MixFishSim: highly resolved spatiotemporal simulations for exploring mixed fishery dynamics

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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

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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 i) a simulated fixed-site sampling design commonly used for fisheries monitoring purposes, and ii) the true underlying population structures input to the simulation. We use the results to establish the potential and limitations of fishery-dependent data in providing a robust picture of spatiotemporal distributions. Finally, we simulate an area closure based on areas defined from the known ("real-population") distribution, commercial catch data and survey data at different 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

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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-unselective fishing gear. In doing so fisheries catch an assemblage of species and may discard overquota catch when managed by single species quotas and fishers exhaust or more quota, may lead to overexploitation of fish populations (Ulrich et al., 2011; Batsleer et al., 2015). This discarding of fish in excess of quota hampers the ability to limit fishing mortality to 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 ways of reducing 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). However, implementation of avoidance measures is hampered by lack of knowledge of fish and fishery spatiotemporal dynamics and understanding of the scale at which processes are important for management. Understanding the correct scale for spatial measures is crucial in order to implement measures 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). However, such information is 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

In order to understand the consequences of using VMS-linked landings to draw inference on the underlying population structure we develop a simulation model where population dynamics are highly-resolved in space and time. 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. 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.

Using our model we simulate 50 years of exploitation of the fish populations. We use the results

1. to understand how sampling-derived data reflects the underlying population structures. We compare at different spatial and temporal aggregations of the simulated population distributions to:
   (a) the inferred population from a stratified fixed-site sampling survey design commonly used for fisheries monitoring purposes, otherwise know as a fisheries-independent survey,
   (b) the inferred population from our fishery-dependent model which includes fishery-induced sampling dynamics.

2. to understand the impact of data aggregation and data source on spatial fisheries management measures we simulate a fishery closure to protect a species based on different spatial and temporal data aggregations:
   (a) as if the real spatial population structure were known,
   (b) the fishery-independent inferred population structure
   (c) the fishery-dependent inferred population structure

   We evaluate the theoretical "benefit" to the population of the closure(s), the effect on the other three populations and fishery catch.

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 valida-

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. Recruitment takes place periodcally 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). 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`).

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 as 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 is incremented each day as follows (the full parameter list is detailed in Table 1):

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

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 weight of fish prior to recruitment, while Wt_R is the 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 $F_{c,d}$:

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

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):

$$\bar{R}_{c,d} = \frac{(\alpha * B_{c,d})}{(\beta + B_{c,d})}$$

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

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

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

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

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.

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 $S = \{S(c1), \ldots S(c_n)\}$ 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).

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

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

Not clear how habitat/GRF affect local abundances, only have $B_{y,d}$Have included cell reference, c to make spatial link explicit

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 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:

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

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.

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^2_p so that each cell and population temperature suitability is defined that:

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

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^2_p 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),

$$Rev = \sum_{p=1}^{P} L_p \cdot Pr_p \tag{3}$$

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:

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

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

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

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 are exploiting 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.

3. Calculation

3.1. Population parametrisation

We parametrised the simulation model for four populations with differing habitat preference, temperature tolerances (Figures S1, S3, S4, S5, S6, S7), population demographics and recruitment functions. In addition, each of the populations has two defined spawning areas which result in the populations moving towards these areas in given weeks (Figure S2) and 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 where the fishing location yields in a top quartile of the value experienced in each year (as defined per fleet in Table 5).

With an increasing probability throughout the simulation fishing locations were chosen based on experience built up in the same month from previous years and from past trip fishing success. 'Success' in this context was defined as the locations where the top 75 % 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 ∼ 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 some trips overlaid on the value field, 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. Simulation settings

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 X 100 square grid, 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, and subsequently close 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' - where the underlying populations assumed to be known perfectly) used at different spatial and temporal scales.

Is there equilibrium after 5 years or still some trend in BNot at equilibrium yet...I need to rerun until steady state, looks 20 years. Will update

The following steps are undertaken to determine closures:

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

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

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

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 year at different spatial resolutions.

The finer spatial grid for the the real population (top left) and commercial data (top middle) show similar patterns, though there are unsampled gaps 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 shows very sparse and uninformative 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 loses a significant amount of information about the spatial resolutions for all data sources, and some differences between the commercial and 'real population' data emerge.

