

MixFishSim: highly resolved spatiotemporal simulations for exploring mixed fishery dynamics

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

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

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

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

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

Abstract

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

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

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

*Corresponding author

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

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

We simulate 5 years of fishing and use the results from the fisheries catch to draw inference on the underlying population structures. We compare this inference to a simulated fixed-site sampling design commonly used for fisheries monitoring purposes and the true underlying population structures. We i) use the results to establish the potential and limitations of fishery-dependent data in providing a robust picture of spatiotemporal distributions; and ii) simulate an area closure based on areas defined from the different data sources at a range of temporal and spatial resolutions and assess their effectiveness on reducing catches of a fish population.

Our framework allows users to explore the assumptions in modelling observational data and evaluate the underlying dynamics of such approaches at a fine spatial and temporal scale. We conclude from our simulations that commercial data, while containing bias, provides a useful tool for managing catches in mixed fisheries if applied at the correct spatiotemporal scale.

Keywords: Some, keywords, here. Max 6

2010 MSC: 00-01, 99-00


1. Introduction


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

quotas and fishers exhaust one or more quota. This may lead to overexploitation of fish populations (Ulrich et al., 2011; Batsleer et al., 2015). Discarding of fish in excess of quota limits the ability to maintain fishing mortality within sustainable limits (Alverson et al., 1994; Crowder et al., 1998; Rijnsdorp et al., 2007) and the ability to manage for the biological and economic sustainability of fisheries. As such, 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).

Changes to spatial fishing patterns have been proposed as a method to reduce discards (Holmes et al., 2011; Little et al., 2014; Dunn et al., 2014). Implementation of avoidance measures is, however, restricted by lack of knowledge of fish and fishery spatiotemporal dynamics and understanding of the scale at which processes become important for management. Understanding the correct scale for spatial measures is crucial for implementation a resolution that ensures effective management (Dunn et al., 2016) while minimising economic impact. For example, a scale that promotes species avoidance for vulnerable or low quota species while allowing continuance of sustainable fisheries for available quota species.

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

37 grounds through an explore-exploit strategy (Bailey et al., 2018) where they
38 search for areas with high catches and then use experience to return to areas
39 where they’ve experienced high catch in the past 

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

- 43 1. How does sampling-derived data reflect ~~the~~ underlying population struc-
44 tures?
- 45 2. How does data aggregation and source impact ~~on~~ spatial fisheries man-
46 agement measures?

47 To answer these questions we i) develop a simulation model where population
48 dynamics are highly-resolved in space and time. Being known directly rather
49 than inferred from sampling or commercial catch, we can use the population
50 model to validate how inference from fisheries-dependent and fisheries indepen-
51 dent sampling relates to the real population structure in a way we could not
52 with real data. We ii) compare, at different spatial and temporal aggregations,
53 the ‘real population’ distributions to samples from fisheries-dependent and fish-
54 eries independent catches to test if these are a true reflection of the relative
55 density of the populations. We then iii) simulate a fishery closure to protect a
56 species based on different spatial and temporal data aggregations. We use these
57 evaluations to draw inference on the utility of commercial data in supporting
58 management decisions.


59
60 [We find..] 

61 2. Materials and Methods

62 A simulation model that is modular and discrete-event based was developed.
63 This approach enables efficient computation by allowing for sub-modules imple-
64 mented on time-scales appropriate to capture the characteristic of the different

65 processes (Figure 1). The following sub-modules were included to capture the
66 full system: 1) Population dynamics, 2) Recruitment dynamics, 3) Population
67 movement, 4) fishery dynamics.

68

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



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



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

79 *2.1. Population dynamics*

80 The basic population level processes are simulated using a modified two-stage
 81 Deriso-Schnute delay difference model (Deriso, 1980; Schnute, 1985; Dichmont
 82 et al., 2003) occurring at a daily time-step. A daily time-step was chosen to
 83 discretise continuous population processes on a biologically relevant and com-
 84 putationally tractable timescale. Under the population dynamics module pop-
 85 ulation biomass growth and depletion for pre-recruits and recruited fish are
 86 modelled separately as a function of previous recruited biomass, intrinsic popu-
 87 lation growth and recruitment functionally linked to the adult population size.
 88 Biomass for each cell c is incremented each day d as follows (the full parameter
 89 list is detailed in Table 1):

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

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

95
 96 Mortality $Z_{c,d}$ can be decomposed to natural mortality, $M_{c,d}$, and fishing
 97 mortality, $F_{c,d}$, where both $M_{c,d}$ and $F_{c,d}$ are instantaneous rates with $M_{c,d}$
 98 fixed and $F_{c,d}$ calculated by solving the Baranov catch equation (Hilborn and
 99 Walters, 1992) for $F_{c,d}$:

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

100 where $C_{c,d}$ is the summed catch from the fishing model across all fleets and
 101 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 the adult biomass to recruits at time of recruitment. In *MixFishSim*, it can be modelled either either as a stochastic Beverton-Holt stock-recruit form (Beverton and Holt, 1957):

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

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


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

where α is the maximum productivity per spawner and β the density dependent reduction in productivity as the SSB increases. In our example application the Beverton-Holt form of stock recruit relationship was used for all populations though either functional form can be chosen.

