

# Highly resolved spatiotemporal simulations for exploring mixed fishery dynamics

Paul J. Dolder<sup>a,b,\*</sup>, C  il  n Minto<sup>a</sup>, Jean-Marc Guarini<sup>c</sup>, Jan Jaap Poos<sup>d,e</sup>

<sup>a</sup>*Marine and Freshwater Research Centre, Galway-Mayo Institute of Technology (GMIT), Dublin Road, Galway, Ireland*

<sup>b</sup>*Centre for Environment, Fisheries and Aquaculture Science (Cefas), Pakefield Road, Lowestoft, UK*

<sup>c</sup>*Sorbonne Universit  , Faculty of Sciences, 4 Place Jussieu, 75005 Paris, France*

<sup>d</sup>*Wageningen Marine Research, Haringkade 1 1976 CP IJmuiden, Netherlands*

<sup>e</sup>*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 discrete-event simulation model *MixFishSim* incorporating: i) delay-difference population dynamics, ii) population movement using Gaussian Random Fields to simulate patchy, heterogeneously distributed and moving fish populations, and iii) fishery dynamics for multiple fleet characteristics based on population targeting under an explore-exploit strategy.

We applied *MixFishSim* to infer community structure when using data generated from: commercial catch, a fixed-site sampling survey design and the true (simulated) underlying populations. In doing so we thereby establish the potential limitations of fishery-dependent data in providing a robust characterisation of spatiotemporal distributions. Different spatial patterns were evident and the effectiveness of the spatial closure reduced when data were aggregated across larger spatial areas. A simulated area closure showed that aggregation across time periods has less of a negative impact on the closure success than aggregation over space. While not as effective as when based on the true population, closures based on high catch rates observed in commercial data were still able to reduce fishing on a protected species.

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 resolutions. From our application we conclude that com-

---

\*Corresponding author

Email addresses: paul.dolder@cefas.co.uk (Paul J. Dolder), coilin.minto@gmit.ie (C  il  n Minto), jean-marc.guarini@upmc.fr (Jean-Marc Guarini), janjaap.poos@wur.nl (Jan Jaap Poos)

mercial data, while containing bias, provide a useful tool for managing catches in mixed fisheries if applied at the correct spatiotemporal scale.

*Keywords:* spatiotemporal, mixed fisheries, individual based, spatial management, heterogeneity, bycatch avoidance  
*2010 MSC:* 00-01, 99-00

---

## 1. Introduction

Fishers exploit a variety of fish populations that are heterogeneously distributed in space and time. Fishers generally only have partial knowledge of species distributions and so limited control over what species they select when fishing in ‘mixed fisheries’. This results in catches of vulnerable species and species with low-quota. These species may be thrown overboard in a process called discarding and discarding catches that are not recorded leads to biased perception of the effects of fisheries on ecosystems. Ultimately the unaccounted discards limit our ability to control fishing mortality (Alverson et al., 1994; Crowder et al., 1998; Rijnsdorp et al., 2007) and the ability to manage biological and economic sustainability of fisheries (Ulrich et al., 2011; Batsleer et al., 2015).

There is increasing interest in technical solutions such as gear adaptations and spatial closures as measures to reduce discarding of unwanted catches (Kennelly and Broadhurst, 2002; Catchpole and Revill, 2008; Bellido et al., 2011; Cosgrove et al., 2019). Adaptive spatial management strategies have been proposed as a way of reducing over-quota discards (Holmes et al., 2011; Little et al., 2015; Dunn et al., 2014). However, to reduce unwanted catch through spatial measures requires an in-depth understanding of the spatiotemporal dynamics of the fishery.

Effective spatial management requires implementation at appropriate spatial scales. These spatial scales shape the trade-offs between protection of populations and economic impacts on fisheries (Dunn et al., 2016). In mixed fisheries, the problem is to identify a scale that promotes species avoidance for vulnerable or low-quota species while allowing continuance of sustainable fisheries for available quota species. Identifying the appropriate spatial scale remains challenging because collecting data on fish distribution at high temporal and spatial resolutions is expensive and difficult. Proxies for the spatial distributions are usually inferred from fisheries-dependent data or from fisheries-independent data. Fisheries-dependent data includes all data on catch and effort from commercial fishing operations while fisheries-independent data includes data collected on board scientific research vessels.

Inferences on fish distributions are hampered where spatial and temporal information is coarse. Sampling designs for scientific research vessel surveys

generally aim for unbiased estimates of local abundance. However, high costs of these surveys generally results in restrictions in terms the number of samples. As a result, sampling is usually restricted to a few weeks a year, and sampling stations are usually coarsely spaced. Moreover, the gear chosen for the survey determines the selectivity for certain species and size classes within fish communities. This selectivity determines the usefulness of relative occurrence in survey catches as proxies for abundances in the fish communities.

Proxies for spatial distribution derived from commercial fisheries in theory allow for much larger sample sizes. These commercial fisheries are often at sea throughout the year, making many fishing hauls. However, spatial information from fisheries is often limited because data on catch and effort is collected or aggregated across larger gridded areas (Branch et al., 2005). If spatially aggregated data does not allow identification of spatial features it may lead to poorly designed spatial management measures that are ineffectual or have unintended consequences (Costello et al., 2010; Dunn et al., 2016). For example, increased benthic impact on previously unexploited areas from the cod closure in the North Sea were observed without the intended effect of reducing cod exploitation (Rijnsdorp et al., 2001; Dinmore et al., 2003).

Even where high-resolution spatiotemporal information is available (see e.g. Lee et al., 2010; Bastardie et al., 2010; Gerritsen et al., 2012; Mateo et al., 2017) commercial catch per unit of effort may still be biased because of fisheries dynamics. Fishers establish favoured fishing grounds through an explore-exploit strategy (Rijnsdorp et al., 2011; Bailey et al., 2019) where they search for areas with high catches and then use experience to return to areas where they have experienced high catch in the past. This leads to inherently biased sampling where target species are over-represented in the catch because fishers exploit areas of high abundance. For effective adaptive spatial management the effects of spatiotemporal aggregation in data and fishery targeting need to be understood.

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

1. Do different sources of sampling-derived fisheries data reflect the underlying community structure?
2. How do data aggregation and data source impact on the success of spatial fisheries management measures?

To answer these questions we i) develop a simulation model where population dynamics are highly-resolved in space and time, using a Gaussian spatial process to define suitable habitat for different populations. As the precise locations of the fish are known directly rather than inferred from sampling or commercial catch, we can use the population model to validate how inference

82 from fisheries-dependent and fisheries-independent sampling relates to the real  
 83 community structure in a way we could not with real data. We ii) compare, at  
 84 different spatial and temporal aggregations, the real (simulated) population dis-  
 85 tributions to samples from fisheries-dependent and fisheries-independent catches  
 86 to test if these are a true reflection of the relative density of the populations.  
 87 We then iii) simulate a fishery closure to protect a species based on different  
 88 spatial and temporal data aggregations.

89  
 90 We use these evaluations to draw inference on the utility of commercial data  
 91 in supporting management decisions.

## 92 2. Materials and Methods

93 A Discrete-event simulation (DES) model of a hypothetical fishery was de-  
 94 veloped as a software package (*MixFishSim*). The modular approach enabled  
 95 efficient computation by allowing for sub-modules implemented on time-scales  
 96 appropriate to capture the characteristics of the different processes (Figure 6).  
 97 Sub-modules to capture the full system comprised: 1) population dynamics, 2)  
 98 recruitment dynamics, 3) population movement, 4) fishery dynamics.

99  
 100 Population dynamics for any number of species, as chosen by the user, oper-  
 101 ate on a daily time-step (with recruitment occurring only during defined seasons  
 102 for each population), while population movement occurs on a weekly time-step,  
 103 with the fishing module operating on a tow-by-tow basis (i.e., multiple events a  
 104 day).

### 106 2.1. Population dynamics

107 The basic population level processes were simulated using a modified two-  
 108 stage Deriso-Schnute delay difference model that models the fish populations in  
 109 terms of aggregate biomass of recruits and mature components rather than keep-  
 110 ing track of individuals (Deriso, 1980; Schnute, 1985; Dichmont et al., 2003). A  
 111 daily time-step was chosen to discretise continuous population processes on a bi-  
 112 ologically relevant and computationally tractable timescale. Population biomass  
 113 growth was modelled as a function of previous recruited biomass, intrinsic pop-  
 114 ulation growth and recruitment functionally linked to the adult population size.  
 115 Biomass for each cell  $c$  was incremented each day  $d$  as follows (see Table 1 for  
 116 all parameter details):

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

117 where  $\rho$  is Ford's growth coefficient shown to be equal to  $e^{-K}$  when  $K$  is the  
 118 Brody growth coefficient, the rate at which the asymptote is approached from a  
 119 von Bertalanffy growth model (Schnute, 1985).  $W_{R-1}$  is the average weight of  
 120 fish prior to recruitment, while  $W_R$  is the average recruited weight.  $\alpha_d$  repre-  
 121 sents the proportion of fish recruited during that day for the year, while  $R_{c,\tilde{y}(c)}$   
 122 is the annual recruits in year  $y$  for cell  $c$ .