Figure 3 shows the consequences of different temporal aggregations of the data, with 156 weekly (top), 36 monthly (middle) and 3 yearly (bottom) catch compositions across a 20 x 20 area.

As can be seen from 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. The monthly data shows some consistency between the 'real population' and commercial data for species 2 - 4, though species 1 remains underrepresented. On an annual basis, interestingly the commercial data underrepresents the first species (in red) while the survey overrepresents 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 overrepresentation 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 (linestyles), while Figure 5 shows the change in fishing mortality from before the closure (average F years 2 - 4) to after the closure (average F years 8 - 10).

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 resulted in increased fishing mortalities (> 30 % - N.B. Note though, this is consistent with the increasing trends in F, which is probably more related to the fact that Fs hadn't stabilised in the simulation from the fishing vessels "learning" the best locations - I will rerun the sims for a longer time (20 - 30 years).

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 I'd posit is due to the increase amount of data available from the commercial sampling across a month compared to a week.i Commercial data used at an annual timestep 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 timeframe, 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

6. Conclusions

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 6: Fishing mortality effects of the closure scenarios

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 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	-

Abbreviations

Detail any unusual ones used.

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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	-

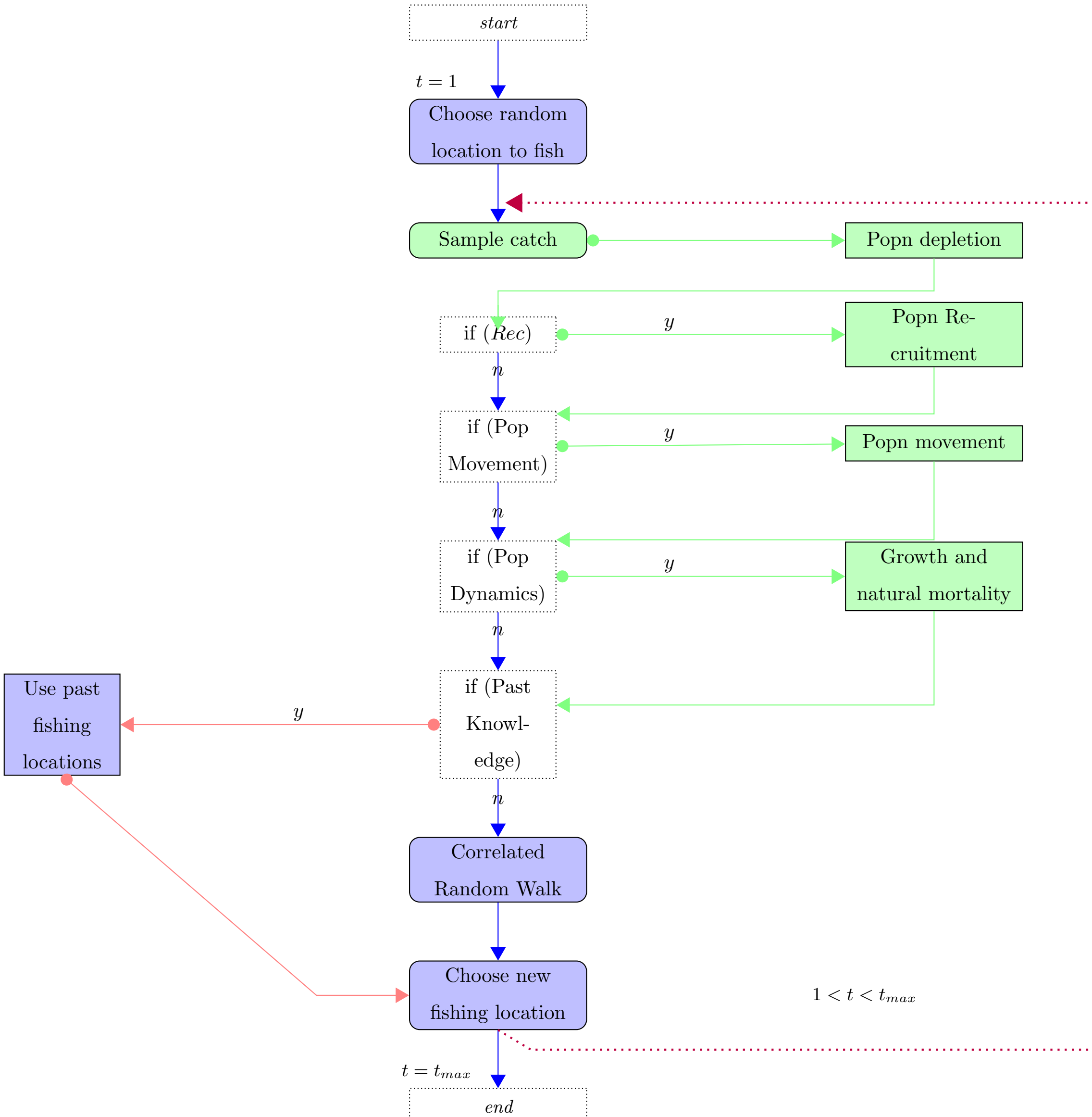

Figure 1: Overview Schematic of simulation model. The blue boxes indicate fleet dynamics processes, the green boxes population dynamics processes while the white boxes are the time steps at which processes occur; t = tow, $tmax$ is the total number of tows; (Rec), (Pop Movement), (Pop Dynamics) logic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

