MixFishSim: highly resolved spatiotemporal simulations for exploring mixed fishery dynamics

Paul J. Dolder[a,b,*], Cóilín 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 Université, 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, often with sparse data at limited spatial and temporal resolution.

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

*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 via a mix of correlated random walk movement (for exploration) and learned behaviour (for exploitation) phases of the fisheries.

We simulate 50 years of fishing and use the results from the fisheries catch to draw inference on the underlying population structures. We compare this inference to a simulated fixed-site sampling design commonly used for fisheries monitoring purposes and the true underlying population structures input to the simulation. 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.

We conclude from our simulations that commercial data, while containing bias, provides a useful tool for managing catches in mixed fisheries if applied at the correct spatiotemporal scale.

[333 words]

Keywords: Some, keywords, here. Max 6

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 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 which may lead to overexploitation of fish populations (Ulrich et al., 2011; Batsleer et al., 2015). This 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).

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 at 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.

This comes as a surprise: I thought this was going to be about discardsAgree, have removed this to avoid confusion

We ask two fundamental questions regarding spatiotemporal inference derived from observational data:

1. How does sampling-derived data reflects the underlying population structures?
2. How does data aggregation and source impact on monitoring spatial fisheries management measures ?

We i) develop a simulation model where population dynamics are highly-resolved in space and time to answer these questions. Being known directly rather than inferred from sampling or commercial catch, we can use the population model to evaluate how inference from fisheries-dependent and fisheries independent sampling relates to the real population structure. We ii) compare at different spatial and temporal aggregations of the simulated population distributions to samples from fisheries-dependent and fisheries independent catches. We then iii) simulate a fishery closure to protect a species based on different spatial and temporal data aggregations.

We compare the catch composition from fisheries independent and dependent sampling against the real population composition, as well as the theoretical "benefit" to the population spatial closures using the different data sources. We use these evaluations to draw inference on the utility of commercial data in supporting management decisions.

2. Materials and Methods

A modular event-based simulation model was developed with sub-modules implemented on independent time-scales appropriate to capture the characteristic of the different processes (Figure 1). The following sub-modules were included to capture the full system: 1) Population dynamics, 2) Recruitment dynamics, 3) Population movement, 4) fishery dynamics.

Population dynamics (fishing and natural mortality, growth) operate on a daily time-step, while population movement occurs on a weekly time-step. Re-

If the paper has two goals this should be clear from the start, but may be better over 2 MSsI would like to keep both parts, but have made clearer in how its set out. The closure scenarios form validation of the data aggregation, rather than effectiveness of the closures themselves - so its a continuation of the same question in my eyes cruitment takes place periodically each year for a set time duration specified for each population, while the fishing module operates on a tow-by-tow basis (i.e. multiple events a day).

In our model system population movement is driven by random (diffusive) and directed (advective) processes and we incorporate characterisation of a number of different fishing fleet dynamics exploiting four fish populations with different spatial and population demographics. We use the model to simulate 50 years of exploitation of the fish populations.