2.3. Population movement dynamics



To simulate fish population distribution in space and time a Gaussian spatial process was employed to model habitat suitability for each of the populations on a 2d grid

125 We first defined a Gaussian random field process, $\{S(c) : c \in \mathbb{R}^2\}$, where
 126 for any set of cells c_1, \dots, c_n , the joint distribution of $S = \{S(c_1), \dots, S(c_n)\}$
 127 is multivariate Gaussian with a *Matérn* covariance structure, where the corre-
 128 lation strength weakens with distance. This enables us to model the spatial
 129 autocorrelation observed in animal populations where density is more similar
 130 in nearby locations (Tobler, 1970; F. Dormann et al., 2007) and we change the
 131 parameters to implement different spatial structures for the populations.

132
 133 The habitat for each of the populations was generated with the *RFSimulate*
 134 function of the *RandomFields* R package (Schlatter et al., 2015), that simulates
 135 a Gaussian Random Field process given a user defined error model and cor-
 136 relation structure. We define a stationary habitat field and combine with a
 137 temporally dynamic thermal tolerance field to imitate two key drivers of pop-
 138 ulation dynamics. Each population was initialised at a single location, and
 139 subsequently moved  according to a probabilistic distribution based on habitat
 140 suitability (represented by the normalised values from the GRFs), temperature
 141 and distance from current cell:

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

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

146
 147 During pre-defined weeks of the year the habitat quality  modified with
 148 user-defined spawning habitat locations, resulting in each population having
 149 concentrated areas where spawning takes place. In the simulations the popu-
 150 lations move towards these cells in the weeks prior to spawning, resulting in
 151 directional movement towards the spawning grounds. 

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

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

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

161
 162 The final process results in a population structure and movement pattern
 163 unique to each species with population movement occurring on a weekly basis.
 164 The decision to model population movement on a weekly timescale was to reflect
 165 that fish tend to aggregate in species specific locations that have been observed
 166 to last around one to two weeks (Poos and Rijnsdorp, 2007b). Therefore this
 167 process approximated the demographic shifts in fish populations throughout a
 168 year with seasonal spawning patterns (e.g. Figure S5).

169 2.4. Fleet dynamics

170 The fleet dynamics can be broadly categorised into three components; fleet
 171 targeting - that determines the fleet catch efficiency and preference towards a
 172 particular species; trip-level decisions, that determine the initial location to be
 173 fished at the beginning of a trip; and within-trip decisions, determining move-
 174 ment from one fishing spot to another within a trip. Together, these elements
 175 implement an explore-exploit type strategy for individual vessels to maximise
 176 their catch from an unknown resource distribution Bailey et al. (2018). The
 177 decision to use an individual based model for fishing vessels was taken because
 178 fishers are heterogeneous in their location choice behaviour due to different
 179 objectives, risk preference and targeting preference (Van Putten et al., 2012).

180 Therefore in the simulations fleet dynamics are the productive of individual
181 experiences rather than pre-defined group dynamics.

182 2.4.1. Fleet targeting

183 Each fleet of n vessels was characterised by both a general efficiency, Q_{fl} ,
184 and a population specific efficiency, $Q_{fl,p}$. Thus, the product of these parame-
185 ters $[Q_{fl} \cdot Q_{fl,p}]$ affects the overall catch rates for the fleet and the preferential
186 targeting of one population over another. This, in combination with the param-
187 eter choice for the step-function defined below (as well as some randomness from
188 the exploratory fishing process) determined the preference of fishing locations
189 for the fleet. All species prices were kept the same across fleets and seasons.

190 2.4.2. Trip-level decisions

191 Several studies (e.g. Hutton et al., 2004; Tidd et al., 2012; Girardin et al.,
192 2015) have confirmed past activity and past catch rates are strong predictors of
193 fishing location choice. For this reason, the fleet dynamics sub-model included a
194 learning component, where a vessel's initial fishing location in a trip was based
195 on selecting from previously successful fishing locations. This was achieved by
196 calculating an expected revenue based on the catches from locations fished in
197 the preceding trip as well as the same month periods in previous years and the
198 travel costs from the port to the fishing grounds, and choosing randomly from
199 the top 75 % of fishing events as defined by the expected profit, that has a
200 seasonal component.

201 2.4.3. Within-trip decisions

202 Fishing locations within a trip are initially determined by a modified ran-
203 dom walk process. As the simulation progresses the within-trip decision become
204 gradually more influenced by experience gained from past fishing locations (as
205 per the initial trip-level location choice), moving location choice towards areas
206 of higher perceived profit. A random walk was chosen for the exploratory fishing
207 process as it is the simplest assumption commonly used in ecology to describe
208 optimal animal search strategy for exploiting homogeneously 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).