123  
 124 Mortality  $Z_{c,d}$  can be decomposed to natural mortality,  $M_{c,d}$ , and fishing  
 125 mortality,  $F_{c,d}$ , where both  $M_{c,d}$  and  $F_{c,d}$  are instantaneous rates with  $M_{c,d}$   
 126 fixed and  $F_{c,d}$  calculated by solving the Baranov catch equation (Hilborn and  
 127 Walters, 1992) for  $F_{c,d}$ :

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

128 where  $C_{c,d}$  is the summed catch from the fishing model across all fleets and  
 129 vessels in cell  $c$  for the population during the day  $d$ , and  $B_{c,d}$  the daily biomass  
 130 for the population in the cell. Here, catch is the sum of those across all fleets  
 131 and vessels,  $C_{c,d} = \sum_{fl=1}^{FL} \sum_{v=1}^{V_{fl}} E_{fl,v,c,d} \cdot Q_{fl} \cdot D_{c,d}$  with  $fl$  and  $FL$  the fleet and  
 132 total number of fleets,  $v$  and  $V_{fl}$  the vessel and total number of vessels per fleet  
 133 respectively and  $E_{fl,v,c,d}$  and  $Q_{fl}$  fishing effort and catchability of the gear, and  
 134  $D_{c,d}$  is the density of the population at the location fished.

## 136 2.2. Recruitment dynamics

137 Recruitment is modelled as a function of adult biomass. In *MixFishSim*, it  
 138 can either take the form of a stochastic Beverton-Holt stock recruitment relation-  
 139 ship, or a stochastic Ricker stock recruitment relationship. The Beverton-Holt  
 140 relationship is defined as (Beverton and Holt, 1957):

$$\bar{R}_{c,d} = \frac{(\alpha S_{c,d})}{(\beta + S_{c,d})} \quad (3)$$

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

141 where  $\alpha$  is the maximum recruitment rate,  $\beta$  the spawning stock biomass (SSB)  
 142 required to produce half the maximum stock size,  $S$  current stock size and  $\sigma^2$   
 143 the variability in the recruitment due to stochastic processes. The stochastic  
 144 Ricker form (Ricker, 1954) is:

$$\bar{R}_{c,d} = B_{c,d} \cdot e^{(\alpha - \beta \cdot B_{c,d})} \quad (4)$$

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

145 where  $\alpha$  is the maximum productivity per spawner and  $\beta$  the density-dependent  
 146 reduction in productivity as the SSB increases.

### 147 2.3. Population movement dynamics

148 Population movement is a combination of directed (advective) movement  
 149 where at certain times of year the population moves towards spawning grounds  
 150 by increasing the probabilities of moving into the spawning grounds from adja-  
 151 cent cells, and random (diffusive) movement, governed by a stochastic process  
 152 where movement between adjacent cells is described by a set of probabilities.  
 153 Stochastic probabilities are affected by the suitability of habitat, temperature  
 154 in a cell and the thermal tolerance of a population to that temperature.

155  
 156 The combined process results in a population structure and movement pat-  
 157 tern unique to each population, with population movement occurring on a  
 158 weekly basis. Modelling population movement on a weekly timescale reflects  
 159 that fish tend to aggregate in species-specific locations that have been observed  
 160 to last between one and two weeks (Poos and Rijnsdorp, 2007b). Therefore this  
 161 process approximated the demographic shifts in fish populations throughout a  
 162 year with seasonal spawning patterns (Figure S1).

163  
 164 To simulate fish population distribution in space and time a Gaussian spa-  
 165 tial process was employed to model habitat suitability for each of the popula-  
 166 tions on a 2d grid. We first defined a Gaussian random field process,  $\{S(c) :$   
 167  $c \in \mathbb{R}^2\}$ , where for any set of cells  $c_1, \dots, c_n$ , the joint distribution of  $S =$   
 168  $\{S(c_1), \dots, S(c_n)\}$  is multivariate Gaussian with a *Matérn* covariance structure,  
 169 where the correlation strength weakens with distance controlled by two param-  
 170 eters, with  $\nu$  a scale parameter in the units of distance and  $\kappa$  a shape parameter  
 171 which determines the smoothness of the process. We use the most commonly  
 172 used Matérn covariance structure as it is a flexible form that contains the expo-  
 173 nential and double exponential as special cases and it enables us to model the  
 174 spatial autocorrelation observed in animal populations where density is more  
 175 similar in nearby locations (Tobler, 1970; F. Dormann et al., 2007; Poos and  
 176 Rijnsdorp, 2007b).

177  
 178 We change the parameters to implement different spatial structures for the  
 179 different populations using the *RandomFields* R package (Schlather et al., 2015).  
 180 We define a stationary habitat field with an anisotropic pattern (to simulate a  
 181 depth gradient) and combine it with a temporally dynamic thermal tolerance  
 182 field to imitate two key drivers of population dynamics without modelling the  
 183 processes explicitly. Each population was initialised at a single location, and  
 184 subsequently moved across the entire space according to a probabilistic distri-  
 185 bution based on habitat suitability (represented by the normalised values from  
 186 the GRFs), temperature tolerance and distance from current cell:

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

187 Where  $d_{I,J}$  is the euclidean distance between cell  $I$  and cell  $J$ ,  $\lambda$  is a given rate

188 of decay,  $Hab_{c,p}$  is the index of habitat suitability for cell  $c$  and population  $p$ ,  
 189 with  $Tol_{c,p,wk}$  the temperature tolerance for cell  $c$  by population  $p$  in week  $wk$   
 190 (see below).

191  
 192 During pre-defined weeks of the year the habitat suitability is modified with  
 193 user-defined spawning habitat locations, resulting in each population having  
 194 concentrated areas where spawning takes place. The populations then move to-  
 195 wards these cells in the weeks prior to spawning, resulting in directional move-  
 196 ment towards the spawning grounds.

197  
 198 A time-varying temperature covariate changes the interaction between time  
 199 and suitable habitat on a weekly time-step. Each population  $p$  was assigned a  
 200 thermal tolerance with mean,  $\mu_p$  and standard deviation,  $\sigma_p$  so that each cell  
 201 and population temperature tolerance is defined as:

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

202 Where  $Tol_{c,p,wk}$  is the tolerance of population  $p$  for cell  $c$  in week  $wk$ ,  $T_{c,wk}$  is  
 203 the temperature in the cell given the week and  $\mu_p$  and  $\sigma_p$  the mean and stan-  
 204 dard deviation of the population temperature tolerance (see Table 2 for variable  
 205 descriptions).

## 207 2.4. Fleet dynamics

208 Fleet dynamics were broadly categorised into three components. *Fleet tar-*  
 209 *geting* determined the fleet catch efficiency and preference towards a particular  
 210 population; *trip-level decisions* determined the initial location to be fished at  
 211 the beginning of a trip; and *within-trip decisions* determined fishing locations  
 212 within a trip. This results in an explore-exploit strategy for individual vessels  
 213 to maximise their catch from an unknown resource distribution (Bailey et al.,  
 214 2019). The decision to use an individual based model for fishing vessels was  
 215 taken because fishers are heterogeneous in their location choice behaviour due  
 216 to different objectives, risk preference and targeting preference (Van Putten  
 217 et al., 2012; Boonstra and Hentati-Sundberg, 2016). Therefore fleet dynamics  
 218 are emergent from individual dynamics rather than pre-defined group dynamics.

### 219 2.4.1. Fleet targeting

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

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

Several studies (for a review see Girardin et al., 2017) have confirmed past activity and past catch rates are strong predictors of fishing location choice. For this reason, the fleet dynamics sub-model included a learning component, where a vessel’s initial fishing location in a trip was based on selecting from previously successful fishing locations. This was achieved by calculating an 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 70 % of fishing events (defined as the ‘threshold’) in terms of expected profit within that season.

#### 2.4.3. Decision about where to fish within a 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,  $Rev$ );

$$Rev_{c,d} = \sum_{p=1}^P L_{c,d,p} \cdot Pr_p \quad (7)$$

where  $L_{c,d,p}$  is landings of a population  $p$ , and  $Pr_p$  price of a population. All population 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 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:

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



Where  $\beta_1$ ,  $\beta_2$  and  $\beta_3$  are parameters determining the shape of the step function in its relation to revenue, so that, a step from  $(x_t, y_t)$  to  $(x_{t+1}, y_{t+1})$  is defined by:

$$\begin{aligned} (x_{t+1}, y_{t+1}) &= x_t + Le \cdot \cos\left(\frac{\pi \cdot Br_{t+1}}{180}\right), \\ y_t &+ Le \cdot \sin\left(\frac{\pi \cdot Br_{t+1}}{180}\right) \end{aligned} \quad (9)$$

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

where  $Le$  is the step length,  $Br_t$  is the bearing at time  $t$ ,  $k$  the concentration parameter from the von Mises distribution that we correlate with the revenue so that  $k = (Rev + 1/RefRev) \cdot max_k$ , where  $max_k$  is the maximum concentration value,  $k$ , and  $RefRev$  is parametrised as for  $\beta_3$  in the step length function. Details of the variables, meaning and units for fleet dynamics are provided in Table 3.

#### 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). 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.

#### 2.5. Fisheries-independent survey

A fisheries-independent survey is simulated where fishing on a regular grid begins each year at the same time for a given number of stations (a fixed station survey design). Catches of the populations at each station are recorded but not removed from the population (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](https://www.github.com/pdolder/MixFishSim)).

### 3. Model calibration

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

#### 3.1. Population models

We calibrated the simulation model for four example populations with different demographics, growth rates, natural mortality and recruitment (Table 4). Habitat preference (Figure S7) and temperature (Figures S9, with temperature tolerance S10) defined to be unique to each population resulting in differently weekly distribution patterns (Figures S1-S3). 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 S8) with population-specific movement rates (Table 4). The population demographics were chosen to broadly represent three mobile low-medium value groundfish species and one high value species with low mobility, with the dynamics hypothetical but might be expected in a typical demersal fishery.