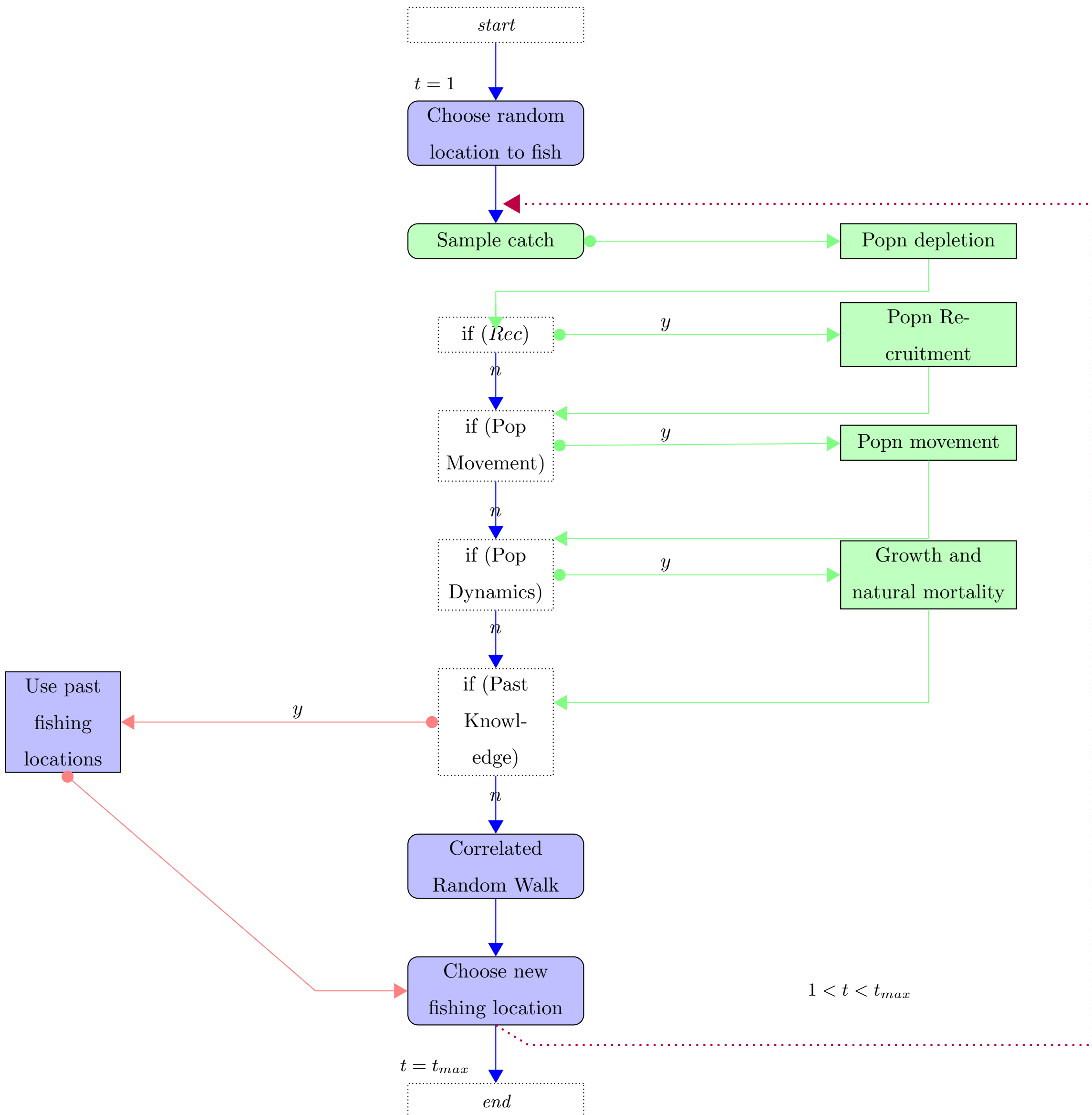

Figure 1: Schematic overview of the simulation model. Blue boxes indicate fleet dynamics processes, the green boxes population dynamics processes while the white boxes are the time steps at which processes occur; t = tow, $tmax$ is the total number of tows; (Rec), (Pop Movement), (Pop Dynamics) logic 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.

2.1. Population dynamics

The basic population level processes are simulated using a modified two-stage Deriso-Schnute delay difference model (Deriso, 1980; Schnute, 1985; Dichmont et al., 2003) occurring at a daily time-step. A daily time-step was chosen to discretise continuous population processes on a biologically relevant and computationally tractable timescale. Under the population dynamics module population biomass growth and depletion for pre-recruits and recruited fish are modelled separately as a function of previous recruited biomass, intrinsic population growth and recruitment. Biomass for each cell c is incremented each day d as follows (the full parameter list is detailed in Table 1):

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

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

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

$$C_{c,d} = \frac{F_{c,d}}{F_{c,d} + M_{c,d}} * (1 - e^{-(F_{c,d}+M_{c,d})}) * B_{c,d} \tag{2}$$

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

[link F to effort and catchability - as I think we have F as an emergent property of the fleets rather than something we solve for (I could be wrong though!) - catch for a vessel is a product of catchability and biomass, i.e. C = qB, but this catch is summed to solve for F. So its both really]

2.2. Recruitment dynamics

Recruitment is modelled through a function relating the mature biomass to recruits at time of recruitment. In *MixFishSim*, it can be modelled either either as a stochastic Beverton-Holt stock-recruit form (Beverton and Holt, 1957):

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

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):

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

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

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. An advection-diffusion process controlled population movement, with a time-varying temperature covariate used to change the spatial bounds of suitable habitat on a weekly time-step.

What have a temperature covariate? Could just use time- Was intended as some biological meaning - species thermal tolerances load onto the temperature effect - so could be different per species

For habitat we first defined a Gaussian random field process, $\{S(c) : c \in \mathbb{R}^2\}$, where for any set of cells $c_1, \ldots, c_n$, the joint distribution of $S =$

Not clear how

$\{S(c1), \ldots S(c_n)\}$ is multivariate Gaussian. The distribution is specified by its *mean function*, $\mu(c) = E[S(c)]$ and its *covariance function*, $\gamma(c, c') = Cov\{S(c), S(c$ (Diggle and Ribeiro, 2007).

Introduce the gamma function, and why this covariance structure? Why correlate values in the random field?to allow populations to have different aggregation densities: have tried to clarify

The covariance structure affects the smoothness of the surfaces which the process generates; we used the *Matérn* covariance structure, where the correlation strength weakens with distance. This enables us to model the spatial autocorrelation observed in animal populations where density is more similar in nearby locations (Tobler, 1970; F. Dormann et al., 2007) and we change the parameters to implement different spatial structures for the populations. The *Matérn* correlation is a two-parameter family where:

$$\rho(u) = \{2^{\kappa-1}\Gamma\kappa\}^{-1}(u/\phi)^{\kappa}K_{\kappa}(u/\phi)$$

$K_\kappa(.)$ is a modified Bessel function of order κ, $\phi > 0$ is a scale parameter with the dimensions of distance, and $\kappa > 0$, called the order, is a shape parameter which determines the smoothness of the underlying process (Figure S16).

