

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. If fishers discard over-quota catch of a species for which they have no quota, it limits our ability to control fishing mortality (Alverson et al., 1994; Crowder et al., 1998; Rijnsdorp et al., 2007) and the ability to manage fisheries for the biological and economic sustainability (Ulrich et al., 2011; Batsleer et al., 2015).

10

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 Reville, 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.

18

Understanding the correct scale for spatial management measures to be effective is crucial as it enables implementation of effective solutions which minimise economic impact (Dunn et al., 2016). For example, the problem can be to iden-

22 tify a scale that promotes species avoidance for vulnerable or low quota species
23 while allowing continuance of sustainable fisheries for available quota species.
24 Identifying the correct spatial scale remains a challenge because data on fish
25 location at high temporal and spatial resolutions is expensive and difficult to
26 collect and proxies are usually inferred from scientific surveys or commercial
27 catches with limited spatial and temporal resolution. Thus, implementation of
28 spatial measures is hampered by a lack of knowledge of fish and fishery spa-
29 tiotemporal dynamics and understanding of the scale at which these processes
30 become important for management.

31

32

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

43

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

53 areas of high abundance. There is a need to understand the influence of these
54 biases on any spatial management measures which are implemented based on
55 inference from commercial landings or catch data.

56

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

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

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

77

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

80 2. Materials and Methods

81 An event-based simulation model of a hypothetical fishery was developed as
 82 a software package (*MixFishSim*). The modular approach enabled efficient com-
 83 putation by allowing for sub-modules implemented on time-scales appropriate
 84 to capture the characteristic of the different processes (Figure 1). The following
 85 sub-modules were included to capture the full system: 1) Population dynamics,
 86 2) Recruitment dynamics, 3) Population movement, 4) fishery dynamics.

87
 88 Population dynamics operate on a daily time-step, while population move-
 89 ment occurs on a weekly time-step, with the fishing module operating on a
 90 tow-by-tow basis (i.e. multiple events a day).

91 2.1. Population dynamics

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

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

102 where ρ is Brody's coefficient, shown to be equal to e^{-K} when K is the growth
 103 rate from a von Bertalanffy logistic growth model (Schnute, 1985). Wt_{R-1} is

the average weight of fish prior to recruitment, while Wt_R is the average recruited weight. α_d represents the proportion of fish recruited during that day for the year, while $R_{y,c}$ is the annual recruits in year y for cell c .

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 $F_{c,d}$:

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

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 as a function of adult biomass. In *MixFishSim*, it can either take the form of a stochastic Beverton-Holt stock recruitment relationship, or a stochastic Ricker stock recruitment relationship. The Beverton-Holt relationship is defined as (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, the stochastic

128 Ricker form (Ricker, 1954):

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

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

131 2.3. Population movement dynamics

132 Population movement is a combination of directed (advective) movement
133 where at certain times of year the population moves towards spawning grounds
134 by increasing the probabilities of moving into the spawning grounds from adja-
135 cent cells, and random (diffusive) movement, governed by a stochastic process
136 where movement between adjacent cells is described by a set of probabilities.

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

the GRFs), temperature and distance from current cell:

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

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

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

A time-varying temperature covariate changes the interaction between time and suitable habitat on a weekly time-step. Each population p was assigned a thermal tolerance with mean, μ_p and variance, σ_p^2 so that each cell and population temperature suitability is defined that:

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

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

The final combined process results in a population structure and movement pattern unique to each species, with population movement occurring on a weekly basis. The decision to model population movement on a weekly timescale was to reflect that fish tend to aggregate in species specific locations that have been observed to last around one to two weeks (Poos and Rijnsdorp, 2007b). Therefore this process approximated the demographic shifts in fish populations

179 throughout a year with seasonal spawning patterns (Figure S5).

180 2.4. Fleet dynamics

181 Fleet dynamics can be broadly categorised into three components: fleet tar-
182 geting - that determined the fleet catch efficiency and preference towards a
183 particular species; trip-level decisions, that determines the initial location to
184 be fished at the beginning of a trip; and within-trip decisions, that determines
185 movement from one fishing spot to another within a trip. An explore-exploit
186 type strategy was implemented in the model that combined these three compo-
187 nents for individual vessels to maximise their catch from an unknown resource
188 distribution (Bailey et al., 2018). The decision to use an individual based model
189 for fishing vessels was taken because fishers are heterogeneous in their location
190 choice behaviour due to different objectives, risk preference and targeting pref-
191 erence (Van Putten et al., 2012). Therefore in the simulations fleet dynamics
192 reflect individual experiences rather than pre-defined group dynamics.

193 2.4.1. Fleet targeting

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

201 2.4.2. Decision about where to fish at the start of the trip

202 Several studies (Girardin et al., 2016, for a review) have confirmed past
203 activity and past catch rates are strong predictors of fishing location choice.
204 For this reason, the fleet dynamics sub-model included a learning component,
205 where a vessel's initial fishing location in a trip was based on selecting from
206 previously successful fishing locations. This was achieved by calculating an
207 expected revenue based on the catches from locations fished in the preceding

trip as well as the same month periods in previous years and the travel costs from the port to the fishing grounds. Then a vessel chooses randomly from the top 75 % of fishing events as defined by the expected profit, that has a seasonal component.