#### 3.2. Fleet calibration

Fleets were calibrated to reflect five different characteristic fisheries with unique exploitation dynamics (Table 5). By setting different catchability coefficients ( $Q_{fl,p}$ ) we create different targeting preferences between the fleets and hence different 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 calibrated 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 slope 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 parameter ( $Q_p = 1$ ) for all populations. This approximates a real world survey design with limited seasonal and spatial coverage.

342 *3.4. Example research question*

343 To illustrate the capabilities of *MixFishSim*, we investigate the influence of  
344 the temporal and spatial resolution of different data sources on the reduction in  
345 catches of a population given spatial closures. To do so, we set up a simulation  
346 to run for 50 years based on a  $100 \times 100$  square grid (undetermined units), with  
347 five fleets of 20 vessels each and four fish populations. Fishing takes place four  
348 times a day per vessel and five days a week, while population movement is every  
349 week.

350  
351 *How does sampling-derived fisheries data reflect the underlying population*  
352 *structure?*

353  
354 To answer this question we compare different spatial and temporal aggrega-  
355 tions of the true population distributions to:

- 356 a) **fisheries-independent data:** the inferred population density from a  
357 fixed-site sampling survey design as commonly used for fisheries monitor-  
358 ing purposes;
- 359 b) **fisheries-dependent data:** the inferred population density from our  
360 fleet model that includes fishery-induced sampling dynamics.

361 We allow the simulation to run unrestricted for 30 years, then implement  
362 spatial closed areas for the last 20 years of the simulation based on data (either  
363 derived from the commercial catches, fisheries-independent survey or the true  
364 population) used at different spatial and temporal scales.

365  
366 The following steps are undertaken to determine closures:

- 367 1. Extract data source (true population, commercial or survey),  
368 2. Aggregate according to desired spatial and temporal resolution,  
369 3. Interpolate across entire area at desired resolution using simple bivariate  
370 interpolation using the *interp* function from the R package *akima* (Akima  
371 and Gebhardt, 2016). This is intended to represent a naive spatial model  
372 of catch rates, without knowledge of the spatial population dynamics.
- 373 4. Close area covering top 5 % of catch rates.

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

- 375 • **data types:** commercial logbook data, survey data and true population,  
376 • **temporal resolutions:** weekly, monthly and yearly closures,  
377 • **spatial resolutions:** 1 x 1 grid, 5 x 5 grid, 10 x 10 grid and 20 x 20 grid,

378 We implemented a series of spatial closures targeted at reducing fishing mor-  
 379 tality on population 3, given the different data sources and spatial and temporal  
 380 resolutions above. We use the effectiveness of these closures in reducing fishing  
 381 mortality as a way of evaluating the trade-offs in data sources and resolution.  
 382 Survey closures were on an annual basis only, as this was the most temporally  
 383 resolved survey data available. We evaluated the factors contributing to the suc-  
 384 cess of the closures through a regression tree (using the R package REEMtree  
 385 (Sela and Simonoff, 2011)) to identify the factor most contributing to differences  
 386 in fishing mortality before and after the closure.

## 387 4. Results

### 388 4.1. Emergent simulation dynamics

389 Individual habitat preferences and thermal tolerances result in different spa-  
 390 tial habitat use for each population (Figure S5) and consequently different sea-  
 391 sonal exploitation patterns (Figure S6).

392 It can be seen from a single vessels movements during a trip that the ves-  
 393 sel exploits three different fishing grounds, each of them multiple times (Figure  
 394 2A), while across several trips fishing grounds that are further apart are fished  
 395 (Figure 2B). These different locations relate to areas where the highest revenue  
 396 were experienced, as shown by Figure 2D, where several vessels tracks are over-  
 397 laid on the revenue field.

398  
 399 Vessels from the same fleet (and therefore targeting preference) may exploit  
 400 some shared and some different fishing grounds depending on their own personal  
 401 experience during the exploratory phase of the fishery (Figure 2 (C)). This  
 402 results from the randomness in the correlated random walk step function, with  
 403 distance moved during the exploitation phase and the direction stochastically  
 404 related to the revenue experienced on the fishing ground (Figure 2 (D)).

### 405 4.2. How does sampling-derived fisheries data reflect the underlying population 406 structure?

407 Catch composition aggregated at different spatial resolutions from each of  
 408 the data sources (average seasonal patterns over a ten-year period) highlights dif-  
 409 ferent patterns in perceived community structure depending on the data source  
 410 and aggregation level (Figure 3). The finer spatial grid for the true popula-  
 411 tion (top left) and commercial data (top middle) show visually similar patterns,  
 412 though there are large unsampled areas in the commercial data from a lack  
 413 of fishing activity (particularly in the lower left part of the sampling domain).  
 414 Survey data at this spatial resolution displays very sparse information about  
 415 the spatial distributions of the populations. The slightly aggregated data on a  
 416 5 x 5 grid shows similar patterns and, while losing some of the spatial detail,  
 417 there remains good consistency between the true population and the commercial  
 418 data. Survey data starts to pick out some of the similar patterns as the other  
 419 data sources, but lacks spatiotemporal coverage. The spatial catch information

on a 10 x 10 and 20 x 20 grid lose a significant amount of information about the spatial resolutions for all data sources, and some differences between the survey, commercial and true population data emerge.

Different perceptions of the proportion of each stock in an area are seen when we aggregate the data at different timescales, with weekly (top), monthly (middle) and yearly (bottom) catch compositions from across an aggregated 20 x 20 area showing different patterns (Figure 4). In the true population, the monthly aggregation captures the major patterns of composition seen in the weekly data with the percentage of different populations in the catch having similar mean and standard deviations (Table 7). In the weekly and monthly data population 2 dominates. However, some of the variation was lost when aggregated to an annual level, as indicated from the lower standard deviations (Table 7).

Weekly commercial data shows some of the same patterns as the true population, though population 1 is less well represented and some weeks are missing catches from the area. Here, weekly and monthly compositions were nearly identical (Figure 4; Table 7). Yearly values had a similar mean but smaller standard deviation. The survey data was only available on an annual basis, and showed again a slightly different composition from the true population and the commercial data; in particular a greater proportion of population 4 (Figure 4).

#### 4.3. *How does data aggregation and source impact on spatial fisheries management measures?*

In most cases the fishery closure was successful in reducing fishing mortality on the species of interest (population 3; Figure 5). Interestingly the largest reductions in fishing mortality happened immediately after the closures, following which the fisheries “adapted” to the closures by finding new areas of high abundance to fish. This led to fishing mortality increasing again, though not to past levels (Figure 5). The exception to the success was the closures implemented based on the coarsest spatial (20 x 20) and temporal resolution (yearly) that was ineffective (i.e. failed to reduce fishing mortality) with all data sources. As expected, closures based on the “known” population distribution were most effective, with differing degrees of success using the commercial data. Fishing mortality rates on the other species changed in different proportions, depending on whether the displaced fishing effort moved to areas where the populations were found in greater or lesser density.

The factor most contributing to differences in fishing mortality before and after the closure was the population (72 % showing that the closures were effective for population 3), followed by spatial data resolution (21 %), data type (7 %) with the least important factor the timescale (< 1 %). In general the finer the spatial resolution of the data used the greater reduction in fishing mortality for population 3 after the closures (Figure 6). The notable outliers are the commercial data at the coarsest spatial resolution (20 x 20) at a yearly and weekly timescale, where closures were nearly as effective as the fine-scale resolution. In

this case the closures were sufficiently large to protect a core area of the habitat for the population, but this was achieved in a fairly crude manner by closing a large area - including area where the species was not found (Figure 7) that may have consequences in terms of restricting the fishery in a much larger area than necessary. We found that these trade-offs existed, with high catches maintained with an effective closure when the highest resolution data was used, with the effect being linear when the true population distribution was known and also persisting for closures based on commercial information (Figure 8).

## 5. Discussion

Our study presents a new highly resolved fisheries simulation framework to evaluate the importance of data scaling and considers potential bias introduced through data aggregation when using fisheries data to infer spatiotemporal dynamics of fish populations. Understanding how fishers exploit multiple heterogeneously distributed fish populations with different catch limits or conservation status requires detailed understanding of the overlap of resources; this is difficult to achieve using conventional modelling approaches due to species targeting in fisheries resulting in preferential sampling (Martínez-Minaya et al., 2018). Often data are aggregated or extrapolated which requires assumptions about the spatial and temporal scale of processes. Our study explores the assumptions behind such aggregation and preferential sampling to identify potential impacts on management advice. With modern management approaches increasingly employing more nuanced spatiotemporal approaches to maximise productivity while taking account of both the biological and human processes operating on different time-frames (Dunn et al., 2016), understanding assumptions behind the data used - increasingly a combination of logbook and positional information from vessel monitoring systems - is vital to ensure measures are effective.

### 5.1. Simulation dynamics

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

Our approach is unique in that it captures fine scale population and fishery dynamics and their interaction in a way not usually possible with real data and thus not usually considered in fisheries simulations. While other simulation frameworks seek to model individual vessel dynamics based on inferred dynamics from VMS and logbook records (Bastardie et al., 2010), or as a system to identify measures to meet particular management goals (Bailey et al., 2019), our framework allows users to explore assumptions in modelling observational

data and to evaluate the underlying dynamics of such approaches at fine spatial and temporal scales. This offers the advantage that larger scale fishery patterns are emergent properties of the system and results can be compared to those obtained under a statistical modelling framework.