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

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

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

where L_p is landings of a population p , and Pr_p price of a population. Here, when fishing is successful vessels remain in a similar location and continue to exploit the local fishing grounds. When unsuccessful, they move some distance

away from the current fishing location. The movement distance retains some degree of stochasticity, that can be controlled separately, but is determined by the relationship:

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

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

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

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

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

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

2.4.4. Local population depletion

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

259 2.5. Fisheries independent survey

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

267 2.6. Software


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


272 3. Parameterisation

273 3.1. Population models

274 We parametrised the simulation model for four populations with different
275 demographics; growth rates, natural mortality and recruitment functions (Table
276 4). Habitat preference (Figure S1) and temperature tolerances (Figures S3,
277 S4) were unique to each population resulting in differently weekly distribution
278 patterns (Figures S5-S7). In addition, each of the populations has two defined
279 spawning areas that result in the populations moving towards these areas in
280 pre-defined weeks (Figure S2) with population-specific movement rates (Table
281 4). The individual habitat preferences and thermal tolerances result in different
282 spatial habitat use for each population (Figure S9) and consequently different
283 seasonal exploitation patterns (Fishing mortality in Figure S10).

284 3.2. Fleet parametrisation

285 The fleets were parametrised to reflect five different characteristic fisheries
286 with unique exploitation dynamics (Table 5). By setting different catchability
287 parameters ($Q_{fl,p}$) we create different targeting preferences between the fleets
288 and hence spatial dynamics. The stochasticity in the random alk process
289 ensures that within a fleet different vessels have slightly different spatial dis-
290 tributions based on individual experience. The step function was parametrised
291 dynamically within the simulations as the maximum revenue obtainable was
292 not known beforehand. This was implemented so that vessels take smaller steps
293 when fishing at a location that yields landings value in the top 90th percentile
294 of the value experienced in that year so far (as defined per fleet in Table 5).

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

306 3.3. Survey settings

307 The survey simulation was set up with a fixed gridded station design with
308 100 stations fished each year, starting on day 92 and ending on day 112 (5
309 stations per day) with same catchability parameters for all populations ($Q_p =$
310 1). This approximates a real world survey design with limited seasonal and
311 spatial coverage.


312 3.4. Example research question

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

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

324

325 The following steps are undertaken to determine closures:

- 326 1. Extract data source
- 327 2. Aggregate according to desired spatial and temporal resolution
- 328 3. Interpolate across entire area at desired resolution using simple kriging 
329 using the *interp* function from the R package *akima* (Akima, 2006).
- 330 4. Close area covering top 5 % of catch rates

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

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


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

338 4. Results

339 4.1. Simulation dynamics

It can be seen from a single vessels movements during a trip that the vessel exploits four different fishing grounds, three of them multiple times (Figure S11), while across several trips fishing grounds that are further apart are fished (Figure S12). These different locations relate to areas where the highest revenue were experienced, as shown by Figure S13, where several trips for the vessel overlaid on the revenue field, i.e.

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

340 Vessels from the same fleet (and therefore targeting preference) exploit sim-
341 ilar but slightly different fishing grounds depending on their own personal ex-
342 perience during the explore phase of the fishery (Figure S14), that is the result
343 of the randomness in the correlated random walk step function, with distance
344 moved during the exploitation phase and the direction stochastically related to
345 the revenue experienced on the fishing ground (Figure S15) 

346 4.2. How does sampling-derived data reflect the underlying population structure?

347 In order to answer this question we compare different spatial and temporal
348 aggregations of the 'real population' distributions to:

- 349 a) **fisheries-independent data:** the inferred population from a fixed-site
350 sampling survey design as commonly used for fisheries monitoring pur-
351 poses;
- 352 b) **fisheries-dependent data:** the inferred population from our fleet model
353 that includes fishery-induced sampling dynamics.

354 Figure 2 shows the aggregated catch composition from each of the data
355 sources over a ten-year period (to average seasonal patterns) at different spa-
356 tial resolutions. The finer spatial grid for the real population (top left) and
357 commercial data (top middle) show visually similar patterns, though there are

358 large unsampled areas in the commercial data from a lack of fishing activity
 359 (particularly in the lower left part of the sampling domain). The survey data at
 360 this spatial resolution displays very sparse information about the spatial distri-
 361 butions of the populations. The slightly aggregated data on a 5 x 5 grid shows
 362 similar patterns and, while losing some of the spatial detail, there remains good
 363 consistency between the 'real population' and the commercial data. Survey data
 364 starts to pick out some of the similar patterns as the other data sources, but
 365 lacks spatiotemporal coverage. The spatial catch information on a 10 x 10 and
 366 20 x 20 grid lose a significant amount of information about the spatial resolu-
 367 tions for all data sources, and some differences between the survey, commercial
 368 and 'real population' data emerge.

369


370 Figure 3 shows the consequences of different temporal aggregations of the
 371 data over a ten-year period, with weekly (top), monthly (middle) and yearly
 372 (bottom) catch compositions from across an aggregated 20 x 20 area. By com-
 373 parison to the 'real population', the monthly aggregation captures the major
 374 patterns seen in the weekly data, albeit missing more subtle difference. The
 375 yearly data results in a constant catch pattern due to the aggregation process
 376 (sometimes known as an aggregation bias). The commercial data on a weekly
 377 basis shows some of the same patterns as the 'real population', though the first
 378 species (in red) is less well represented and some weeks are missing catches
 379 from the area. The monthly data shows some consistency between the 'real
 380 population' and commercial data for species 2 - 4, though species 1 remains
 381 under-represented. On an annual basis, interestingly the commercial data un-
 382 der represents the first species (in red) while the survey over represents species
 383 1. This is likely due to the biases in commercial sampling, with the fisheries
 384 not targeting the areas where species 1 are present, and the biases in the survey
 385 sampling from over representation of the spatial distribution.