The habitat for each of the populations was generated with the *RFSimulate* function of the *RandomFields* R package (Schlater et al., 2015). Each population was initialised at a single location, and subsequently moveed according to a probabilistic distribution based on habitat suitability (represented by the normalised values from the GRFs), temperature and distance from current cell:

$$Pr(J|I) = \frac{e^{-\lambda * d_{IJ}} \cdot (Hab^2_{J,p} \cdot Tol_{J,p,wk})}{\sum\limits_{c=1}^{C} e^{-\lambda * d} \cdot (Hab^2_{c,p} \cdot Tol_{c,p,wk})} \tag{5}$$

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

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

What does it mean concisely? Areas are assigned? Yes, the areas are pre-defined - I have amended to reflect and tried to clarify

The temperature field was defined on a gradient from a South-Westerly to North-Easterly direction, with temperature in each cell changing gradually on a week-by-week basis so that initially high temperature areas cycled to lower temperatures and low temperature areas *vice versa*. Each population p was assigned a thermal tolerance with mean, μ_p and variance, σ_p^2 so that each cell and population temperature suitability is defined that:

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

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

The final process resulted in independent populations structure and movement patterns, with population movement occurring on a weekly basis. This process approximated the demographic shifts in fish populations throughout a year with seasonal spawning patterns (e.g. Figure S5).

2.4. Fleet dynamics

The fleet dynamics can be broadly categorised into three components; fleet targeting - which determined the fleet catch efficiency and preference towards a particular species; trip-level decisions, which determined the initial location to be fished at the beginning of a trip; and within-trip decisions, determining movement from one fishing spot to another within a trip. Together, these element implement an explore-exploit type strategy for individual vessels to maximise their catch from an unknown resource distribution (Bailey et al. (2018)).

2.4.1. *Fleet targeting*

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

2.4.2. *Trip-level decisions*

Several studies (e.g. Hutton et al., 2004; Tidd et al., 2012; Girardin et al., 2015) 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, and choosing randomly from the top 75 % of fishing events as defined by the expected profit. Simulation testing indicated that this learning increased the mean value of catches for the vessels, over just relying on the correlated random walk function as described for the 'within trip' decisions below (MIGHT NEED TO INCLUDE IN SUPPLEMENTARY).

Correlated random walk of what

2.4.3. *Within-trip decisions*

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 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),

$$Rev = \sum_{p=1}^{P} L_p \cdot Pr_p \tag{7}$$

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, which can be controlled separately, but is determined by the relationship:

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

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:

So step length increases with increasingly gross revenue?No, the opposite

$$\begin{aligned}
(x2, y2) = & x1 + StepL \cdot \cos(\frac{\pi \cdot Br}{180}), \\
& y1 + StepL \cdot \sin(\frac{\pi \cdot Br}{180}) \\
with \quad & Br_{t-1} < 180, Br_t = 180 + \sim vm[(0, 360), k] \\
& Br_{t-1} > 180, Br_t = 180 - \sim vm[(0, 360), k]
\end{aligned} \tag{9}$$

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

2.4.4. Local population depletion

Where several fishing vessels 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, 2007). In order to account for this behaviour, the fishing sub-model operates spatially on a daily time-step so that for future days the biomass available to the fishery is reduced in the areas fished. The cumulative effect is to make heavily fished areas less attractive as future fishing opportunities.

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. 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

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

3. Calculation - used by journal / Parameterisation

3.1. Population parametrisation

We parametrised the simulation model for four populations with different population demographics; growth rates, natural mortality and recruitment functions (Table 4). Habitat preference (Figure S1) and temperature tolerances (Figures S3, S4) were unique to each population resulting in differently weekly distribution patterns (Figures S5-S7). In addition, each of the populations has two defined spawning areas which result in the populations moving towards these areas in pre-defined weeks (Figure S2) with population-specific movement rates (Table 4). The realised movement of the populations for a number of weeks is shown in Figure S9 while the realised daily fishing mortality are shown in Figure S10.

3.2. Fleet parametrisation

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

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

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

Move some of the supplementary figures to the manuscript

3.3. Survey settings

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

3.4. Example research question scenario

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

move to start of methods sectionI think ecological modelling wants the 'calculations' section here..will check

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

Is there equilibrium after 5 years or still some trend in B? I have rerun to ensure some steady state dynamics

The following steps are undertaken to determine closures:

Procedure unclear. Refer to symbols in methods section or switch order starting with description of data type etc..Yes, will redo

1. Extract data source
2. Aggregate according to desired spatial and temporal resolution
3. Interpolate across entire area at desired resolution
4. Close area covering top 5 % of catch

In total 56 closure scenarios were run which represent combinations of:

- **data types:** commercial logbook data, survey data and 'real population',
- **temporal resolutions:** weekly, monthly and yearly closures,

- **spatial resolutions:** 1 x 1 grid, 5 x 5 grid, 10 x 10 grid and 20 x 20 grid,
- **closure basis:** high catch rates of protected species, or high ratio of protected species v secondary species.