Typically, simulation models that treat fish as individuals are focussed on exploring the inter- and intra- specific interactions among fish populations (e.g. OSMOSE; Shin et al. (2004)) in order to understand how they vary over space 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. This shows how realised catch distributions may differ from the underlying populations, as identified by 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 preferences 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 profitable 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., 2019).

## 5.2. *How does sampling-derived fisheries 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 (Figures 2 and S5).

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 even spatial coverage the survey captured some of the same spatial patterns as the true population, but missed others due to gaps between survey stations limiting spatial and temporal coverage (Figure 3). 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 given locations over the course of the year (Figure S5).

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 population 2 - 4, though population 1 remains under-represented. On an annual basis, interestingly the commercial data under represents the first species 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 population 1 are present and the survey sampling areas where population 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 reduce fishing mortality. The likely cost of poor spatial and temporal resolution is associated with reduced effectiveness and potentially closing fishing opportunities for other fisheries (Figure 8).

Two contrasting real world approaches in this respect were the spatial closures 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 substantially (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 of considering fishing effort reallocation following spatial closures, and our simulation allows us to consider the spatiotemporal reasons for these changes.

#### 5.4. Model assumptions and caveats

We modelled 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 necessarily had to make a number of simplifying assumptions.

Fish populations in our simulations move in pre-defined timescales and according to fixed habitat preferences and temperature gradients (Figures S7, S9). Our assumptions in calibrating the model (movement rates, temperature tolerances) will have a direct impact on our conclusions on the relative importance of spatial and temporal processes. These assumptions could be explored in a future study by varying the parameters and assessing the robustness of our conclusions. For our example application we have chosen movement rates to reflect aggregation periods observed in past studies (Poos and Rijnsdorp, 2007b).

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

#### 5.5. Future applications of *MixFishSim*

We consider that the increased availability of high resolution catch and locational information from commercial fisheries will make it a key source of data for ensuring management is implemented at the right scale in future. For example, identifying hot-spots for bycatch reduction or identifying spatial overlaps in mixed fisheries (Dolder et al., 2018; Gardner et al., 2008; Little et al., 2015; Dedman et al., 2015; Ward et al., 2015). Our simulation model has the potential to test some of the assumptions behind the modelling approaches in identifying such hotspots and indeed behind spatiotemporal modelling in general, e.g. comparing GAMs, GLMMs, Random Forests and geostatistical models under different data generation processes as exemplified by Stock et al. (2019).

Other novel applications of our framework could be: testing different survey designs given multiple species and data generating assumptions (Xu et al.,

2015); commercial index standardisation methods and approaches and understanding of appropriate scales and data aggregations and non-proportionality in catch rate and abundance (Harley et al., 2001; Maunder and Punt, 2004); exploring assumptions about the distribution of natural mortality and fishing mortality throughout the year and importance of capturing in-year dynamics in estimating stock status (Liu and Heino, 2014); 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., 2017); 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 greater spatial than temporal heterogeneity. 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 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.

679 **Funding and Acknowledgements**

680       This work was supported by the MARES doctoral training program (MARES\_14\_15)  
681 and the Centre for Environment, Fisheries and Aquaculture Science seedcorn  
682 program (DP227AC). We thank two anonymous reviewers for their helpful com-  
683 ments which greatly improved the final manuscript. The authors declare no  
684 competing interests.

Table 1: Description of variables for population and recruitment dynamics sub-modules.

Variable	Meaning	Units
<b>Population dynamics</b>		
<i>Delay-difference model</i>		
$B_{c,d}$	Biomass in cell $c$ and day $d$	kg
$Z_{c,d}$	Total mortality in cell $c$ for day $d$	-
$R_{c,\tilde{y}}$	Annually recruited fish in cell	yr <sup>-1</sup>
$\rho$	Ford's growth coefficient	yr <sup>-1</sup>
$Wt_R$	Weight of a fully recruited fish	kg
$Wt_{R-1}$	Weight of a pre-recruit fish	kg
$\alpha_d$	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
$F_{c,d}$	Rate of fishing mortality in cell $c$ on day $d$	$d^{-1}$
$M_{c,d}$	Rate of natural mortality in cell $c$ on day $d$	$d^{-1}$
$B_{c,d}$	Biomass in cell $c$ on day $d$	kg
<b>Recruitment dynamics</b>		
$\tilde{R}_{c,d}$	is the number of fish recruited in cell $c$ for day $d$	$d^{-1}$
$\alpha$	the maximum recruitment rate (Beverton Holt) or maximum productivity per spawner (Ricker)	number fish
$\beta$	the stock size required to produce half the maximum rate of recruitment (Beverton Holt) or density dependent reduction in productivity per capita of SSB	number fish

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

Variable	Meaning	Units
<i>Thermal tolerance</i>		
$T_{c,wk}$	Temperature for cell $c$ in week $wk$	°C
$\mu_p$	Mean of the thermal tolerance for population $p$	°C
$\sigma_p$	Standard deviation of thermal tolerance for population $p$	°C
<i>Population movement model</i>		
$\lambda$	Decay rate for population movement	-
$Hab_{c,p}$	Habitat suitability for cell $c$ and population $p$	-
$Tol_{c,wk,p}$	Thermal tolerance for in cell $c$ at week $wk$ for population $p$	-
$d_{I,J}$	Euclidean distance between cell $I$ and cell $J$	-

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

Variable	Meaning	Units
$Rev$	Revenue from fishing tow	€
$RefRev$	Reference revenue for determining the step function	€
$L_p$	Landings of population $p$	kg
$Pr_p$	Average price of population $p$	€/kg <sup>-1</sup>
$Le$	Step length for vessel	-
$Br$	Bearing	degrees
$k$	Concentration parameter for von mises distribution	-
$\beta_1$	shape parameter for step function	-
$\beta_2$	shape parameter for step function	-
$\beta_3$	shape parameter for step function	-

Table 4: Population dynamics and movement parameter settings.

Parameter	Pop 1	Pop 2	Pop 3	Pop 4
Habitat quality				
Matérn $\nu$	1/0.015	1/0.05	1/0.01	1/0.005
Matérn $\kappa$	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				
Movement $\lambda = 0.1$				
Population dynamics				
Starting Biomass	1e5	2e5	1e5	1e4
Beverton-Holt Recruit $\alpha$	6	27	18	0.3
Beverton-Holt Recruit $\beta$	4	4	11	0.5
Beverton-Holt Recruit $\sigma^2$	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
$K = 0.3$				
$wt = 1$				
$wt_{d-1} = 0.1$				
M (annual)	0.2	0.1	0.2	0.1
Movement dynamics				
$\mu_p$	12	15	17	14
$\sigma_p^2$	8	9	7	10

Table 5: Fleet dynamics parameter setting.

Parameter	Fleet 1	Fleet 2	Fleet 3	Fleet 4	Fleet 5
Targeting preferences	pop 2/4	pop 1/3	-	pop 4	pop 2/3
Price $Pr_p1 = 100$					
Price $Pr_p2 = 200$					
Price $Pr_p3 = 350$					
Price $Pr_p4 = 600$					
$Q_p$	0.01	0.02	0.02	0.01	0.01
$Q_p$	0.02	0.01	0.02	0.01	0.03
$Q_p$	0.01	0.02	0.02	0.01	0.02
$Q_p$	0.02	0.01	0.02	0.05	0.01
Exploitation dynamics					
$\beta_1$	1	2	1	2	3
$\beta_2$	10	15	8	12	7
$\beta_3$ , the landings value $nth$ quantile	90	90	85	90	80
step function $rate$	20	30	25	35	20
Past Knowledge = TRUE					
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 on population 3 (ordered by most effective first). The fishing mortality rate before the closure was 1.08.

Scenario No	F after closure	% F change	data type	timescale	resolution
9	0.29	-73.47	true Population	weekly	1.00
10	0.29	-72.94	true Population	monthly	1.00
11	0.35	-68.04	true Population	yearly	1.00
45	0.58	-46.70	commercial	yearly	20.00
1	0.58	-46.21	commercial	weekly	1.00
23	0.59	-45.27	true Population	weekly	5.00
2	0.59	-45.06	commercial	monthly	1.00
7	0.60	-44.48	survey	yearly	1.00
24	0.61	-43.20	true Population	monthly	5.00
3	0.64	-40.82	commercial	yearly	1.00
25	0.65	-39.94	true Population	yearly	5.00
17	0.67	-38.11	commercial	yearly	5.00
15	0.71	-34.38	commercial	weekly	5.00
43	0.71	-34.31	commercial	weekly	20.00
16	0.73	-32.58	commercial	monthly	5.00
51	0.78	-27.92	true Population	weekly	20.00
37	0.78	-27.76	true Population	weekly	10.00
39	0.79	-26.98	true Population	yearly	10.00
38	0.81	-25.47	true Population	monthly	10.00
21	0.81	-25.21	survey	yearly	5.00
35	0.81	-25.05	survey	yearly	10.00
44	0.87	-19.91	commercial	monthly	20.00
52	0.88	-18.39	true Population	monthly	20.00
30	0.96	-11.06	commercial	monthly	10.00
29	0.98	-9.80	commercial	weekly	10.00
31	1.03	-4.36	commercial	yearly	10.00
53	1.06	-1.64	true Population	yearly	20.00
49	1.07	-1.01	survey	yearly	20.00

Table 7: Mean and standard deviation of proportions of each species at different levels of temporal aggregation