386 *4.3. How does data aggregation and source impact on spatial fisheries manage-*
387 *ment measures?*

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

393 The trend in fishing mortality for each species show that in most cases the
394 fishery closure was successful in reducing fishing mortality on the species of in-
395 terest (species 3; Figure 4), though interestingly the largest reductions in fishing
396 mortality happened immediately after the closures, following which the fisheries
397 "adapted" to the closures and fishing mortality increased again somewhat. The
398 exception to the success was the closures implemented based on the coarsest
399 spatial (20 x 20) and temporal resolution (yearly) that was ineffective with all
400 data sources. As expected, closures based on the "known" population distribu-
401 tion were most effective, with differing degrees of success using the commercial
402 data. Fishing mortality rates on the other species changed in different propor-
403 tions, depending on whether the displaced fishing effort moved to areas where
404 the populations were found in greater or lesser density.

405
406 A regression tree (using the R package REEMtree (Sela and Simonoff, 2012))
407 highlights that the factor most contributing to differences in fishing mortality
408 before and after the closure was the population (72 % showing that the closures
409 were effective for population 3), followed by data resolution (21 %), data type
410 (7 %) with the least important factor the timescale (< 1 %). In general the finer
411 the spatial resolution of the data used the greater reduction in fishing mortality
412 for population 3 after the closures (Figure 5). The notable outliers are the com-
413 mercial data at the coarsest spatial resolution (20 x 20) at a yearly and weekly
414 timescale, where closures were nearly as effective as the fine-scale resolution. In
415 this case the closures were sufficiently large to protect a core area of the habitat
416 for the population, but this was achieved in a fairly crude manner by closing a

417 large area - including area where the species was not found (Figure S17) that
418 may have consequences in terms of restricting the fishery in a much larger area
419 than necessary 

420

421 5. Discussion

422 Our study evaluates the importance of data scaling and considers poten-
423 tial bias introduced through data aggregation when using fisheries data to infer
424 spatiotemporal dynamics of fish populations. Understanding how fishers ex-
425 ploit multiple heterogeneously distributed fish populations with different catch
426 limits or conservation status requires detailed understanding of the overlap of
427 resources; this is difficult to achieve using conventional modelling approaches
428 due to species targeting in fisheries resulting in preferential sampling (Martínez-
429 Minaya et al., 2018). Often data are aggregated or extrapolated which requires
430 assumptions about the spatial and temporal scale of processes. Our study ex-
431 plores the assumptions behind such aggregation and preferential sampling to
432 identify potential impacts on management advice. With modern management
433 approaches increasingly employing more nuanced spatiotemporal approaches in
434 order to maximise productivity while taking account of both the biological and
435 human processes operating on different time-frames (Dunn et al., 2016), un-
436 derstanding assumptions behind the data used - increasingly a combination of
437 logbook and positional information from vessel monitoring systems - is vital to
438 ensure measures are effective.

439

440 5.1. Simulation dynamics


441 We employ a simulation approach to model each of the population and fish-
442 ery dynamics in a hypothetical 'mixed fishery', allowing us to i) evaluate the
443 consequences of different aggregation assumptions on our understanding of the
444 spatiotemporal distribution of the underlying fish populations, and ii) evaluate

445 the effectiveness of a spatial closure given those assumptions.

446

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

458

459 Typically, simulation models that treat fish as individuals are focussed on
460 exploring the inter- and intra- specific interactions among fish populations (e.g.
461 OSMOSE Shin et al. (2004)) in order to understand how they vary over space
462 and time. Our focus was on understanding the strengths and limitations of
463 inference from catch data obtained through commercial fishing activity with
464 fleets exploiting multiple fish populations and realising catch distributions that
465 may differ from the underlying populations. As such, we favoured a minimum
466 realistic model of the fish populations (Plagányi et al., 2014), while incorporating
467 detailed fishing dynamics that take account of different drivers in a mechanistic
468 way. In this way we take account of heterogeneity in fleet dynamics due to
469 different preferences and drivers similarly to other approaches (Fulton et al.,
470 2011), but at an individual vessel rather than fleet level. We do not explicitly
471 define fleets as rational profit maximisers at the outset, but consider there are
472 several stages to development of the fishery; information gathering through
473 search where the resource location is not known, followed by individual learnt
474 behaviour of profitable locations. This provides a realistic model  how fishing
475 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 data reflect the underlying population structure?

Our results demonstrate the importance of considering data scale and resolution 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.

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. 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 S9). 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

505 and temporal resolution is associated with reduced effectiveness and potentially
506 closing fishing opportunities for other fisheries.