2.4.3. *Decision about where to fish within the trip*

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

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 relating recent fishing success, measured as the summed value of fish caught (revenue, Rev);

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

where L_p is landings of a population p , and Pr_p price of a population. All species prices were kept the same across fleets and seasons. Here, when fishing is successful vessels remain in a similar location and continue to exploit the local

236 fishing grounds. When unsuccessful, they move some distance away from the
 237 current fishing location. The movement distance retains some degree of stochas-
 238 ticity, that can be controlled separately, but is determined by the relationship:

$$239 \quad StepL = e^{\log(\beta_1) + \log(\beta_2) - \left(\log\left(\frac{\beta_1}{\beta_3}\right)\right)} \cdot Rev \quad (8)$$

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

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

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

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

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

246 2.4.4. Local population depletion

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

256 2.5. Fisheries independent survey

257 A fisheries-independent survey is simulated where fishing on a regular grid
 258 begins each year at the same time for a given number of stations (a fixed station

survey design). Catches of the populations at each station are recorded but not removed from the population (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 within a fleet different vessels have different spatial distributions based on individual experience. The step function was parametrised dynamically within the simulations as the maximum revenue obtainable was not known beforehand. This was implemented so that vessels take smaller steps when fishing at a location that yields landings value in the top 90th percentile of the value experienced in that year so far (as defined per fleet in Table 5).

Fishing locations were chosen based on random search and, with increasing proportion as time progressed, 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 revenue from previous trips 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 that ensures the upper asymptote (where decisions are mainly based on past knowledge) is reached approximately halfway through the simulation.

3.3. Survey settings

The survey simulation was set up with 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 ($Q_p = 1$). This approximates a real world survey design with limited seasonal and spatial coverage.

3.4. Example research question

To illustrate the capabilities of *MixFishSim*, we investigate the influence of the temporal and spatial resolution of different data sources on the reduction in catches of a population given spatial closures. To do so, we set up a simulation to run for 50 years based on a 100×100 square grid (undetermined units), with

315 five fleets of 20 vessels each and four fish populations. Fishing takes place four
316 times a day per vessel and five days a week, while population movement is every
317 week.

318

319 *How does sampling-derived fisheries data reflect the underlying population*
320 *structure?*

321

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

324 a) **fisheries-independent data:** the inferred population from a fixed-site
325 sampling survey design as commonly used for fisheries monitoring pur-
326 poses;

327 b) **fisheries-dependent data:** the inferred population from our fleet model
328 that includes fishery-induced sampling dynamics.

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

333

334 The following steps are undertaken to determine closures:

- 335 1. Extract data source (real population, commercial or survey),
- 336 2. Aggregate according to desired spatial and temporal resolution,
- 337 3. Interpolate across entire area at desired resolution using simple bivariate
338 interpolation using the *interp* function from the R package *akima* (Akima,
339 2006). This is intended to represent a naive spatial model of catch rates,
340 without knowledge of the spatial population dynamics.
- 341 4. Close area covering top 5 % of catch rates

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

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

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

349 4. Results

350 4.1. Emergent simulation dynamics

351 Individual habitat preferences and thermal tolerances result in different spa-
352 tial habitat use for each population (Figure 2) and consequently different sea-
353 sonal exploitation patterns (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.

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

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

360 *4.2. How does sampling-derived fisheries data reflect the underlying population*
 361 *structure?*

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

378
 379 Different perceptions of the proportion of each stock in an area are seen when
 380 we aggregate the data over a smaller geographical region at different timescales,
 381 with weekly (top), monthly (middle) and yearly (bottom) catch compositions
 382 from across an aggregated 20 x 20 area (Figure 7). In the real population, the
 383 monthly aggregation captures the major patterns of composition seen in the
 384 weekly data with the percentage of different species in the catch having simi-
 385 lar mean and standard deviations. In the weekly data species 1 = 9.36 (3.99),
 386 species 2 = 83.2 (5.60), species 3 = 3.57 (1.23), species 4 = 3.91 (1.59); in the
 387 monthly data species 1 = 9.23 (3.87), species 2 = 83.3 (5.52), species 3 = 3.62
 388 (1.15), species 4 = 3.86 (1.52). While means were similar some of the variation
 389 was lost when aggregated to an annual level; species 1 = 9.90 (0.173), species 2
 390 = 82.2 (0.308), species 3 = 3.82 (0.119), species 4 = 4.03 (0.0502).

391

392 The commercial data on a weekly basis shows some of the same patterns
393 as the real population, though the species 1 (in red) is less well represented
394 and some weeks are missing catches from the area. Here, weekly and monthly
395 compositions were nearly identical, with monthly composition of species 1 =
396 0.0472 (0.0139), species 2 = 94.4 (1.47), species 3 = 3.12 (1.47), species 4 =
397 2.40 (0.444). Again, yearly values head a similar mean but smaller standard
398 deviation.

399

400 The survey data was only available on an annual basis, and showed again
401 a slightly different composition; species 1 = 0.372 (0.00473), species 2 = 87.7
402 (0.193), species 3 = 0.729 (0.0200), species 4 = 11.2 (0.172).