Data type	Timescale	Population 1	Population 2	Population 3	Population 4
commercial	monthly	0.047(0.014)	94.435(1.47)	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)
True Population	monthly	9.225(3.872)	83.287(5.522)	3.624(1.151)	3.864(1.519)
True Population	weekly	9.358(3.992)	83.165(5.596)	3.567(1.233)	3.91(1.592)
True Population	yearly	9.899(0.173)	82.25(0.308)	3.821(0.119)	4.031(0.05)
survey	yearly	0.372(0.005)	87.667(0.193)	0.729(0.02)	11.232(0.172)



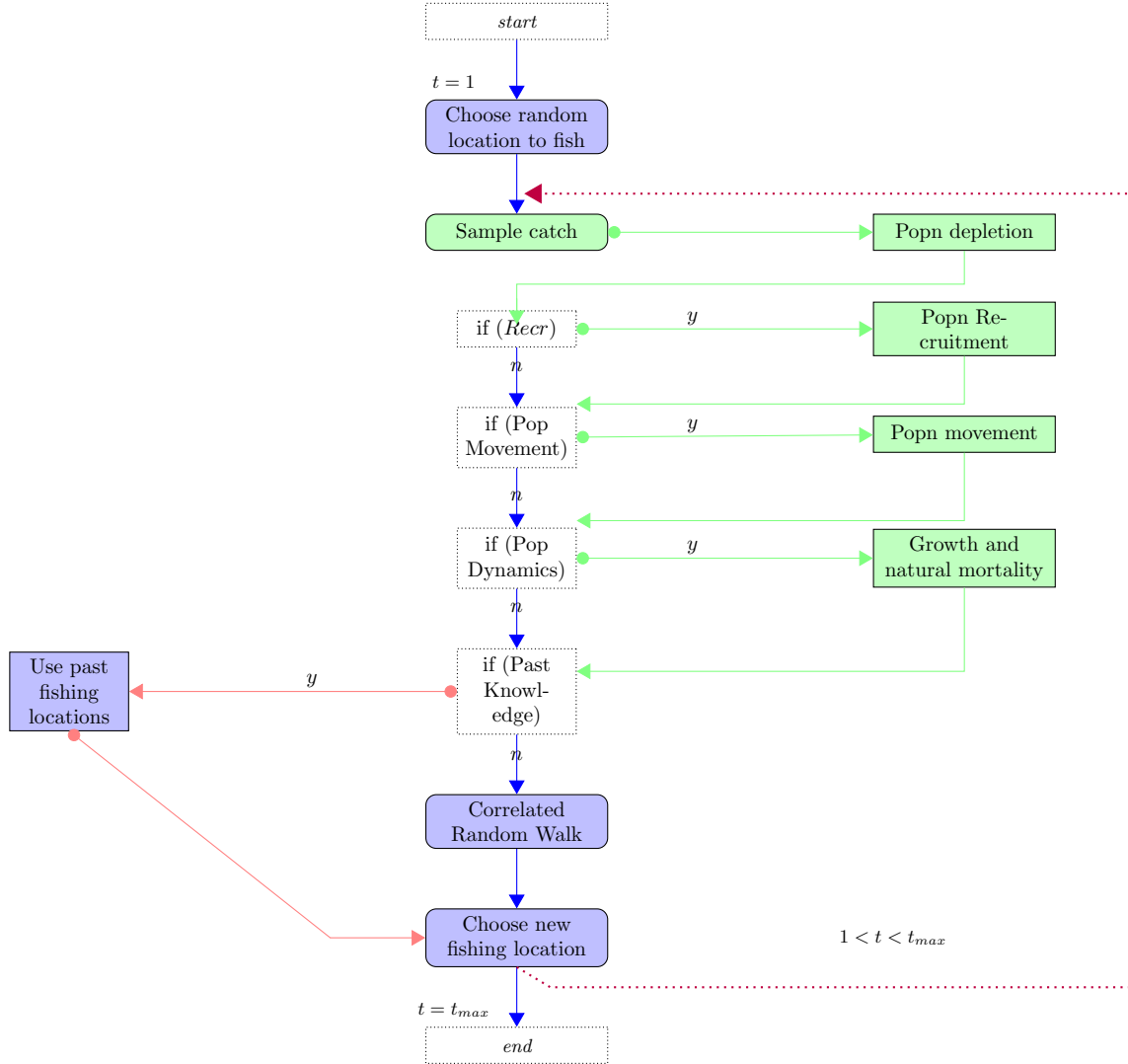


Figure 1: Schematic overview of the simulation model. Blue boxes indicate fleet dynamics processes, the green boxes population dynamics processes while the white boxes are the time steps at which processes occur;  $t = \text{tow}$ ,  $t_{max}$  is the total number of tows; (Recr), (Pop Movement), (Pop 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.

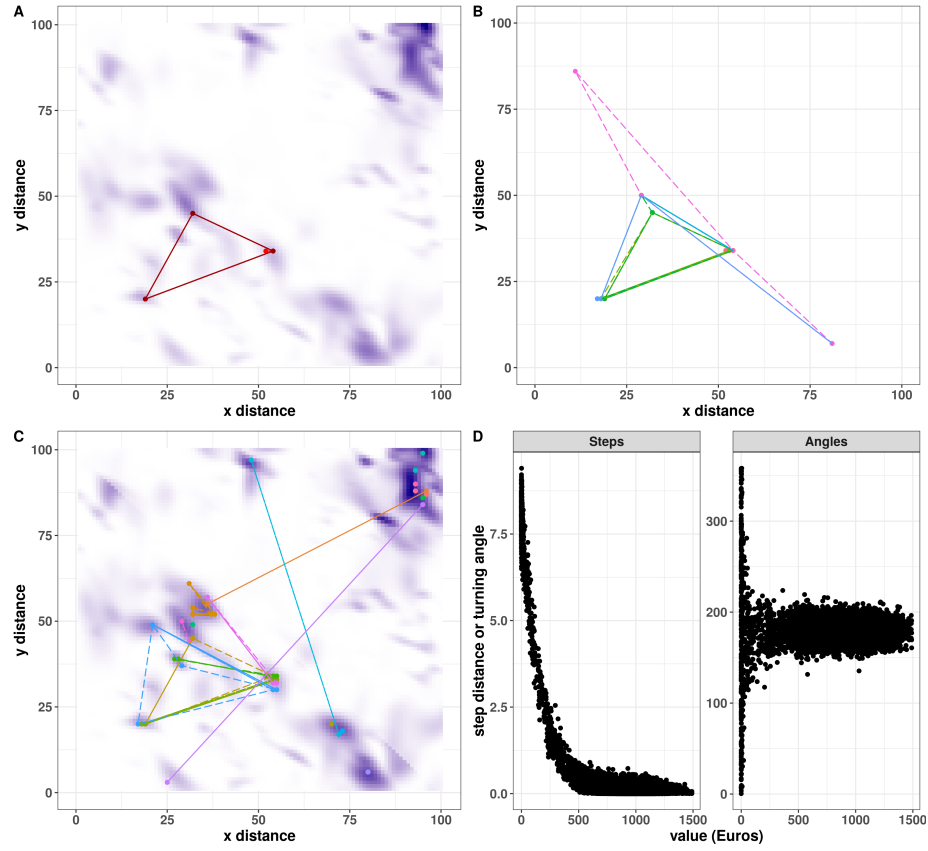


Figure 2: (A) The fishing locations (points) and movements (lines) of a single vessel during a trip overlaid on the revenue of a fishing site (landings  $\times$  price; darker purple = higher revenue); (B) the fishing locations of the vessel over several trips (value field changes over the period so not shown). Note that movements are a mixture of correlated random walk (solid lines) and experience-based (dashed lines), and that the field is wrapped on a torus so that opposite sides of the spatial domain are considered spatially close; (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.