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

4. Results

In order to answer the question of how sampling-derived data reflects the underlying population structure we compare different spatial and temporal aggregations of the simulated population distributions to:

a) **fisheries-independent data:** the inferred population from a fixed-site sampling survey design as commonly used for fisheries monitoring purposes;

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

The consequences of different spatial aggregations of the data are shown in Figure 2, which represents the aggregation of catch from each of the data sources over a ten-year period (to average seasonal patterns) at different spatial resolutions.

The finer spatial grid for the real population (top left) and commercial data (top middle) show visually similar patterns, though there are large unsampled areas in the commercial data from a lack of fishing activity (particularly in the lower left part of the sampling domain). The survey data at this spatial resolution displays very sparse information about the spatial distributions of the populations. The slightly aggregated data on a 5 x 5 grid shows similar patterns and, while losing some of the spatial detail, there remains good consistency between the ‘real population’ and the commercial data. Survey data starts to pick out some of the similar patterns as the other data sources, but lacks 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 'real population' data emerge.

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

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

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

For the closures based on 'real population' (bottom row), the most disaggregated data (a weekly timescale and 1 x 1 resolution) was most effective, reducing fishing mortality on species 1 (left) by ~ 60 %. Next was the monthly closures ($< \sim 30$ %). The least effective were the yearly closures (blue lines) at all spatial resolutions, which conversely resulted in increased fishing mortalities (> 30 %).

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

For the commercial data, the most effective closure scenario was based on 1 x 1 data at a monthly temporal resolution. This results in ~ 10 % reduction in F for species 1. This was the only closure scenario to have positive effect according to Figure 5, though looking at the trend in Figure 4 this looks more related to the continued increased in F trend, as other scenarios had an initial effect. Interestingly the monthly data scenario was more effective than weekly data, which we posit is due to the increased data available from the commercial sampling across a month compared to a week. Commercial data used at an annual time-step was ineffective in bringing fishing mortality down for species 1.

Given the scenarios above, it seems clear that spatial disaggregation is more important than the temporal disaggregation of the commercial data, except when its used at an annual time-frame, which is the scenario that gave the worst results.

For the other species in the simulation (population 2 - 4) there was little difference in fishing mortalities across scenarios.

Note: The monthly commercial data scenario is the most effective of the realistic scenarios, as the 'real population' can only be seen as a baseline comparison.

5. Discussion

Our study evaluates the importance of data scaling and considers potential bias introduced through data aggregation when using commercial fisheries data to infer spatio-temporal dynamics in fisheries. 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 is 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 spatio-temporal approaches in order 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.

We employ a simulation approach to model each of the population and fishery processes in a hypothetical 'mixed fishery', allowing us to i) evaluate the consequences of different aggregation assumptions on our understanding of the spatio-temporal distribution of the underlying fish populations, and ii) evaluate the effectiveness of a spatial closure given those assumptions. Our approach captures fine scale population and fishery dynamics not usually considered (although see Bastardie et al. (2010); Bailey et al. (2018)) which offers the advantage that larger scale fishery patterns are emergent properties of the system rather than the result of a statistical modelling framework.

Our results show commercial data can provide at right scale and resolution - depends on scale of process: pop movement etc... Important to consider how fishers interact / adapt to changes with the resource and mgmt.

Closure scenarios demonstrate potential tor reduce F - not as high as with real pop, but good. Make link to other studies – read up on these.

<u>The what next:</u>

Real world spatiotemp closures rarely been able to consider these issues / designed with these issues fully in mind - NS cod closures, plaice and trevose box...

Use of commercial data increasing - likely to become more important in future. Also collaborative approach with industry, e.g. hotspot mapping, spatiotemp advice...

Other potential uses of the model

Survey design

commercial index standardization methods

Sampling scheme design

Testing fleet dynamics models at an aggregated level

Bigger picture stuff:: LO, increasing desire for more nuanced spatiotemp mgmt... Wider applicability: birds, wildlife ??

6. Conclusions

Study shows ....

This is important because ....

How we might apply this in future ....

Abbreviations

Detail any unusual ones used.

Acknowledgements

those providing help during the research..

Funding

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

Appendices

Table 1: Description of variables for population dynamics sub-module

Variable	Meaning	Units
	Population dynamics	
Delay-difference model		
$B_{c,d}$	Biomass in cell c and day d	kg
$Z_{c,d}$	Total mortality in cell c for day d	-
$R_{c,\tilde{y}}$	Annualy 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	-
Baranov catch equation		
$C_{c,d}$	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	
Habitat model		
a	b	c
Thermal tolerance		
$T_{c,wk}$	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
Population movement model		
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 1	Fleet 2	Fleet 3	Fleet 4	Fleet 5
Targeting preferences					
Price Pop1	100	100	100	100	100
Price Pop2	200	200	200	200	200
Price Pop3	350	350	350	350	350
Price Pop4	600	600	600	600	600
Q Pop1	0.01	0.02	0.02	0.01	0.01
Q Pop2	0.02	0.01	0.02	0.01	0.03
Q Pop3	0.01	0.02	0.02	0.01	0.02
Q Pop4	0.02	0.01	0.02	0.05	0.01
Exploitation dynamics					
step function β_1	1	2	1	2	3
step function β_2	10	15	8	12	7
step function β_3	Q90	Q90	Q85	Q90	Q80
step function $rate$	20	30	25	35	20
Past Knowledge	T	T	T	T	T
Past Year & Month	T	T	T	T	T
Past Trip	T	T	T	T	T
Threshold	0.7	0.7	0.7	0.7	0.7
Fuel Cost	3	2	5	2	1

