closure fishing locations based on annual closures with a coarse spatial resolution. Closure location can be seen in red in relation to a) before the closure fishing locations, b) after the closure fishing locations, c) species 3 habitat distribution

657 References

- 658 Akima, H., 2006. Interpolation of irregularly spaced data, The akima Package. Interpolation
659 of Irregularly and Regularly Spaced Data .
- 660 Alverson, D.L., Freeberg, M.H., Murawski, S.A., Pope, J., 1994. A global assessment of
661 fisheries bycatch and discards.
- 662 Bailey, R.M., Carrella, E., Axtell, R., Burgess, M.G., Cabral, R.B., Drexler, M., Dorsett, C.,
663 Madsen, J.K., Merkl, A., Saul, S., 2018. A computational approach to managing coupled
664 human–environmental systems: the POSEIDON model of ocean fisheries.
- 665 Bastardie, F., Nielsen, J.R., Ulrich, C., Egekvist, J., Degel, H., 2010. Detailed mapping
666 of fishing effort and landings by coupling fishing logbooks with satellite-recorded vessel
667 geo-location. *Fisheries Research* 106, 41–53.
- 668 Batsleer, J., Hamon, K.G., Overzee, H.M.J., Rijnsdorp, A.D., Poos, J.J., 2015. High-grading
669 and over-quota discarding in mixed fisheries. *Reviews in Fish Biology and Fisheries* 25,
670 715–736.
- 671 Bellido, J.M., Santos, M.B., Pennino, M.G., Valeiras, X., Pierce, G.J., 2011. Fishery discards
672 and bycatch: Solutions for an ecosystem approach to fisheries management? *Hydrobiologia*
673 670, 317–333.
- 674 Beverton, R.J., Holt, S.J., 1957. On the Dynamics of Exploited Fish Populations , 533.
- 675 Branch, T., Hilborn, R., Bogazzi, E., 2005. Escaping the tyranny of the grid: a more realistic
676 way of defining fishing opportunities. *Canadian Journal of Fisheries and Aquatic Sciences*
677 642, 631–642.
- 678 Catchpole, T.L., Revill, A.S., 2008. Gear technology in Nephrops trawl fisheries. *Reviews in*
679 *Fish Biology and Fisheries* 18, 17–31.
- 680 Codling, E.A., Plank, M.J., Benhamou, S., Interface, J.R.S., 2008. Random walk models in
681 biology. *Journal of the Royal Society, Interface / the Royal Society* 5, 813–34.
- 682 Cosgrove, R., Browne, D., Minto, C., Tyndall, P., Oliver, M., Montgomerie, M., McHugh,
683 M., 2019. A game of two halves: Bycatch reduction in Nephrops mixed fisheries. *Fisheries*
684 *Research* 210, 31–40.
- 685 Costello, C., Rassweiler, A., Siegel, D., De Leo, G., Micheli, F., Rosenberg, A., 2010. The
686 value of spatial information in MPA network design. *Proceedings of the National Academy*
687 *of Sciences* .

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

690 Crowder, B.L.B., Murawski, S.a., Crowder, L.B., Murawski, S.a., 1998. Fisheries Bycatch:
691 Implications for Management. *Fisheries* 23, 8–17.

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

694 Deriso, R.B., 1980. Harvesting Strategies and Parameter Estimation for an Age-Structured
695 Model. *Canadian Journal of Fisheries and Aquatic Sciences* 37, 268–282. [arXiv:1410.7455v3](#).
696

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

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

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

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

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

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

716 Fulton, E.A., Link, J.S., Kaplan, I.C., Savina-Rolland, M., Johnson, P., Ainsworth, C., Horne,
717 P., Gorton, R., Gamble, R.J., Smith, A.D., Smith, D.C., 2011. Lessons in modelling and
718 management of marine ecosystems: The Atlantis experience. *Fish and Fisheries* .

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

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

725 Gillespie, D.T., 1977. Exact stochastic simulation of coupled chemical reactions, in: *Journal*
726 *of Physical Chemistry*.