507

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

517

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

523 *5.4. Model assumptions and caveats*

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

528

529 Fish populations in our simulations move in pre-defined timescales and ac-
530 cording to fixed habitat preferences and temperature gradients (Figures S1, S3).
531 Our assumptions in parametrising the model (movement rates, temperature tol-
532 erances) will have a direct impact on our conclusions on the relative importance
533 of spatial and temporal processes. These assumptions could be explored in a
534 future study by varying the parameters and assessing the robustness of our con-

535 clusions. For our example application we have chosen movement rates to reflect
536 aggregation periods observed in past studies (Poos and Rijnsdorp, 2007b).

537

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

546

547 5.5. *Future applications of MixFishSim*

548 We consider that the increased availability of high resolution catch and lo-
549 cational information from commercial fisheries will require it to be a key source
550 of data for ensuring management is implemented at the right scale in future.
551 For example, identifying hot-spots for bycatch reduction or identifying spatial
552 overlaps in mixed fisheries (Dolder et al., 2018; Gardner et al., 2008; Little et al.,
553 2014; Dedman et al., 2015; Ward et al., 2015). Our simulation model has the
554 potential to test some of the assumptions behind the modelling approaches in
555 identifying such hotspots and indeed behind spatiotemporal modelling in gen-
556 eral (e.g. comparing GAMs, GLMMs, Random Forests and geostatistical mod-
557 els under different data generation processes as exemplified by Stock et al. (2019)).

558

559 Other novel applications of our framework could be; testing different sur-
560 vey designs given multiple species and data generating assumptions (Xu et al.,
561 2015); commercial index standardisation methods and approaches and under-
562 standing of appropriate scales and data aggregations and non-proportionality
563 in catch rate and abundance (Harley et al., 2001; Maunder and Punt, 2004);
564 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 coverage that the features can be distinguished. We found in our application that there was greater spatial heterogeneity than temporal heterogeneity and that when using aggregated data to define spatial closures coarser temporal resolution (months instead of weeks) could still achieve the same results in reducing exploitation rates of a vulnerable species at the highest temporal resolution data. Conversely, reducing the spatial resolution had a negative effect on the

effectiveness of the measures (though importantly, there was still some benefit even with coarse spatial resolution).

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

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

Abbreviations

Detail any unusual ones used.

Acknowledgements

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}
$B_{c,d}$	is the Biomass in cell c for day d	d^{-1}
α	the maximum recruitment rate	kg
β	the biomass required to produce half the maximum rate of recruitment	kg

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

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

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

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

Table 4: Population dynamics and movement parameter setting

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

Table 5: Fleet dynamics parameter setting

Parameter	Fleet	Fleet	Fleet	Fleet	Fleet
	1	2	3	4	5
Targeting preferences	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