403 *4.3. How does data aggregation and source impact on spatial fisheries manage-*
404 *ment measures?*

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

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

421 the populations were found in greater or lesser density.

422

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

437

438 5. Discussion

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

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

457 *5.1. Simulation dynamics*

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

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

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

inference from catch data obtained through commercial fishing activity with
fleets exploiting multiple fish populations and realising catch distributions that
may differ from the underlying populations [(Gillis et al., 2008)]. As such,
we favoured a minimum realistic model of the fish populations (Plagányi et al.,
2014) taking account of environmental but not demographic stochasticity, while
incorporating detailed fishing dynamics that take account of different drivers in
a mechanistic way.

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

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

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

Our results demonstrate the importance of considering data scale and resolu-
tion when using observational data to support management measures. We find
that understanding of the community composition dynamics will depend on the

level of data aggregation and its important to consider the scale of processes; including population movement rates, habitat uniformity and fishing targeting practices if potential biases in data are to be understood and taken into account (Figures X,Y,Z).

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

5.3. How does data aggregation and source impact on spatial fisheries management measures?

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

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

der represents the first species (in red) while the survey over represents species
1. This is likely due to the biases in commercial sampling, with the fisheries
not targeting the areas where species 1 are present and the survey sampling
areas where species 1 is more abundant than on average. This indicates that
fixed closures, at the right resolution, when based on commercially derived data
have the potential to reduced fishing mortality. The likely cost of poor spatial
and temporal resolution is associated with reduced effectiveness and potentially
closing fishing opportunities for other fisheries.

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

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

5.4. Model assumptions and caveats

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

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

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

587 588 5.5. Future applications of *MixFishSim*

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

599

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

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

637

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

643

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

652 **Abbreviations**

653 Detail any unusual ones used.

654 **Acknowledgements**

655 those providing help during the research..

Funding

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

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.

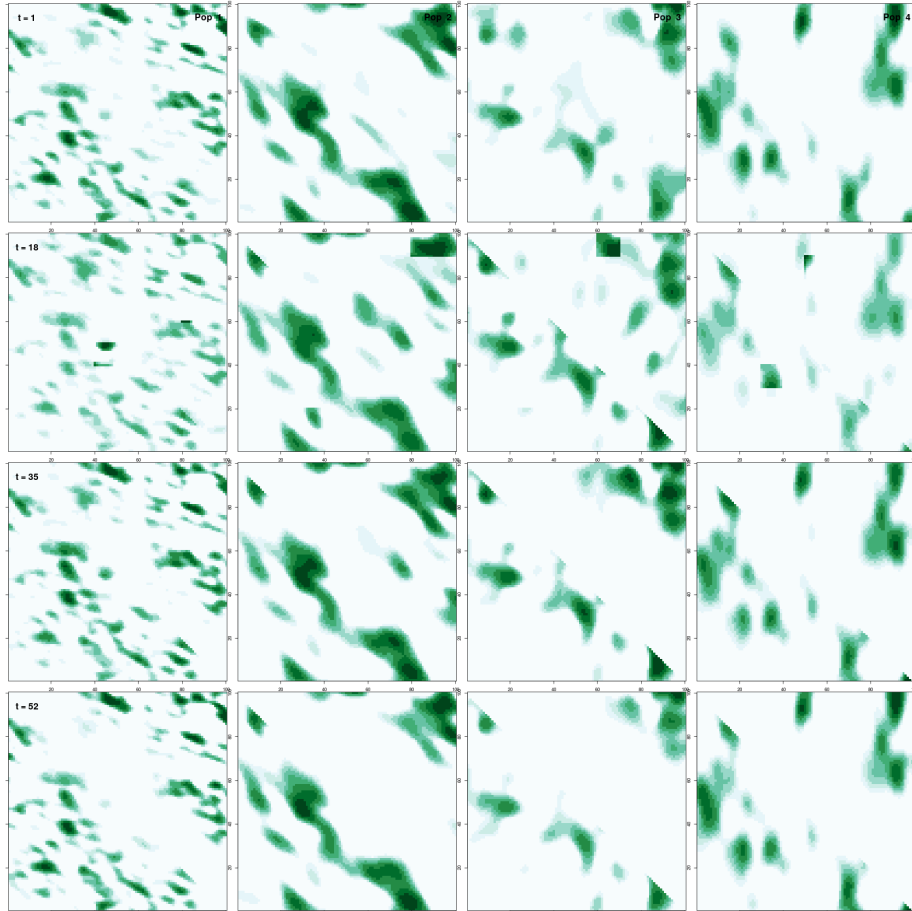


Figure 2: Simulated spatial dynamics - the four populations abundance ($\log+1$) at four time steps.