Table 6: Fishing mortality effects of the closure scenarios (ordered by most effective first)

scenario	metric	pop	before	after	diff	timescale	basis	data_type	resolution
9	F	spp_3	1.08	0.29	-73.47	weekly	high_pop	real_pop	1.00
10	F	spp_3	1.08	0.29	-72.94	monthly	high_pop	real_pop	1.00
11	F	spp_3	1.08	0.35	-68.04	yearly	high_pop	real_pop	1.00
45	F	spp_3	1.08	0.58	-46.70	yearly	high_pop	commercial	20.00
1	F	spp_3	1.08	0.58	-46.21	weekly	high_pop	commercial	1.00
23	F	spp_3	1.08	0.59	-45.27	weekly	high_pop	real_pop	5.00
2	F	spp_3	1.08	0.59	-45.06	monthly	high_pop	commercial	1.00
7	F	spp_3	1.08	0.60	-44.48	yearly	high_pop	survey	1.00
24	F	spp_3	1.08	0.61	-43.20	monthly	high_pop	real_pop	5.00
3	F	spp_3	1.08	0.64	-40.82	yearly	high_pop	commercial	1.00
25	F	spp_3	1.08	0.65	-39.94	yearly	high_pop	real_pop	5.00
17	F	spp_3	1.08	0.67	-38.11	yearly	high_pop	commercial	5.00
15	F	spp_3	1.08	0.71	-34.38	weekly	high_pop	commercial	5.00
43	F	spp_3	1.08	0.71	-34.31	weekly	high_pop	commercial	20.00
16	F	spp_3	1.08	0.73	-32.58	monthly	high_pop	commercial	5.00
51	F	spp_3	1.08	0.78	-27.92	weekly	high_pop	real_pop	20.00
37	F	spp_3	1.08	0.78	-27.76	weekly	high_pop	real_pop	10.00
39	F	spp_3	1.08	0.79	-26.98	yearly	high_pop	real_pop	10.00
38	F	spp_3	1.08	0.81	-25.47	monthly	high_pop	real_pop	10.00
21	F	spp_3	1.08	0.81	-25.21	yearly	high_pop	survey	5.00
35	F	spp_3	1.08	0.81	-25.05	yearly	high_pop	survey	10.00
44	F	spp_3	1.08	0.87	-19.91	monthly	high_pop	commercial	20.00
52	F	spp_3	1.08	0.88	-18.39	monthly	high_pop	real_pop	20.00
30	F	spp_3	1.08	0.96	-11.06	monthly	high_pop	commercial	10.00
29	F	spp_3	1.08	0.98	-9.80	weekly	high_pop	commercial	10.00
31	F	spp_3	1.08	1.03	-4.36	yearly	high_pop	commercial	10.00
53	F	spp_3	1.08	1.06	-1.64	yearly	high_pop	real_pop	20.00
49	F	spp_3	1.08	1.07	-1.01	yearly	high_pop	survey	20.00

Table 7: Fishing mortality effects of the closure scenarios (based on highest ratio, ordered by most effective first)

scenario	metric	pop	before	after	diff	timescale	basis	data_type	resolution
6	F	spp_3	1.08	0.52	-52.27	yearly	high_ratio	commercial	1.00
48	F	spp_3	1.08	0.57	-47.06	yearly	high_ratio	commercial	20.00
50	F	spp_3	1.08	0.63	-41.53	yearly	high_ratio	survey	20.00
18	F	spp_3	1.08	0.71	-34.23	weekly	high_ratio	commercial	5.00
19	F	spp_3	1.08	0.72	-33.42	monthly	high_ratio	commercial	5.00
34	F	spp_3	1.08	0.78	-27.75	yearly	high_ratio	commercial	10.00
5	F	spp_3	1.08	0.80	-25.99	monthly	high_ratio	commercial	1.00
20	F	spp_3	1.08	0.81	-25.27	yearly	high_ratio	commercial	5.00
4	F	spp_3	1.08	0.85	-21.52	weekly	high_ratio	commercial	1.00
54	F	spp_3	1.08	0.89	-17.46	weekly	high_ratio	real_pop	20.00
55	F	spp_3	1.08	0.89	-17.46	monthly	high_ratio	real_pop	20.00
56	F	spp_3	1.08	0.89	-17.46	yearly	high_ratio	real_pop	20.00
26	F	spp_3	1.08	0.92	-14.73	weekly	high_ratio	real_pop	5.00
27	F	spp_3	1.08	0.92	-14.73	monthly	high_ratio	real_pop	5.00
28	F	spp_3	1.08	0.92	-14.73	yearly	high_ratio	real_pop	5.00
13	F	spp_3	1.08	0.96	-11.53	monthly	high_ratio	real_pop	1.00
14	F	spp_3	1.08	0.96	-11.01	yearly	high_ratio	real_pop	1.00
12	F	spp_3	1.08	0.97	-10.66	weekly	high_ratio	real_pop	1.00
32	F	spp_3	1.08	1.02	-5.94	weekly	high_ratio	commercial	10.00
22	F	spp_3	1.08	1.02	-5.64	yearly	high_ratio	survey	5.00
33	F	spp_3	1.08	1.02	-5.29	monthly	high_ratio	commercial	10.00
36	F	spp_3	1.08	1.03	-4.52	yearly	high_ratio	survey	10.00
40	F	spp_3	1.08	1.03	-4.52	weekly	high_ratio	real_pop	10.00
41	F	spp_3	1.08	1.03	-4.52	monthly	high_ratio	real_pop	10.00
42	F	spp_3	1.08	1.03	-4.52	yearly	high_ratio	real_pop	10.00
46	F	spp_3	1.08	1.04	-3.50	weekly	high_ratio	commercial	20.00
8	F	spp_3	1.08	1.06	-2.42	yearly	high_ratio	survey	1.00
47	F	spp_3	1.08	1.09	0.52	monthly	high_ratio	commercial	20.00