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

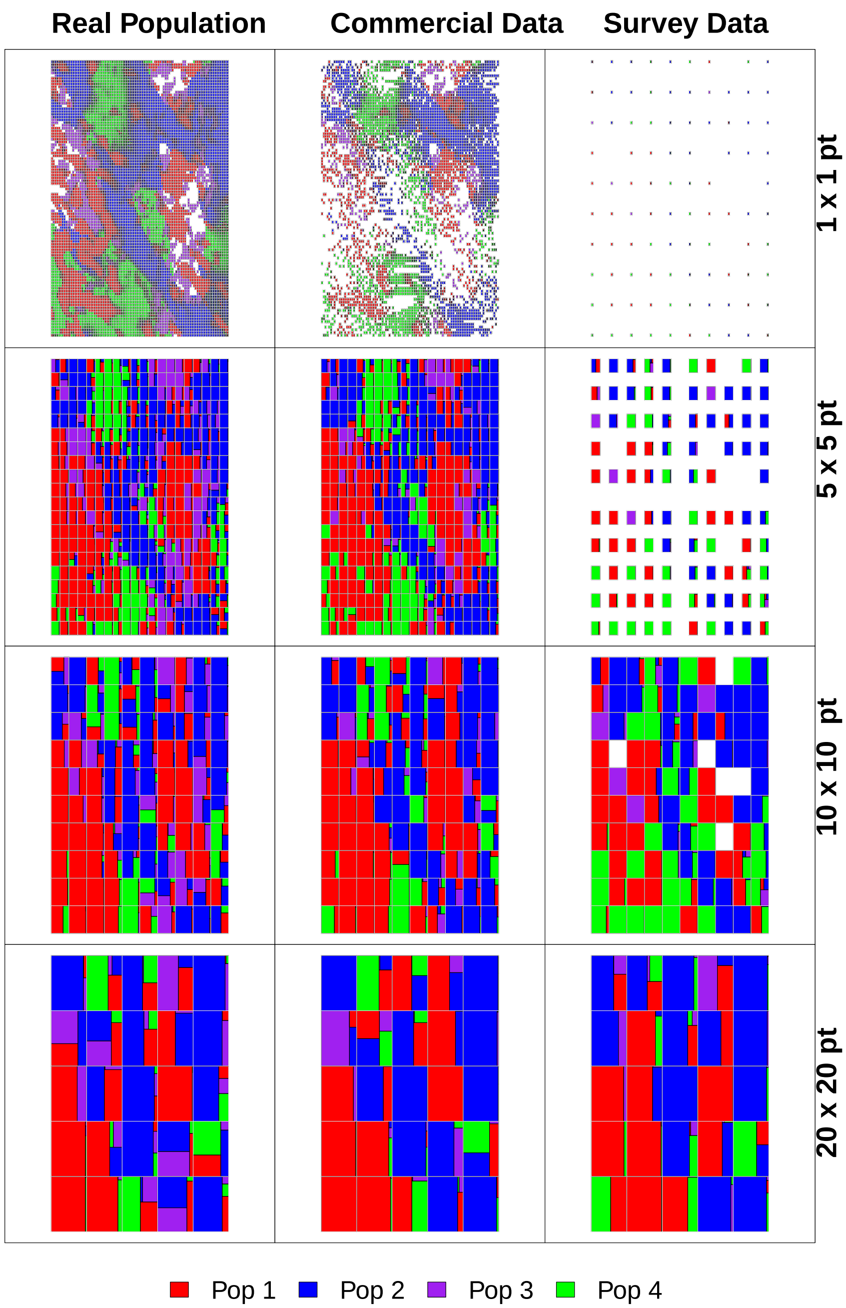

Figure 2: Data aggregation at