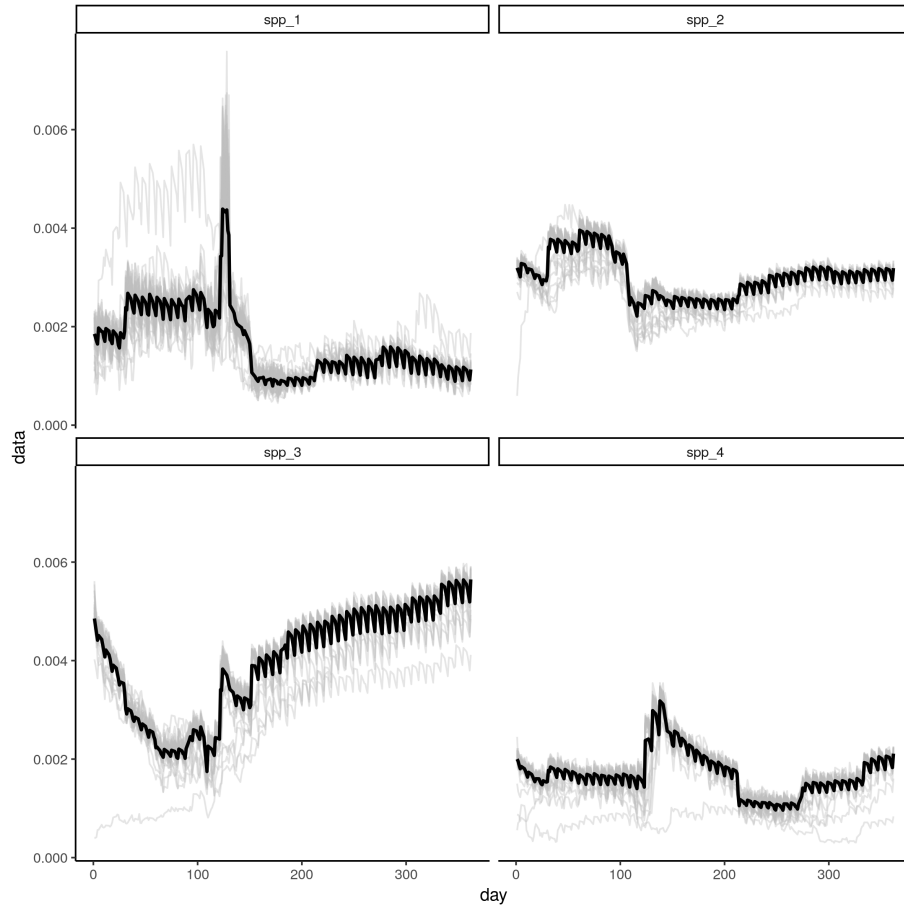


Figure 3: Fishing mortality dynamics - the daily fishing mortalities showing weekly and seasonal patterns in exploitation. Individual years and the light grey lines, the mean of all years the thick black line

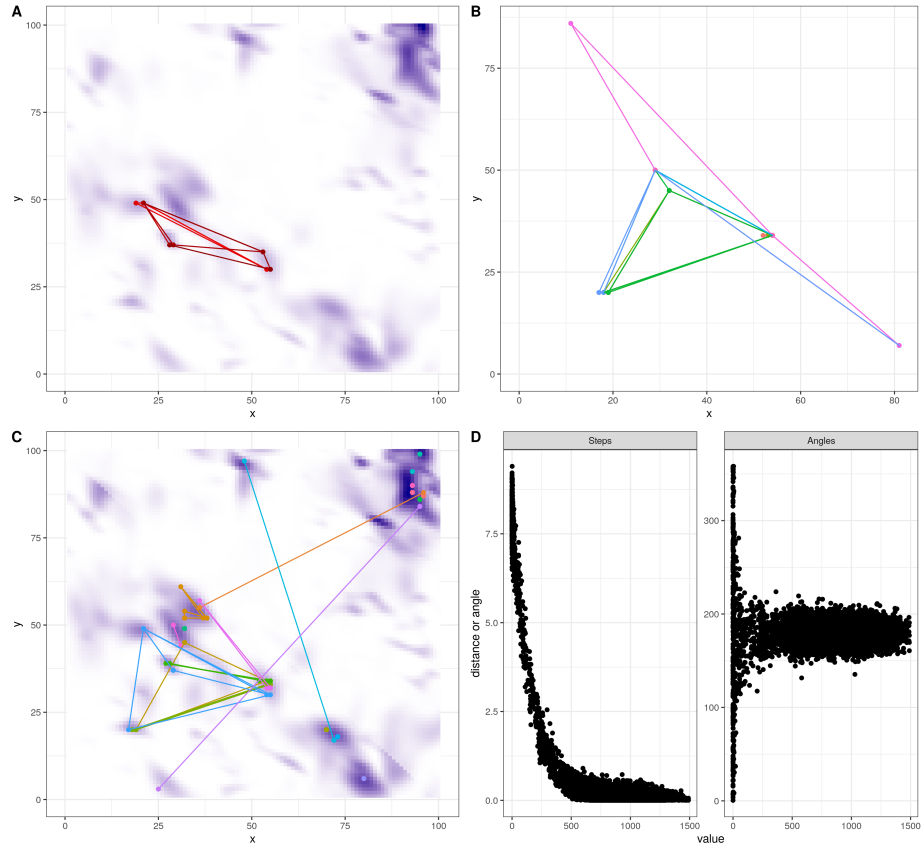


Figure 4: (A) The fishing locations (points) and movements (lines) of a single vessel during a trip overlaid on the relative value of a fishing site; (B) the fishing locations of the vessel over several trips (value field changes over the period so not shown); (C) the locations of multiple vessels from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