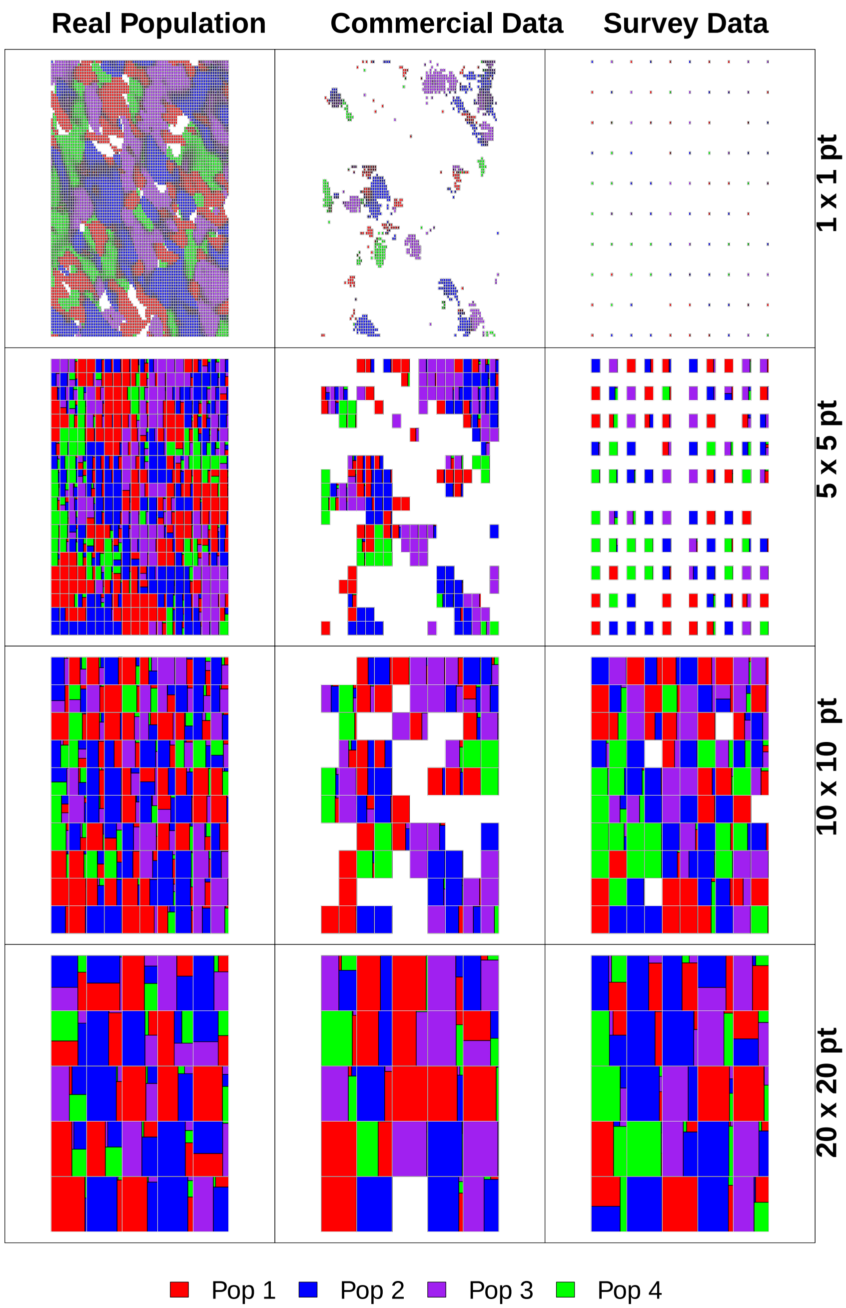

Figure 2: Data aggregation at different spatial resolutions over a ten year period