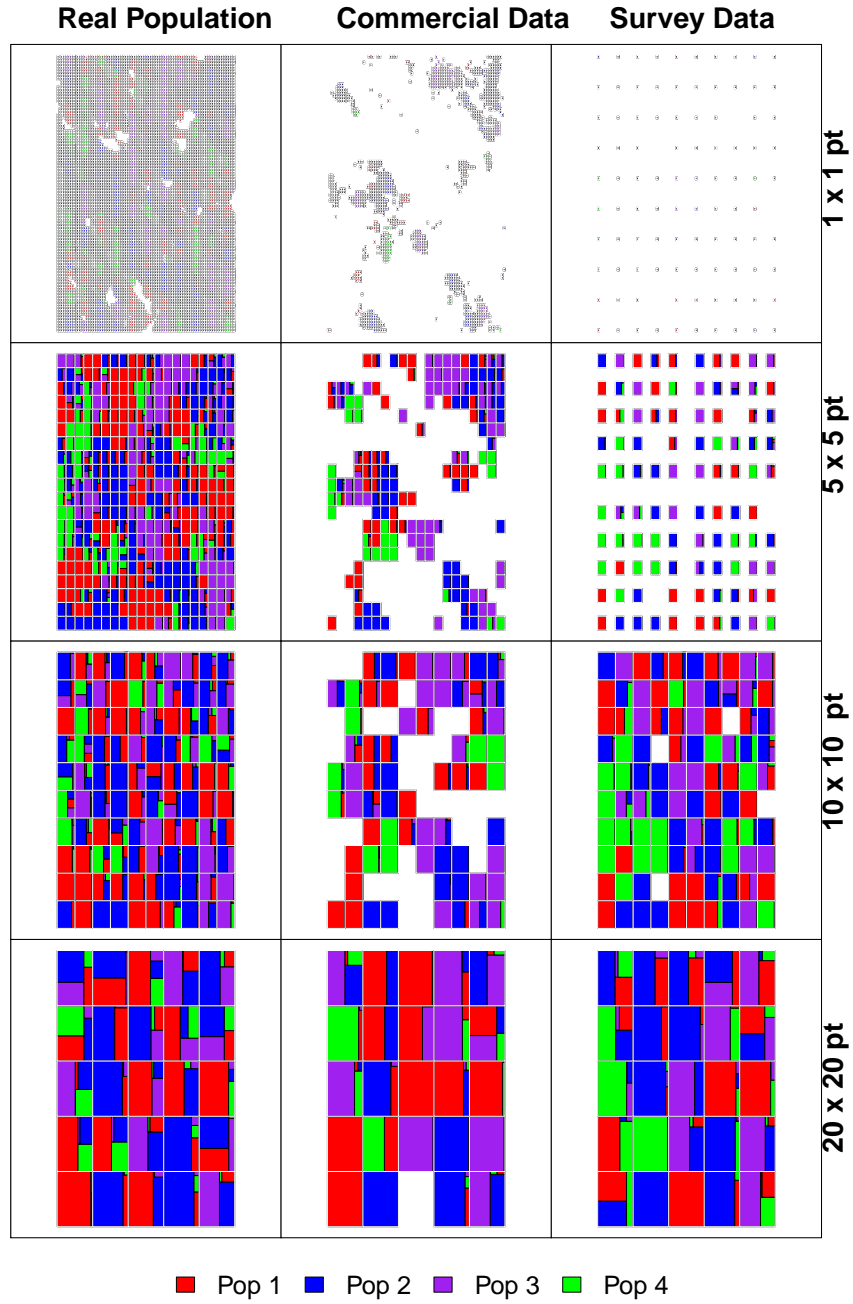


Figure 2: Data aggregation at different spatial resolutions over a ten year period

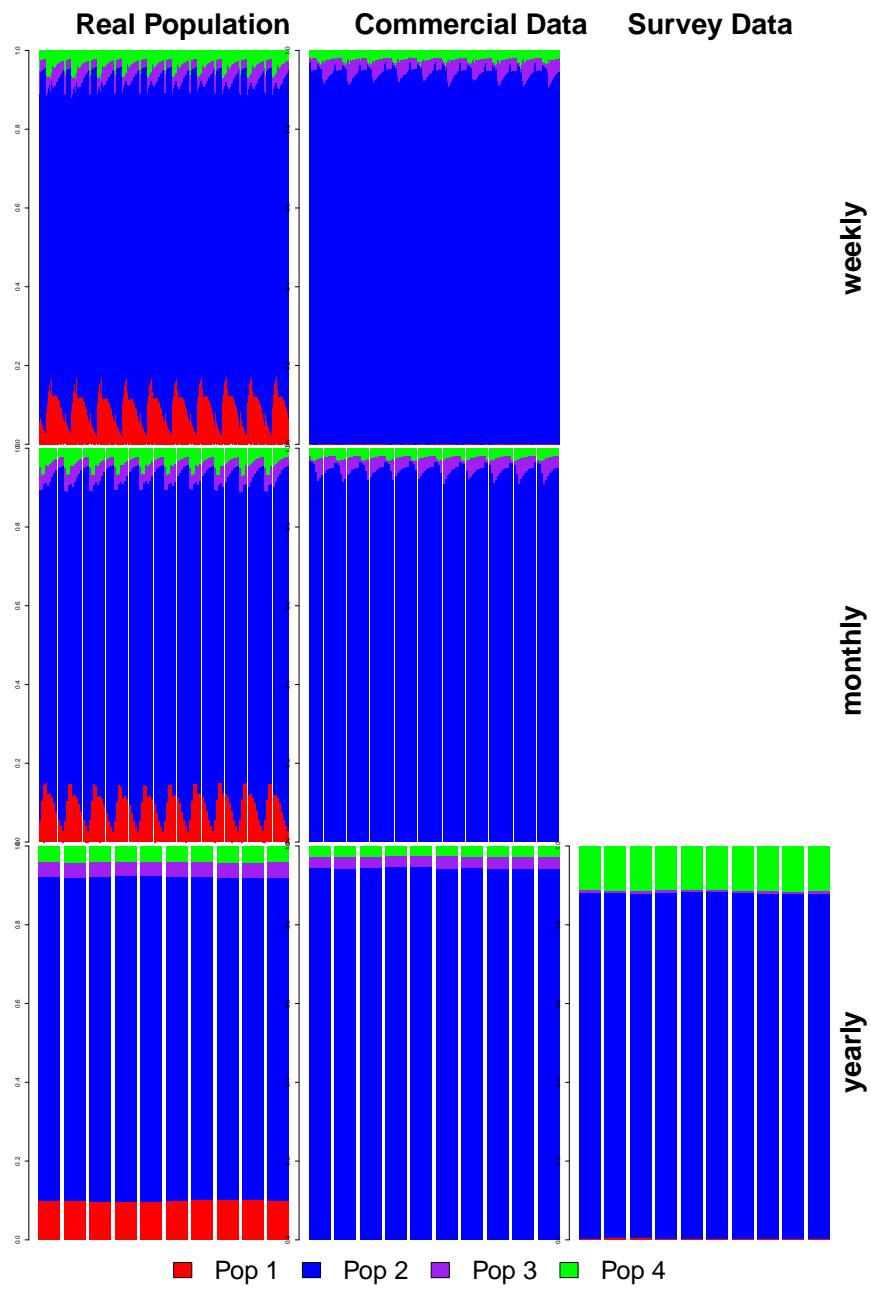


Figure 3: Data aggregation at different temporal resolutions over a ten-year period