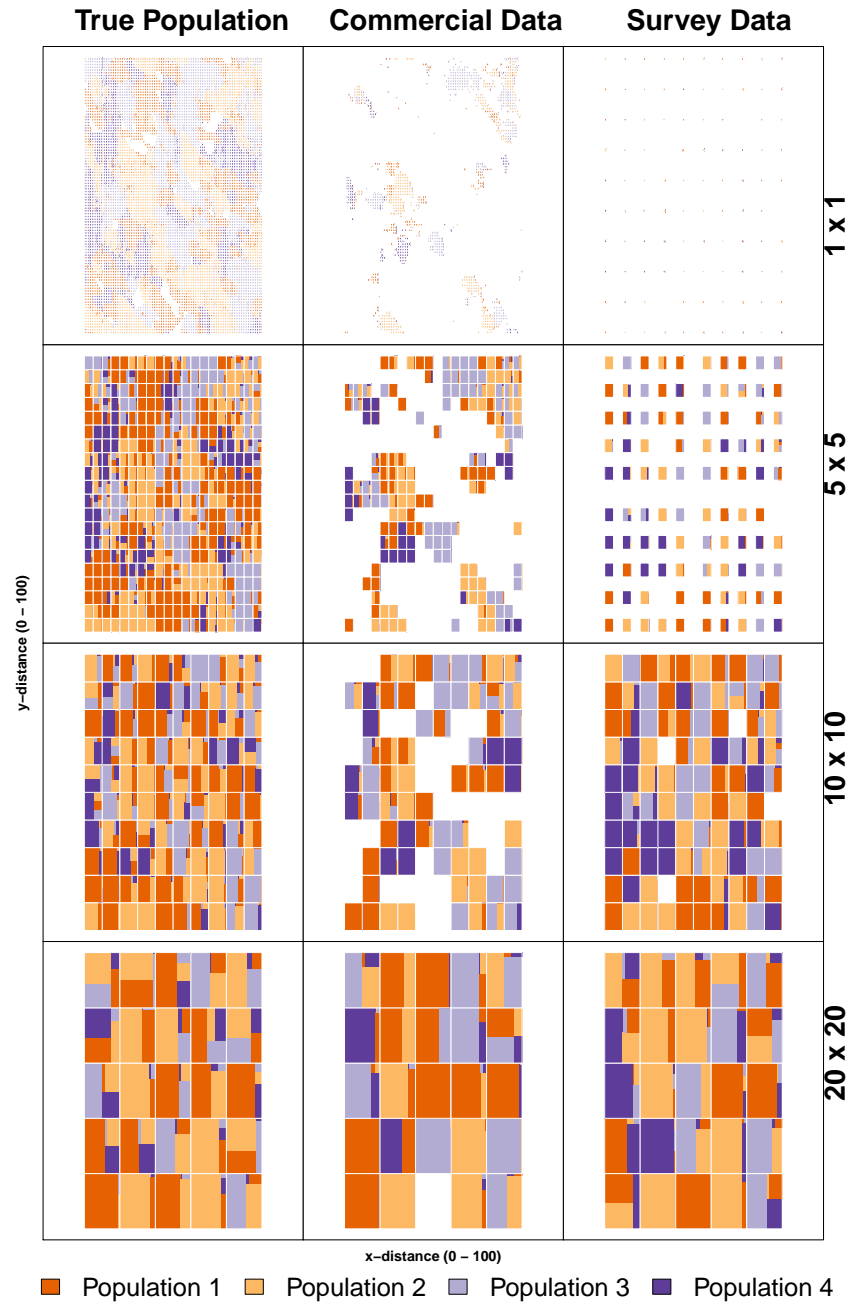


Figure 3: [Colour online] Data aggregation at different spatial resolutions over a ten year period. The figure shows catch composition at each spatial unit represented by a square pie chart of the four populations. The area of each colour is proportional to the weight of each population caught in that unit. Figure produced using the R package ‘mapplots’ (Gerritsen (2014)).

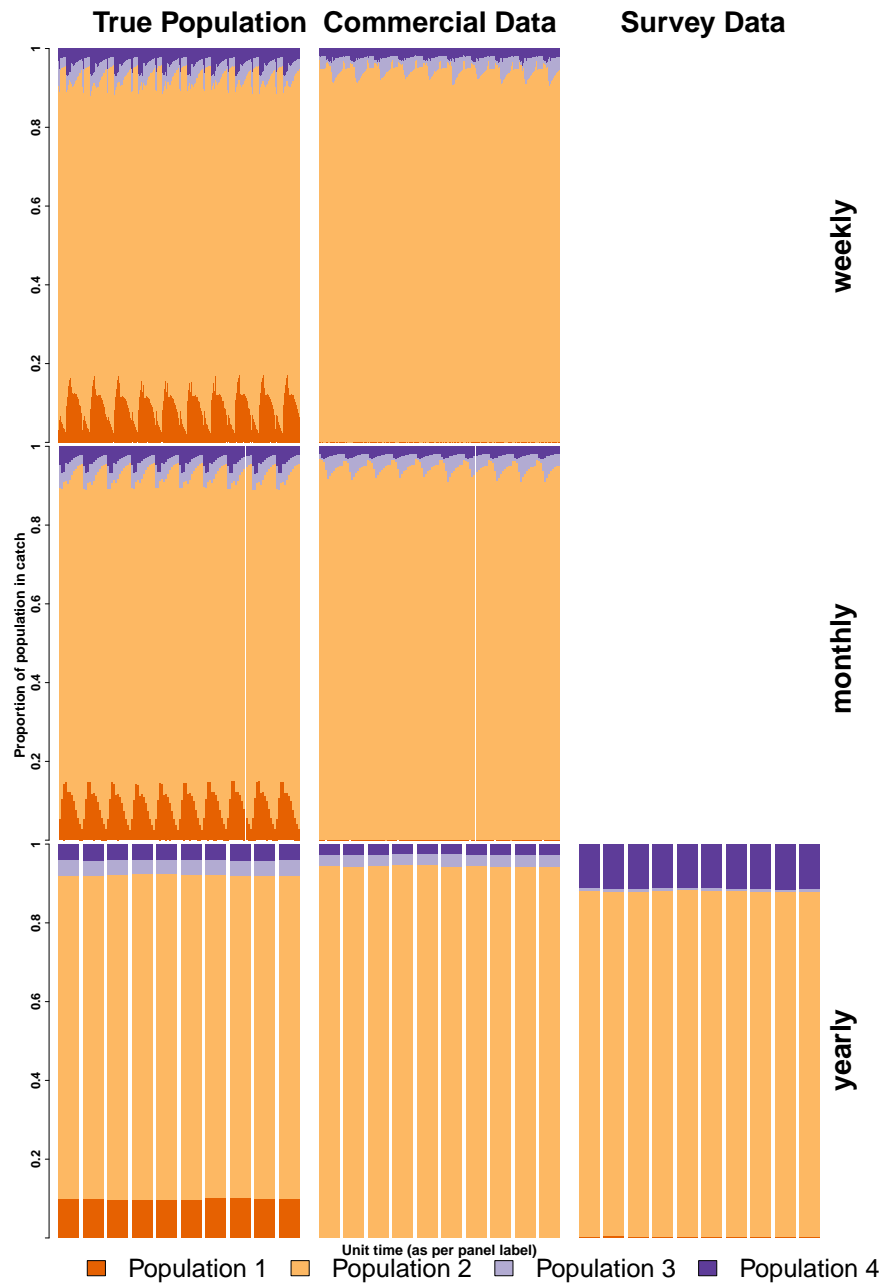


Figure 4: [Colour online] Proportion of each population (y axis) for data aggregated at different temporal resolutions. Data is aggregated over a ten-year period for an area 20 x 20. Each bar represents either a week, month or year respectively.

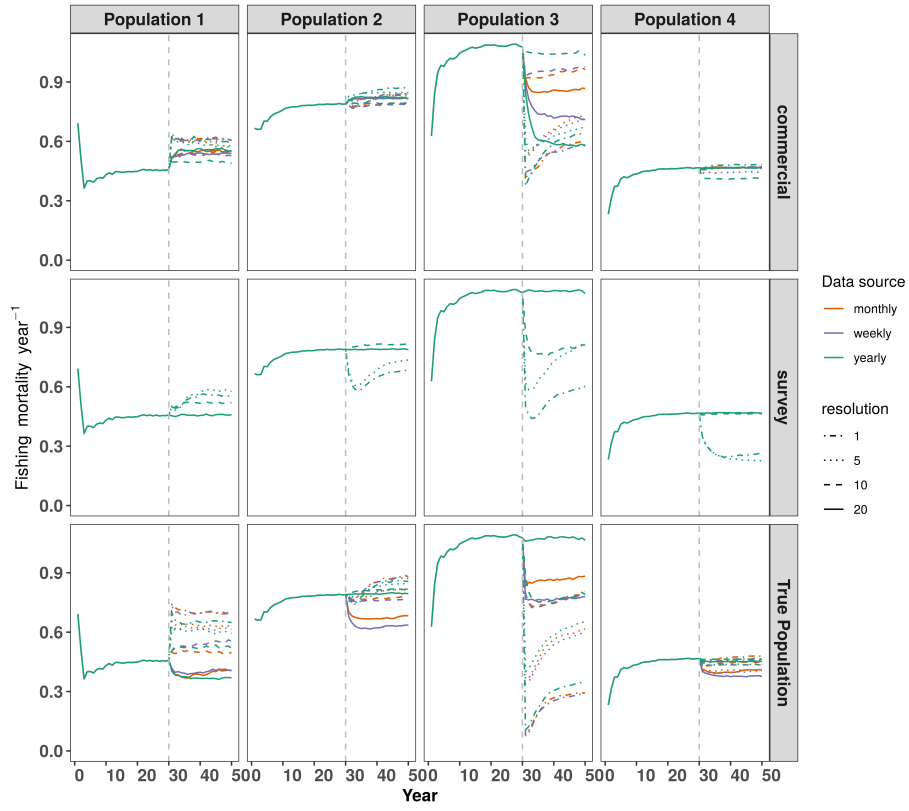


Figure 5: [Colour online] Comparison of closure scenarios effect on fishing mortality trends. Line colour denotes timescale, while linestyle denotes spatial resolution. The vertical dashed line indicates the onset of the spatial closures.