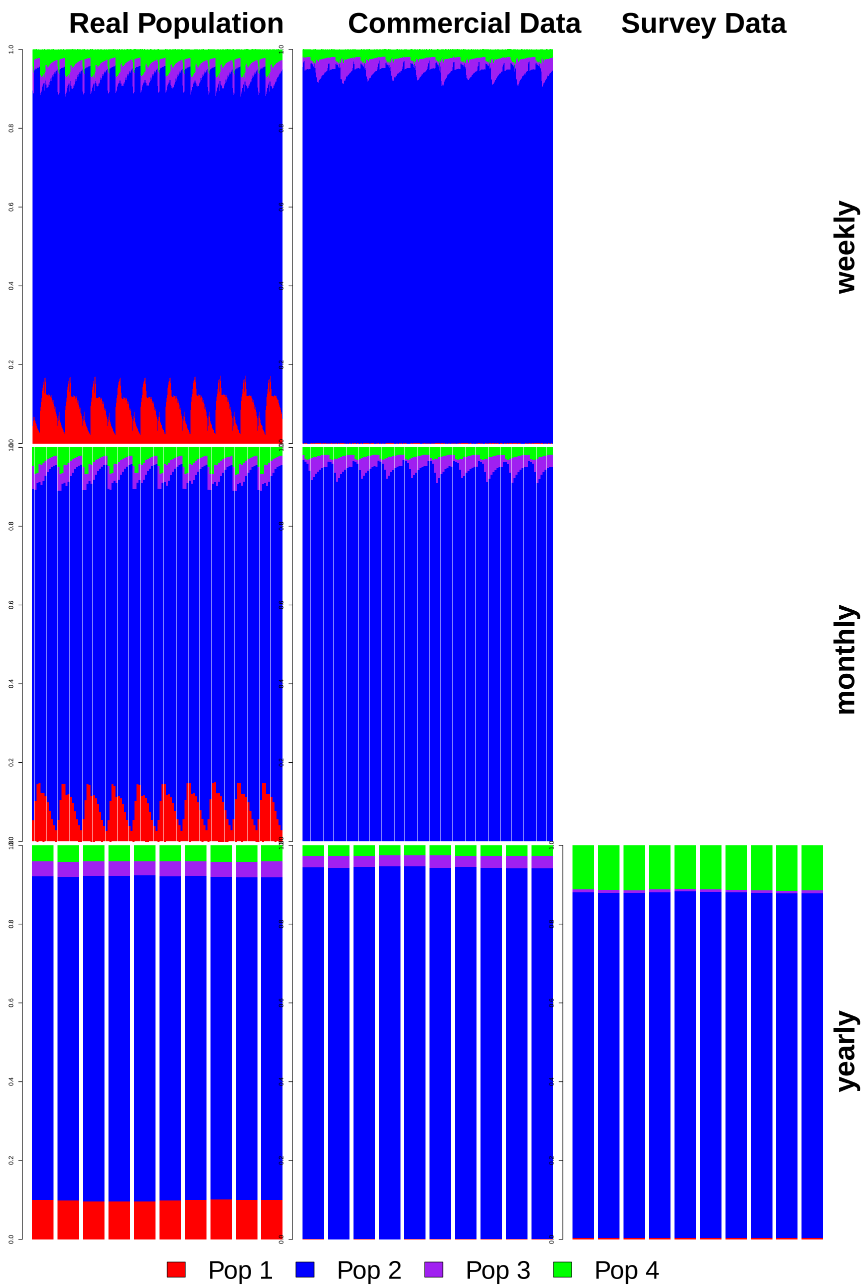

Figure 3: Data aggregation at different temporal resolutions over a ten-year period