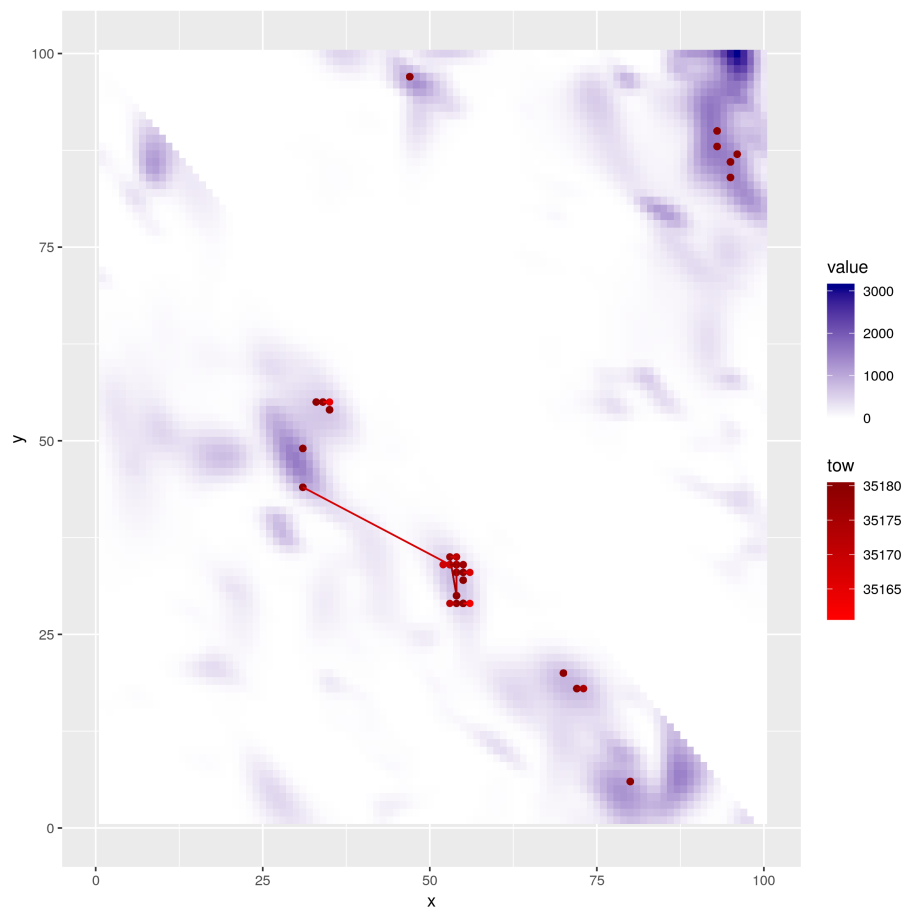


Figure 5: movement of a fleet over a single trip reference overlaid on the value field (i.e. sum of the population abundance \times catchability \times value