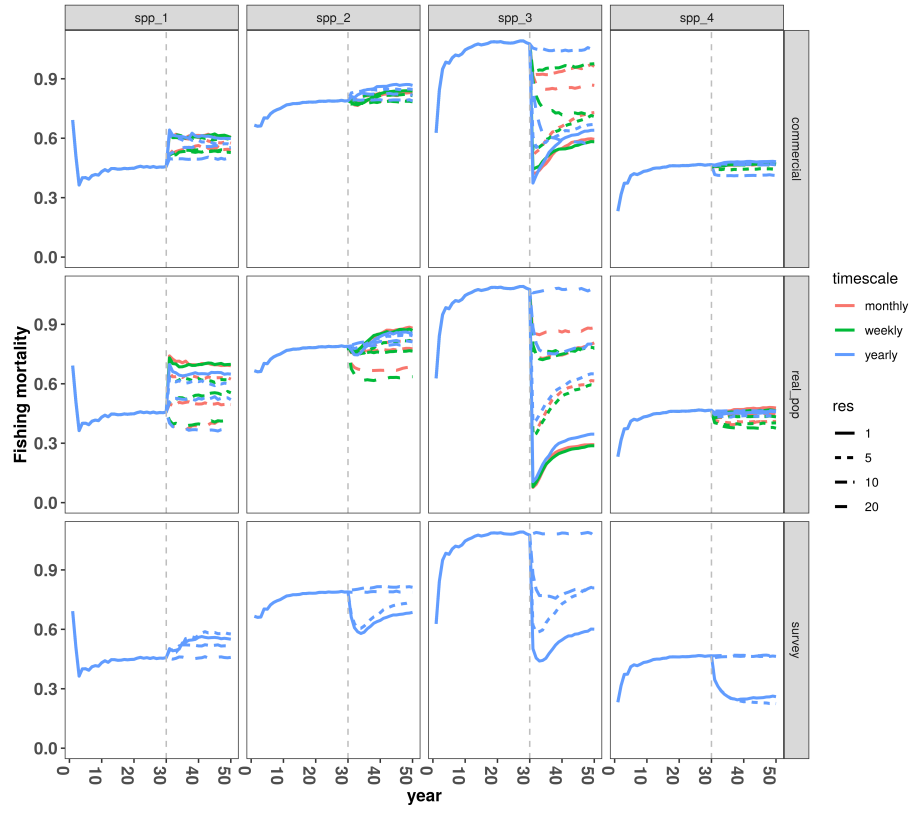


Figure 4: Comparison of closure scenarios effect on fishing mortality trends. Line colour denotes the timescale, while linestyle denotes the spatial resolution.

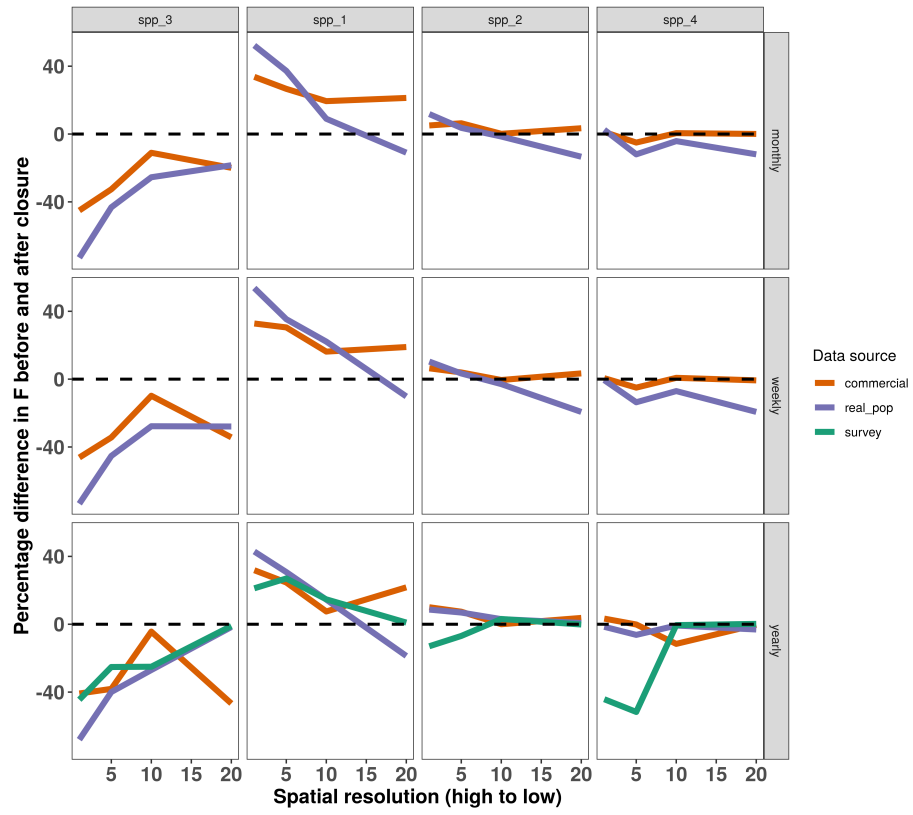


Figure 5: Comparison of closure scenario effectiveness based on different spatial and temporal resolutions.