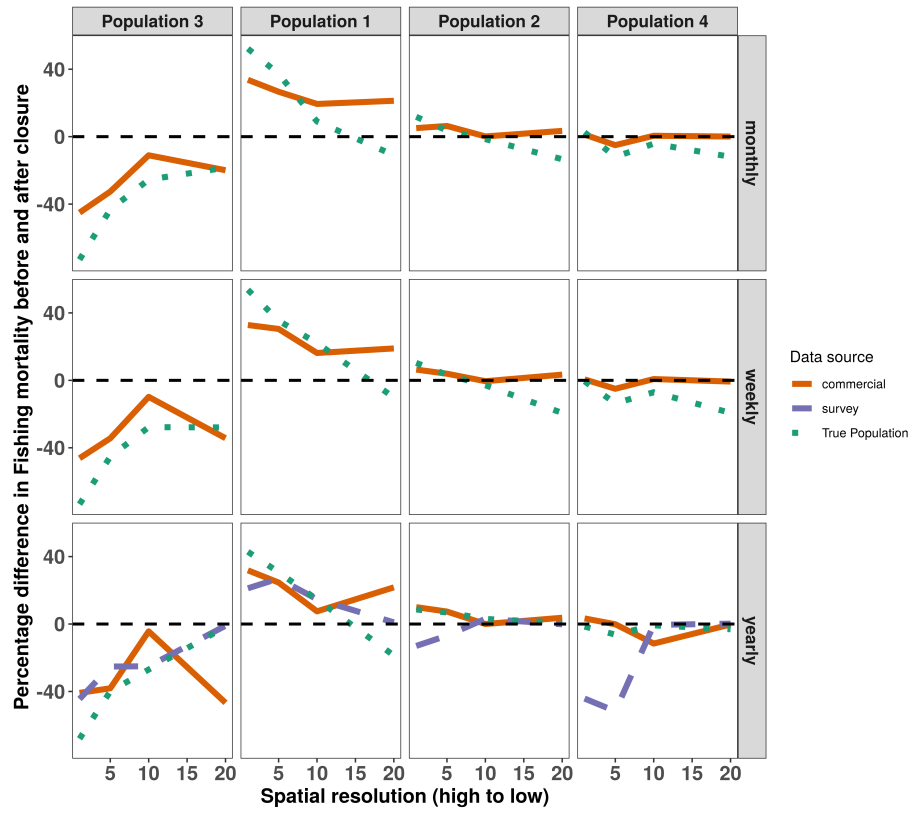


Figure 6: Comparison of closure scenario effectiveness based on different spatial and temporal resolutions.

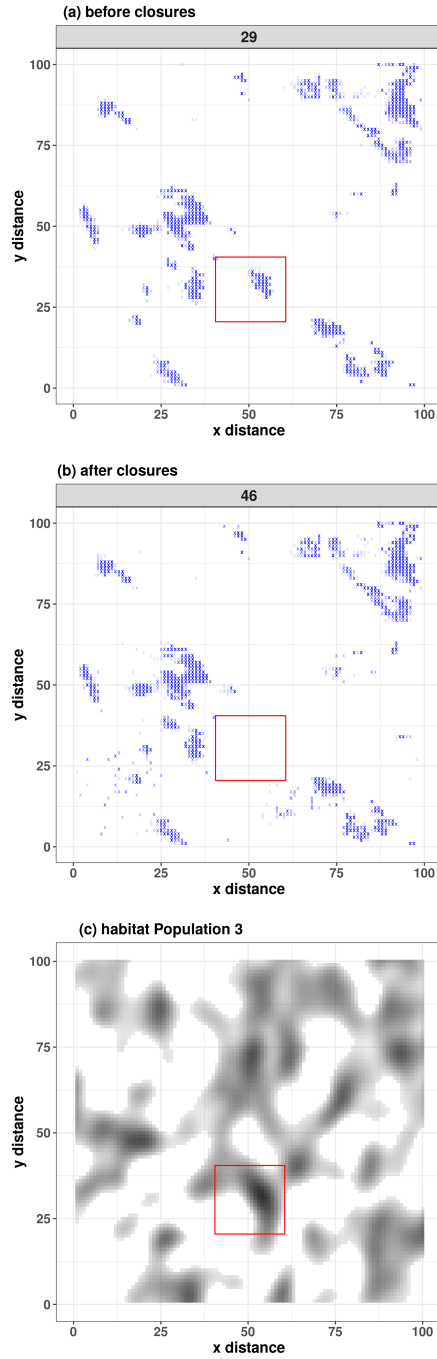


Figure 7: The location of fishing effort, (a) before the spatial closure and (b) after the spatial closure (years in panel), and (c) the suitable habitat for population 3. The site of the closure can be seen in the red box on all three panels.

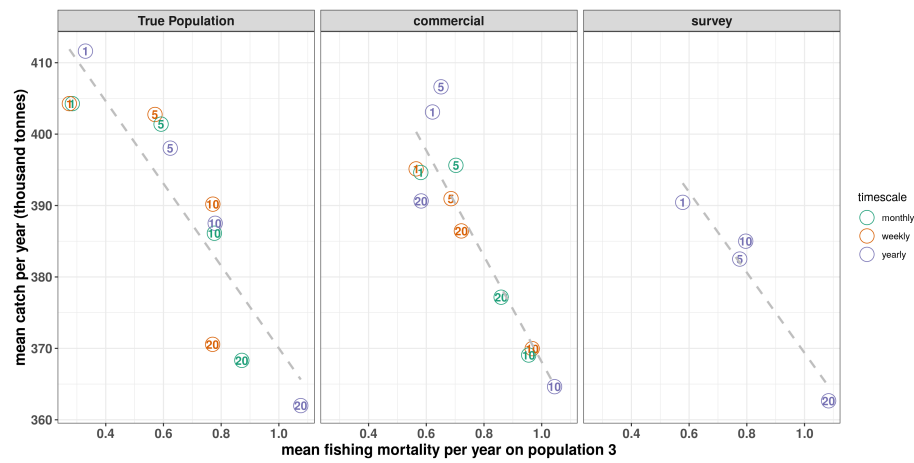


Figure 8: [Colour online] Effectiveness of closure with regards to reducing fishing mortality on protected population (further left on x-axis is best) and maintaining high catches in the fishery (highest on y-axis is best). The numbers indicate the spatial resolution of the data, while grey lines indicate the direction of the trade-off between reducing fishing mortality and overall catches.



## 685 References

- 686 Akima, H., Gebhardt, A., 2016. akima: Interpolation of Irregularly and Regu-  
687 larly Space data. R package version 0.6-2.
- 688 Alverson, D.L., Freeberg, M., Pope, J., Murawski, S., 1994. A Global Assess-  
689 ment of Fisheries By-catch and Discards: A Summary Overview. Technical  
690 Report 339.
- 691 Bailey, R.M., Carrella, E., Axtell, R., Burgess, M.G., Cabral, R.B., Drexler, M.,  
692 Dorsett, C., Madsen, J.K., Merkl, A., Saul, S., 2019. A computational ap-  
693 proach to managing coupled human–environmental systems: the POSEIDON  
694 model of ocean fisheries. *Sustainability Science* 14, 259–275.
- 695 Bastardie, F., Nielsen, J.R., Ulrich, C., Egekvist, J., Degel, H., 2010. De-  
696 tailed mapping of fishing effort and landings by coupling fishing logbooks  
697 with satellite-recorded vessel geo-location. *Fisheries Research* 106, 41–53.
- 698 Batsleer, J., Hamon, K.G., Overzee, H.M.J., Rijnsdorp, A.D., Poos, J.J., 2015.  
699 High-grading and over-quota discarding in mixed fisheries. *Reviews in Fish*  
700 *Biology and Fisheries* 25, 715–736.
- 701 Bellido, J.M., Santos, M.B., Pennino, M.G., Valeiras, X., Pierce, G.J., 2011.  
702 Fishery discards and bycatch: Solutions for an ecosystem approach to fisheries  
703 management? *Hydrobiologia* 670, 317–333.
- 704 Beverton, R.J., Holt, S.J., 1957. On the Dynamics of Exploited Fish Popula-  
705 tions. HM Stationary Office, London.
- 706 Boonstra, W.J., Hentati-Sundberg, J., 2016. Classifying fishers’ behaviour. An  
707 invitation to fishing styles. *Fish and Fisheries* 17, 78–100.
- 708 Branch, T.A., Hilborn, R., Bogazzi, E., 2005. Escaping the tyranny of the grid:  
709 A more realistic way of defining fishing opportunities. *Canadian Journal of*  
710 *Fisheries and Aquatic Sciences* 62, 631–642.
- 711 Catchpole, T.L., Reville, A.S., 2008. Gear technology in Nephrops trawl fisheries.  
712 *Reviews in Fish Biology and Fisheries* 18, 17–31.
- 713 Codling, E.A., Plank, M.J., Benhamou, S., Interface, J.R.S., 2008. Random  
714 walk models in biology. *Journal of the Royal Society, Interface / the Royal*  
715 *Society* 5, 813–34.
- 716 Cosgrove, R., Browne, D., Minto, C., Tyndall, P., Oliver, M., Montgomerie, M.,  
717 McHugh, M., 2019. A game of two halves: Bycatch reduction in Nephrops  
718 mixed fisheries. *Fisheries Research* 210, 31–40.
- 719 Costello, C., Rassweiler, A., Siegel, D., De Leo, G., Micheli, F., Rosenberg, A.,  
720 2010. The value of spatial information in MPA network design. *Proceedings*  
721 *of the National Academy of Sciences of the United States of America* 107,  
722 18294–18299.