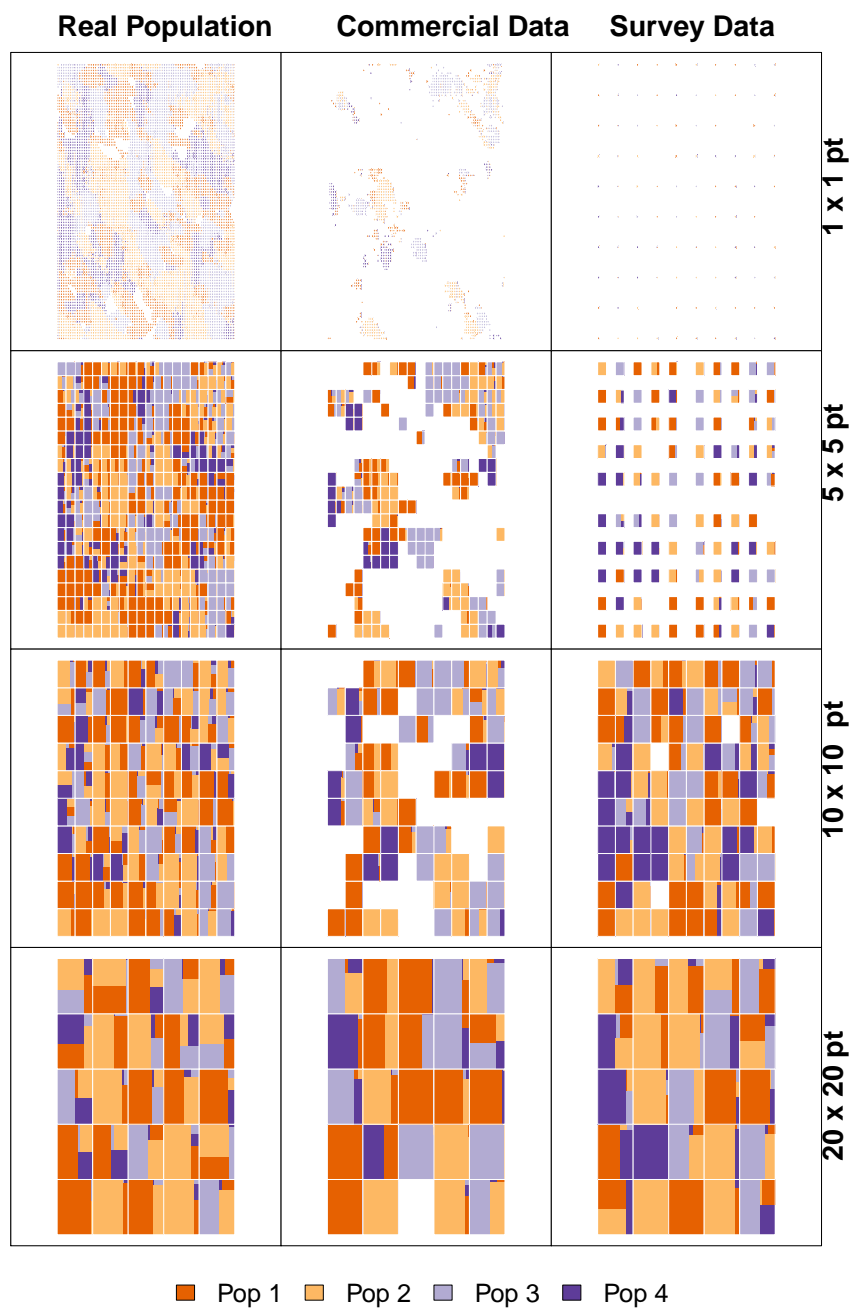


Figure 6: Data aggregation at different spatial resolutions over a ten year period

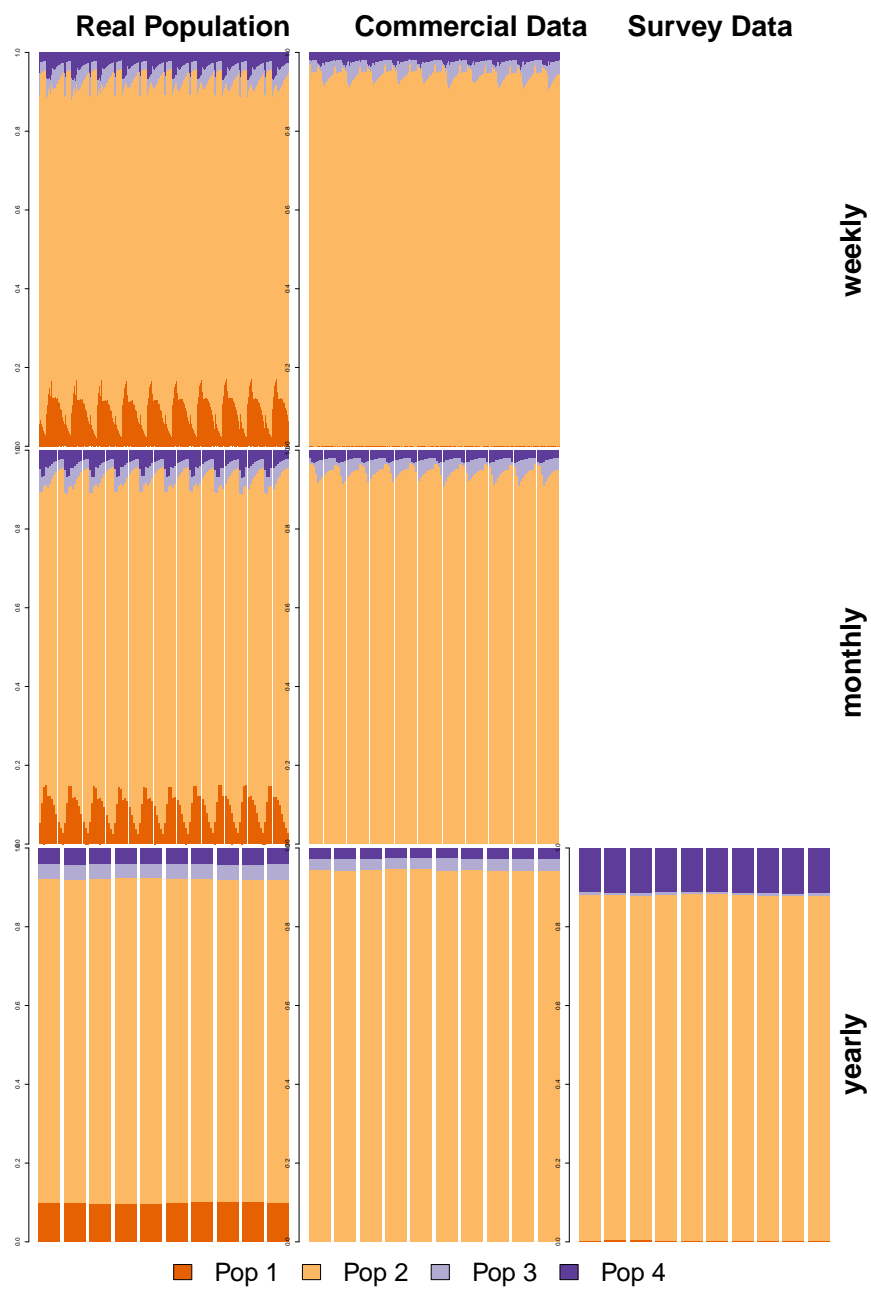


Figure 7: Data aggregation at different temporal resolutions over a ten-year period