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

730 Girardin, R., Hamon, K.G., Pinnegar, J., Poos, J.J., Thébaud, O., Tidd, A., Vermard, Y.,
731 Marchal, P., 2016. Thirty years of fleet dynamics modelling using discrete-choice models:
732 What have we learned? *Fish and Fisheries* , 1–18.

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

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

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

740 Holmes, S.J., Bailey, N., Campbell, N., Catarino, R., Barratt, K., Gibb, A., Fernandes, P.G.,
741 2011. Using fishery-dependent data to inform the development and operation of a co-
742 management initiative to reduce cod mortality and cut discards. *ICES Journal of Marine*
743 *Science* 68, 1679–1688.

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

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

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

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

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

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

759 Liu, X., Heino, M., 2013. Overlooked biological and economic implications of within-season
760 fishery dynamics. *Canadian Journal of Fisheries and Aquatic Sciences* .

761 Mahévas, S., Pelletier, D., 2004. ISIS-Fish, a generic and spatially explicit simulation tool for
762 evaluating the impact of management measures on fisheries dynamics. *Ecological Modelling*
763 .

764 Mangel, M., Clark, C.W., 1983. Uncertainty, search, and information in fisheries. *ICES*
765 *Journal of Marine Science* .

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

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

771 Maunder, M.N., Punt, A.E., 2004. Standardizing catch and effort data: A review of recent
772 approaches. *Fisheries Research* .

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

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

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

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

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

788 Ricker, W.E., 1954. Stock and recruitment. *Journal of the Fisheries Research Board of Canada*
789 11, 559 – 623.

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

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

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

797 Robinson, L.M., Elith, J., Hobday, A.J., Pearson, R.G., Kendall, B.E., Possingham, H.P.,
798 Richardson, a.J., 2011. Pushing the limits in marine species distribution modelling: Lessons
799 from the land present challenges and opportunities. *Global Ecology and Biogeography* 20,
800 789–802.

801 Schlater, M., Malinowski, A., Menck, P.J., 2015. Analysis, Simulation and Prediction of
802 Multivariate Random Fields with Package RandomFields. *Journal of Statistical Software*
803 63, 1–25. [arXiv:1501.0228](https://arxiv.org/abs/1501.0228).

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

806 Sela, R., Simonoff, J., 2012. Package ‘REEMtree’.

807 Shin, Y.J., Shannon, L.J., Cury, P.M., 2004. Simulations of fishing effects on the southern
808 Benguela fish community using an individual-based model: Learning from a comparison
809 with ECOSIM, in: *African Journal of Marine Science*.

810 Stock, B.C., Ward, E.J., Eguchi, T., Jannot, J.E., Thorson, J.T., Feist, B.E., Semmens, B.X.,
811 2019. Comparing predictions of fisheries bycatch using multiple spatiotemporal species
812 distribution model frameworks. *Canadian Journal of Fisheries and Aquatic Sciences* .

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

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

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

820 Van Putten, I.E., Kulmala, S., Thébaud, O., Dowling, N., Hamon, K.G., Hutton, T., Pascoe,
821 S., 2012. Theories and behavioural drivers underlying fleet dynamics models. Fish and
822 Fisheries 13, 216–235.

823 Viswanathan, G.M., Buldyrev, S.V., Havlin, S., Da Luz, M.G.E., Raposo, E.P., Stanley, H.E.,
824 1999. Optimizing the success of random searches. Nature 401, 911–914.

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

826 Ward, E.J., Jannot, J.E., Lee, Y.W., Ono, K., Shelton, A.O., Thorson, J.T., 2015. Using spa-
827 tiotemporal species distribution models to identify temporally evolving hotspots of species
828 co-occurrence. Ecological Applications 25, 2198–2209.

829 Xu, B., Zhang, C., Xue, Y., Ren, Y., Chen, Y., 2015. Optimization of sampling effort for a
830 fishery-independent survey with multiple goals. Environmental Monitoring and Assessment
831 .