References

- Akima, H., 2006. Interpolation of irregularly spaced data, The akima Package. Interpolation of Irregularly and Regularly Spaced Data .
- Alverson, D.L., Freeberg, M.H., Murawski, S.A., Pope, J., 1994. A global assessment of fisheries bycatch and discards.
- Bailey, R.M., Carrella, E., Axtell, R., Burgess, M.G., Cabral, R.B., Drexler, M., Dorsett, C., Madsen, J.K., Merkl, A., Saul, S., 2018. A computational approach to managing coupled human–environmental systems: the POSEIDON model of ocean fisheries.
- Bartumeus, F., Da Luz, M.G.E., Viswanatham, G.M., Catalan, J., 2005. Animal Search Strategies: A Quantitative Random Walk Analysis. Ecological Society of America 86, 3078–3087.
- Bastardie, F., Nielsen, J.R., Ulrich, C., Egekvist, J., Degel, H., 2010. Detailed mapping of fishing effort and landings by coupling fishing logbooks with satellite-recorded vessel geo-location. Fisheries Research 106, 41–53.
- Batsleer, J., Hamon, K.G., Overzee, H.M.J., Rijnsdorp, A.D., Poos, J.J., 2015. High-grading and over-quota discarding in mixed fisheries. Reviews in Fish Biology and Fisheries 25, 715–736.
- Bellido, J.M., Santos, M.B., Pennino, M.G., Valeiras, X., Pierce, G.J., 2011. Fishery discards and bycatch: Solutions for an ecosystem approach to fisheries management? Hydrobiologia 670, 317–333.
- Bertrand, S., Bertrand, A., Guevara-Carrasco, R., Gerlotto, F., 2007. Scale-invariant movements of fishermen: The same foraging strategy as natural predators. Ecological Applications 17, 331–337.
- Beverton, R.J., Holt, S.J., 1957. On the Dynamics of Exploited Fish Populations , 533.
- Catchpole, T.L., Revall, A.S., 2008. Gear technology in Nephrops trawl fisheries. Reviews in Fish Biology and Fisheries 18, 17–31.
- Codling, E.A., Plank, M.J., Benhamou, S., Interface, J.R.S., 2008. Random walk models in biology. Journal of the Royal Society, Interface / the Royal Society 5, 813–34.
- Cosgrove, R., Browne, D., Minto, C., Tyndall, P., Oliver, M., Montgomerie, M., McHugh, M., 2019. A game of two halves: Bycatch reduction in Nephrops mixed fisheries. Fisheries Research 210, 31–40.

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

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

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

657 Deriso, R.B., 1980. Harvesting Strategies and Parameter Estimation for an Age-Structured
658 Model. *Canadian Journal of Fisheries and Aquatic Sciences* 37, 268–282. [arXiv:1410.7455v3](#).
659

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

703 Holmes, S.J., Bailey, N., Campbell, N., Catarino, R., Barratt, K., Gibb, A., Fernandes, P.G.,
704 2011. Using fishery-dependent data to inform the development and operation of a co-
705 management initiative to reduce cod mortality and cut discards. *ICES Journal of Marine*
706 *Science* 68, 1679–1688.

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

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

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

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

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

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

722 Mahévas, S., Pelletier, D., 2004. ISIS-Fish, a generic and spatially explicit simulation tool for
723 evaluating the impact of management measures on fisheries dynamics. *Ecological Modelling*
724 .

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

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

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

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

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

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

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

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

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

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

750 Ricker, W.E., 1954. Stock and recruitment. *Journal of the Fisheries Research Board of Canada*
751 11, 559 – 623.

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

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

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

759 Robinson, L.M., Elith, J., Hobday, A.J., Pearson, R.G., Kendall, B.E., Possingham, H.P.,
760 Richardson, a.J., 2011. Pushing the limits in marine species distribution modelling: Lessons
761 from the land present challenges and opportunities. *Global Ecology and Biogeography* 20,
762 789–802.

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

765 Schlater, M., Malinowski, A., Menck, P.J., 2015. Analysis, Simulation and Prediction of
766 Multivariate Random Fields with Package RandomFields. *Journal of Statistical Software*
767 63, 1–25. [arXiv:1501.0228](https://arxiv.org/abs/1501.0228).

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

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

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

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

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

781 Stock, B.C., Ward, E.J., Eguchi, T., Jannot, J.E., Thorson, J.T., Feist, B.E., Semmens, B.X.,
782 2019. Comparing predictions of fisheries bycatch using multiple spatiotemporal species
783 distribution model frameworks. *Canadian Journal of Fisheries and Aquatic Sciences* .

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

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

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

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

794 Viswanathan, G.M., Buldyrev, S.V., Havlin, S., Da Luz, M.G.E., Raposo, E.P., Stanley, H.E.,
795 1999. Optimizing the success of random searches. *Nature* 401, 911–914.

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

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

800 Xu, B., Zhang, C., Xue, Y., Ren, Y., Chen, Y., 2015. Optimization of sampling effort for a
801 fishery-independent survey with multiple goals. *Environmental Monitoring and Assessment*
802 .