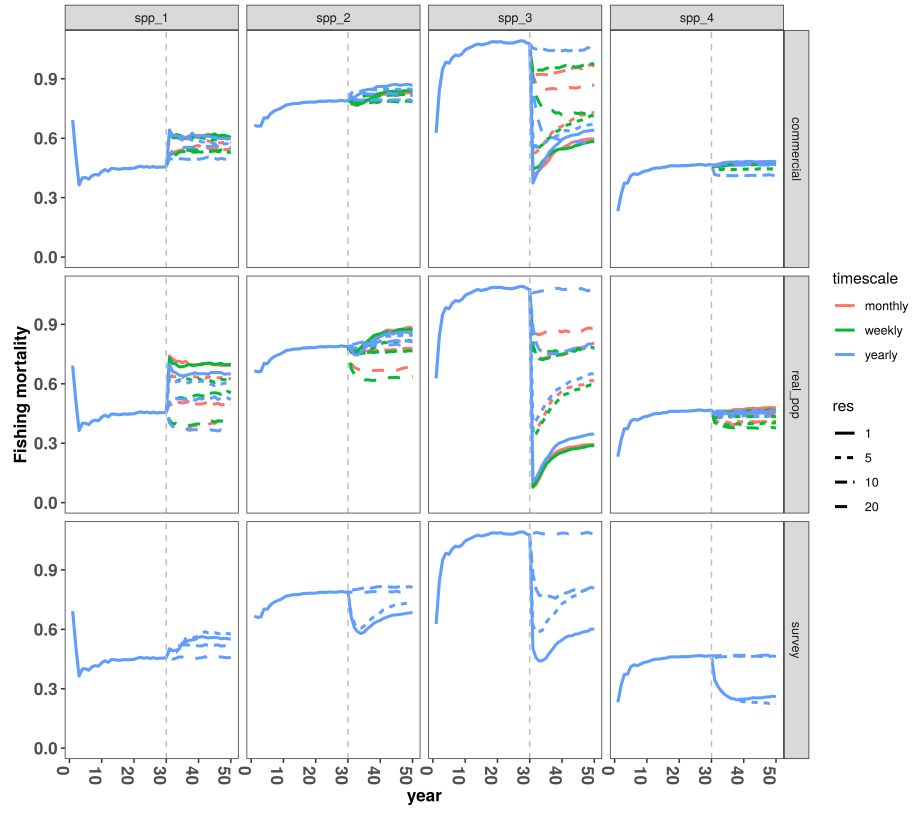


Figure 8: Comparison of closure scenarios effect on fishing mortality trends. Line colour denotes the timescale, while linestyle denotes the spatial resolution.

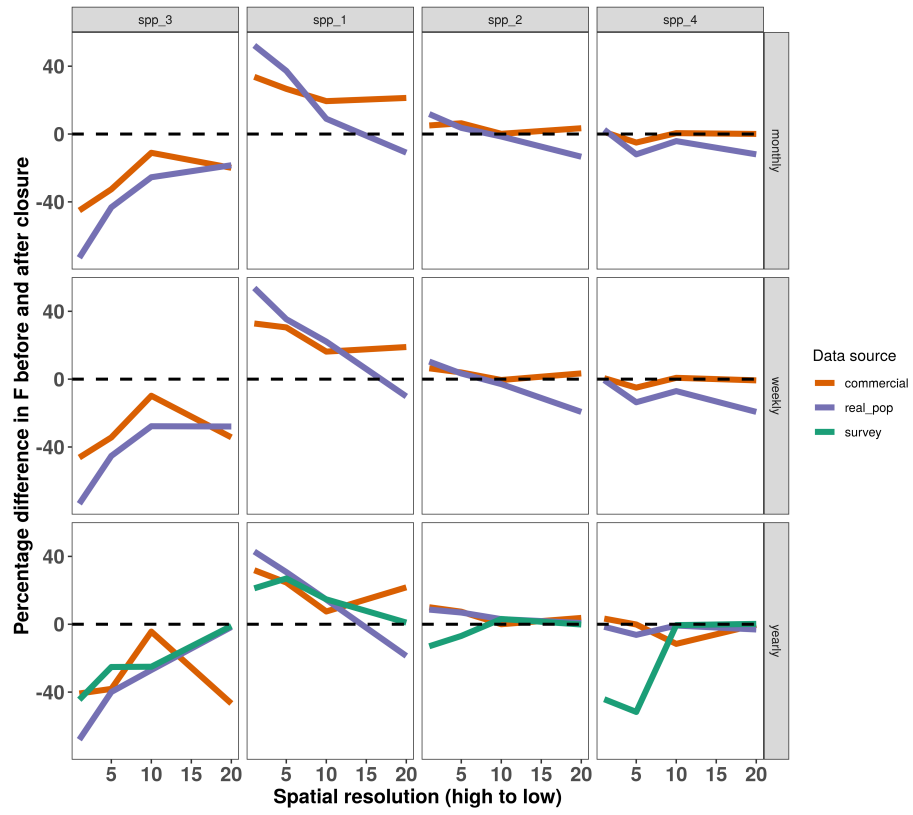


Figure 9: Comparison of closure scenario effectiveness based on different spatial and temporal resolutions.