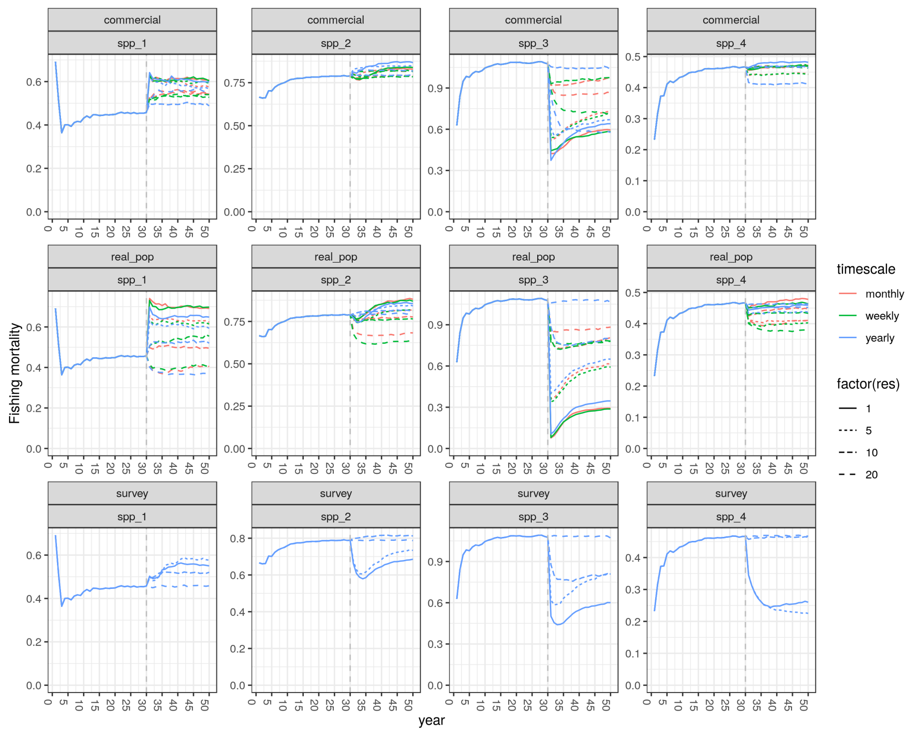

Figure 4: Comparison of closure scenarios - Fishing mortality trends. Only the scenarios based on high catch rates of population 3 are shown.

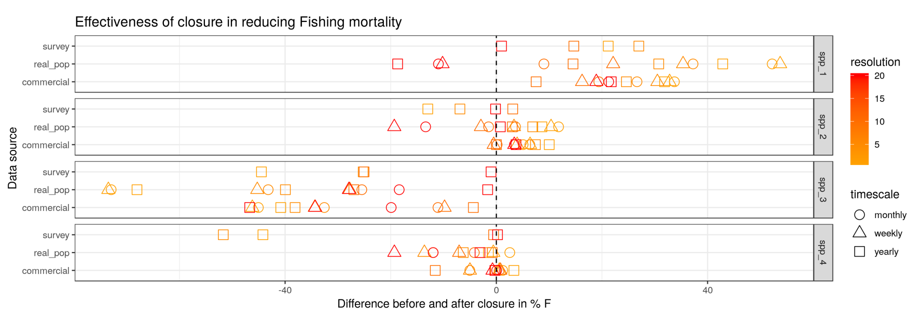

Figure 5: Comparison of closure scenarios. Points indicate the difference between the fishing mortality pre-closure (year 29) and post-closure (year 50) for population 3. Only the scenarios based on high catch rates of population 3 are shown.

References

Alverson, D.L., Freeberg, M.H., Murawski, S.A., Pope, J., 1994. A global assessment of fisheries bycatch and discards.

Bailey, R.M., Carrella, E., Axtell, R., Burgess, M.G., Cabral, R.B., Drexler, M., Dorsett, C., Madsen, J.K., Merkl, A., Saul, S., 2018. A computational approach to managing coupled human–environmental systems: the POSEIDON model of ocean fisheries.

Bartumeus, F., Da Luz, M.G.E., Viswanatham, G.M., Catalan, J., 2005. Animal Search Strategies: A Quantitative Random Walk Analysis. Ecological Society of America 86, 3078–3087.

Bastardie, F., Nielsen, J.R., Ulrich, C., Egekvist, J., Degel, H., 2010. Detailed mapping of fishing effort and landings by coupling fishing logbooks with satellite-recorded vessel geo-location. Fisheries Research 106, 41–53.

Batsleer, J., Hamon, K.G., Overzee, H.M.J., Rijnsdorp, A.D., Poos, J.J., 2015. High-grading and over-quota discarding in mixed fisheries. Reviews in Fish Biology and Fisheries 25, 715–736.

Bellido, J.M., Santos, M.B., Pennino, M.G., Valeiras, X., Pierce, G.J., 2011. Fishery discards and bycatch: Solutions for an ecosystem approach to fisheries management? Hydrobiologia 670, 317–333.

Bertrand, S., Bertrand, A., Guevara-Carrasco, R., Gerlotto, F., 2007. Scale-invariant movements of fishermen: The same foraging strategy as natural predators. Ecological Applications 17, 331–337.

Beverton, R.J., Holt, S.J., 1957. On the Dynamics of Exploited Fish Populations , 533.

Catchpole, T.L., Revill, A.S., 2008. Gear technology in Nephrops trawl fisheries. Reviews in Fish Biology and Fisheries 18, 17–31.

Codling, E.A., Plank, M.J., Benhamou, S., Interface, J.R.S., 2008. Random walk models in biology. Journal of the Royal Society, Interface / the Royal Society 5, 813–34.

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

Deriso, R.B., 1980. Harvesting Strategies and Parameter Estimation for an Age-Structured Model. Canadian Journal of Fisheries and Aquatic Sciences 37, 268–282. arXiv:1410.7455v3.

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

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

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

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

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

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

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

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

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

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

Hilborn, R., Walters, C., 1992. Quantitative fisheries stock assessment: Choice, dynamics and uncertainty. volume 2. arXiv:1011.1669v3.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Schlater, M., Malinowski, A., Menck, P.J., 2015. Analysis, Simulation and Prediction of Multivariate Random Fields with Package RandomFields. Journal of Statistical Software 63, 1–25. arXiv:1501.0228.

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

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

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

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

Tobler, W.R., 1970. A Computer Movie Simulating Urban Growth in the Detroit Region. Economic Geography 46, 234. arXiv:1011.1669v3.

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

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