- 723 Cotter, A.J., Pilling, G.M., 2007. Landings, logbooks and observer surveys:  
724 Improving the protocols for sampling commercial fisheries. *Fish and Fisheries*  
725 8, 123–152.
- 726 Crowder, B.L.B., Murawski, S.A., Crowder, L.B., 1998. Fisheries Bycatch:  
727 Implications for Management. *Fisheries* 23, 8–17.
- 728 Dedman, S., Officer, R., Brophy, D., Clarke, M., Reid, D.G., 2015. Modelling  
729 abundance hotspots for data-poor Irish Sea rays. *Ecological Modelling* 312,  
730 77–90.
- 731 Deriso, R.B., 1980. Harvesting Strategies and Parameter Estimation for an Age-  
732 Structured Model. *Canadian Journal of Fisheries and Aquatic Sciences* 37,  
733 268–282.
- 734 Dichmont, C.M., Punt, A.E., Deng, A., Dell, Q., Venables, W., 2003. Applica-  
735 tion of a weekly delay-difference model to commercial catch and effort data  
736 for tiger prawns in Australia’s Northern Prawn Fishery. *Fisheries Research*  
737 65, 335–350.
- 738 Dinmore, T.A., Duplisea, D.E., Rackham, B.D., Maxwell, D.L., Jennings, S.,  
739 2003. Impact of a large-scale area closure on patterns of fishing disturbance  
740 and the consequences for benthic communities. *ICES Journal of Marine Sci-*  
741 *ence* 60, 371–380.
- 742 Dolder, P.J., Thorson, J.T., Minto, C., 2018. Spatial separation of catches in  
743 highly mixed fisheries. *Scientific Reports* 8.
- 744 Dunn, D.C., Boustany, A.M., Roberts, J.J., Brazer, E., Sanderson, M., Gardner,  
745 B., Halpin, P.N., 2014. Empirical move-on rules to inform fishing strategies:  
746 A New England case study. *Fish and Fisheries* 15, 359–375.
- 747 Dunn, D.C., Maxwell, S.M., Boustany, A.M., Halpin, P.N., 2016. Dynamic  
748 ocean management increases the efficiency and efficacy of fisheries manage-  
749 ment. *Proceedings of the National Academy of Sciences of the United States*  
750 *of America* 113, 668–673.
- 751 F. Dormann, C., M. McPherson, J., B. Araújo, M., Bivand, R., Bolliger, J.,  
752 Carl, G., G. Davies, R., Hirzel, A., Jetz, W., Daniel Kissling, W., Kühn, I.,  
753 Ohlemüller, R., R. Peres-Neto, P., Reineking, B., Schröder, B., M. Schurr,  
754 F., Wilson, R., 2007. Methods to account for spatial autocorrelation in the  
755 analysis of species distributional data: A review. *Ecography* 30, 609–628.
- 756 Fulton, E.A., Link, J.S., Kaplan, I.C., Savina-Rolland, M., Johnson, P.,  
757 Ainsworth, C., Horne, P., Gorton, R., Gamble, R.J., Smith, A.D., Smith,  
758 D.C., 2011. Lessons in modelling and management of marine ecosystems:  
759 The Atlantis experience. *Fish and Fisheries* 12, 171–188.

760 Gardner, B., Sullivan, P.J., Morreale, S.J., Epperly, S.P., 2008. Spatial and  
761 temporal statistical analysis of bycatch data: patterns of sea turtle bycatch  
762 in the North Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences*  
763 65, 2461–2470.

764 Gerritsen, H., 2014. mapplots: Data visualisation on maps.

765 Gerritsen, H.D., Lordan, C., Minto, C., Kraak, S.B., 2012. Spatial patterns  
766 in the retained catch composition of Irish demersal otter trawlers: High-  
767 resolution fisheries data as a management tool. *Fisheries Research* 129-130,  
768 127–136.

769 Gillespie, D.T., 1977. Exact stochastic simulation of coupled chemical reactions.  
770 *Journal of Physical Chemistry* 81, 2340–2361.

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

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

778 Girardin, R., Hamon, K.G., Pinnegar, J., Poos, J.J., Thébaud, O., Tidd, A.,  
779 Vermard, Y., Marchal, P., 2017. Thirty years of fleet dynamics modelling  
780 using discrete-choice models: What have we learned? *Fish and Fisheries* 18,  
781 638–655.

782 Harley, S.J., Myers, R.A., Dunn, A., 2001. Is catch-per-unit-effort proportional  
783 to abundance? *Canadian Journal of Fisheries and Aquatic Sciences* 58, 1760–  
784 1772.

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

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

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

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

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

797 Lee, J., South, A.B., Jennings, S., 2010. Developing reliable, repeatable, and  
798 accessible methods to provide high-resolution estimates of fishing-effort distri-  
799 butions from vessel monitoring system (VMS) data. *ICES Journal of Marine*  
800 *Science* 67, 1260–1271.

801 Little, A.S., Needle, C.L., Hilborn, R., Holland, D.S., Marshall, C.T., 2015.  
802 Real-time spatial management approaches to reduce bycatch and discards:  
803 Experiences from Europe and the United States. *Fish and Fisheries* 16, 576–  
804 602.

805 Liu, X., Heino, M., 2014. Overlooked biological and economic implications of  
806 within-season fishery dynamics. *Canadian Journal of Fisheries and Aquatic*  
807 *Sciences* 71, 181–188.

808 Mahévas, S., Pelletier, D., 2004. ISIS-Fish, a generic and spatially explicit  
809 simulation tool for evaluating the impact of management measures on fisheries  
810 dynamics. *Ecological Modelling* 171, 65–84.

811 Mangel, M., Clark, C.W., 1983. Uncertainty, search, and information in fish-  
812 eries. *ICES Journal of Marine Science* 41, 93–103.

813 Martínez-Minaya, J., Cameletti, M., Conesa, D., Pennino, M.G., 2018. Species  
814 distribution modeling: a statistical review with focus in spatio-temporal is-  
815 sues. *Stochastic Environmental Research and Risk Assessment* 32, 3227–3244.

816 Mateo, M., Pawlowski, L., Robert, M., 2017. Highly mixed fisheries: Fine-scale  
817 spatial patterns in retained catches of French fisheries in the Celtic Sea. *ICES*  
818 *Journal of Marine Science* 74, 91–101.

819 Maunder, M.N., Punt, A.E., 2004. Standardizing catch and effort data: A  
820 review of recent approaches. *Fisheries Research* 70, 141–159.

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

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

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

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

834 R Core Team, 2017. R Core Team (2017). R: A language and environment for  
835 statistical computing.

836 Ricker, W.E., 1954. Stock and Recruitment. *Journal of the Fisheries Research*  
837 *Board of Canada* 11, 559–623.

838 Rijnsdorp, A.D., 2000. Competitive interactions among beam trawlers exploit-  
839 ing local patches of flatfish in the North Sea. *ICES Journal of Marine Science*  
840 57, 894–902.

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

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

847 Rijnsdorp, A.D., Poos, J.J., Quirijns, F.J., Grant, J., 2011. Spatial dimension  
848 and exploitation dynamics of local fishing grounds by fishers targeting several  
849 flatfish species. *Canadian Journal of Fisheries and Aquatic Sciences* 68, 1064–  
850 1076.

851 Robinson, L.M., Elith, J., Hobday, A.J., Pearson, R.G., Kendall, B.E., Poss-  
852 ingham, H.P., Richardson, a.J., 2011. Pushing the limits in marine species  
853 distribution modelling: Lessons from the land present challenges and oppor-  
854 tunities. *Global Ecology and Biogeography* 20, 789–802.

855 Schlather, M., Malinowski, A., Menck, P.J., Oestin, M., Strokorb, K., 2015.  
856 Analysis, simulation and prediction of multivariate random fields with package  
857 randomfields. *Journal of Statistical Software* 63, 1–25. [arXiv:1501.0228](#).

858 Schnute, J., 1985. A genera theory for analysis of catch and effort data. *Cana-  
859 dian Journal of Fisheries and Aquatic Sciences* 42, 414–429.

860 Sela, R., Simonoff, J., 2011. REEMtree: Regression Trees with Random Effects.  
861 R package version 0.90.3.

862 Shin, Y.J., Shannon, L.J., Cury, P.M., 2004. Simulations of fishing effects on the  
863 southern Benguela fish community using an individual-based model: Learning  
864 from a comparison with ECOSIM. *African Journal of Marine Science* 26, 95–  
865 114.

866 Stock, B.C., Ward, E.J., Eguchi, T., Jannot, J.E., Thorson, J.T., Feist, B.E.,  
867 Semmens, B.X., 2019. Comparing predictions of fisheries bycatch using multi-  
868 ple spatiotemporal species distribution model frameworks. *Canadian Journal*  
869 *of Fisheries and Aquatic Sciences* .

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

- 872 Ulrich, C., Reeves, S.A., Vermard, Y., Holmes, S.J., Vanhee, W., 2011. Rec-  
873 onciling single-species TACs in the North Sea demersal fisheries using the  
874 Fcube mixed-fisheries advice framework. *ICES Journal of Marine Science* 68,  
875 1535–1547.
- 876 Van Putten, I.E., Kulmala, S., Thébaud, O., Dowling, N., Hamon, K.G., Hut-  
877 ton, T., Pascoe, S., 2012. Theories and behavioural drivers underlying fleet  
878 dynamics models. *Fish and Fisheries* 13, 216–235.
- 879 Viswanathan, G.M., Buldyrev, S.V., Havlin, S., Da Luz, M.G.E., Raposo, E.P.,  
880 Stanley, H.E., 1999. Optimizing the success of random searches. *Nature* 401,  
881 911–914.
- 882 Walters, C.J., 2007. Is adaptive management helping to solve fisheries problems?  
883 *Ambio* .
- 884 Ward, E.J., Jannot, J.E., Lee, Y.W., Ono, K., Shelton, A.O., Thorson, J.T.,  
885 2015. Using spatiotemporal species distribution models to identify temporally  
886 evolving hotspots of species co-occurrence. *Ecological Applications* 25, 2198–  
887 2209.
- 888 Xu, B., Zhang, C., Xue, Y., Ren, Y., Chen, Y., 2015. Optimization of sampling  
889 effort for a fishery-independent survey with multiple goals. *Environmental*  
890 *Monitoring and Assessment* 187.