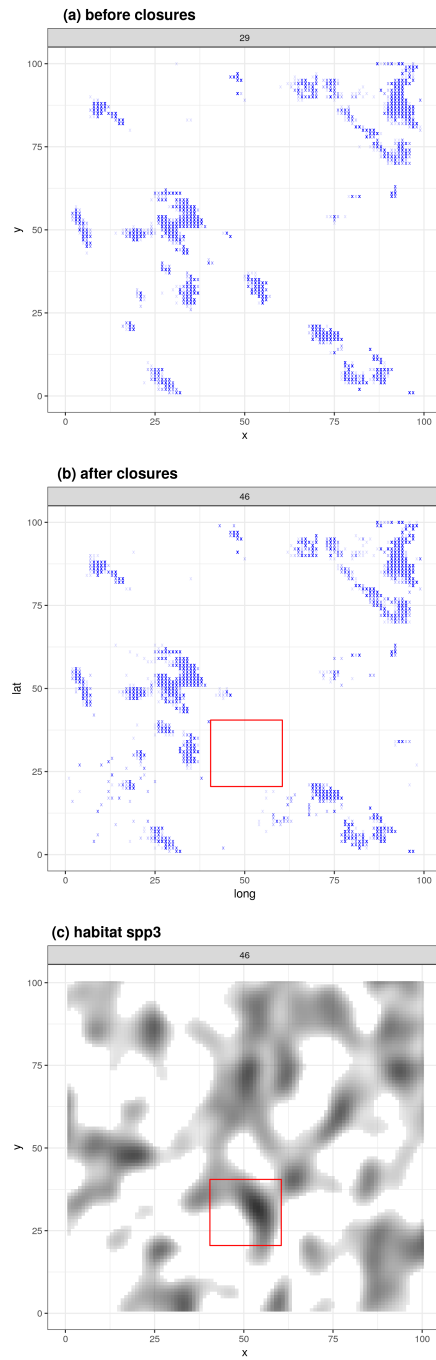


Figure 10: Closure fishing locations based on annual closures with a coarse spatial resolution. Closure location can be seen in red in relation to a) before the closure fishing locations, b) after the closure fishing locations, c) species 3 habitat distribution

661 References

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

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

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

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

698 Deriso, R.B., 1980. Harvesting Strategies and Parameter Estimation for an Age-Structured
699 Model. *Canadian Journal of Fisheries and Aquatic Sciences* 37, 268–282. [arXiv:1410.7455v3](#).
700

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

744 Holmes, S.J., Bailey, N., Campbell, N., Catarino, R., Barratt, K., Gibb, A., Fernandes, P.G.,
745 2011. Using fishery-dependent data to inform the development and operation of a co-
746 management initiative to reduce cod mortality and cut discards. *ICES Journal of Marine*
747 *Science* 68, 1679–1688.

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

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

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

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

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

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

762 Mahévas, S., Pelletier, D., 2004. ISIS-Fish, a generic and spatially explicit simulation tool for
763 evaluating the impact of management measures on fisheries dynamics. *Ecological Modelling*
764 .

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

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

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

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

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

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

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

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

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

789 Ricker, W.E., 1954. Stock and recruitment. *Journal of the Fisheries Research Board of Canada*
790 11, 559 – 623.

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

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

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

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

801 Robinson, L.M., Elith, J., Hobday, A.J., Pearson, R.G., Kendall, B.E., Possingham, H.P.,
802 Richardson, a.J., 2011. Pushing the limits in marine species distribution modelling: Lessons
803 from the land present challenges and opportunities. *Global Ecology and Biogeography* 20,
804 789–802.

805 Schlater, M., Malinowski, A., Menck, P.J., 2015. Analysis, Simulation and Prediction of
806 Multivariate Random Fields with Package RandomFields. *Journal of Statistical Software*
807 63, 1–25. [arXiv:1501.0228](https://arxiv.org/abs/1501.0228).

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

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

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

814 Stock, B.C., Ward, E.J., Eguchi, T., Jannot, J.E., Thorson, J.T., Feist, B.E., Semmens, B.X.,
815 2019. Comparing predictions of fisheries bycatch using multiple spatiotemporal species
816 distribution model frameworks. *Canadian Journal of Fisheries and Aquatic Sciences* .

817 Tobler, W.R., 1970. A Computer Movie Simulating Urban Growth in the Detroit Region.
818 *Economic Geography* 46, 234. [arXiv:1011.1669v3](https://arxiv.org/abs/1011.1669v3).

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

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

825 Viswanathan, G.M., Buldyrev, S.V., Havlin, S., Da Luz, M.G.E., Raposo, E.P., Stanley, H.E.,
826 1999. Optimizing the success of random searches. *Nature* 401, 911–914.

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

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

831 Xu, B., Zhang, C., Xue, Y., Ren, Y., Chen, Y., 2015. Optimization of sampling effort for a
832 fishery-independent survey with multiple goals. *Environmental Monitoring and Assessment*
833 .