different spatial resolutions

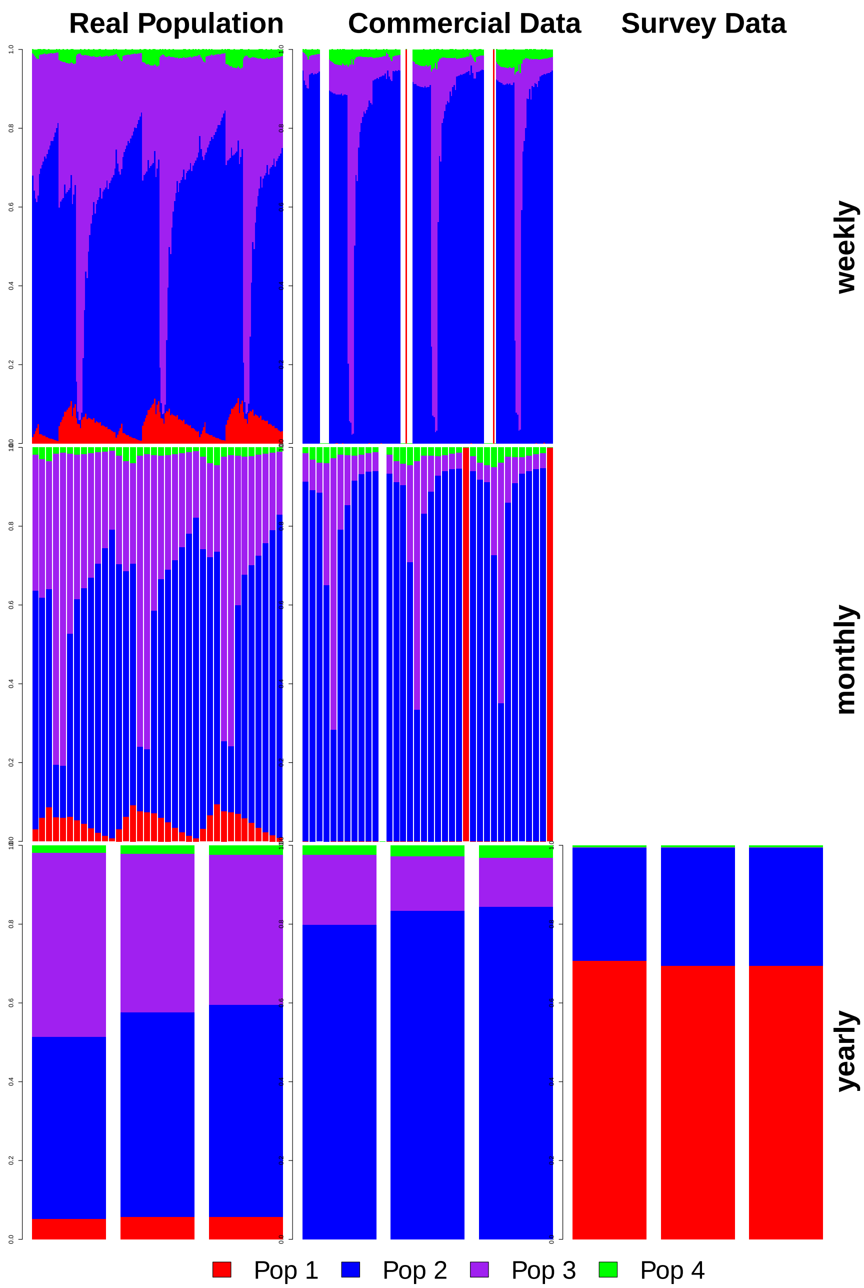

Figure 3: Data aggregation at different temporal resolutions

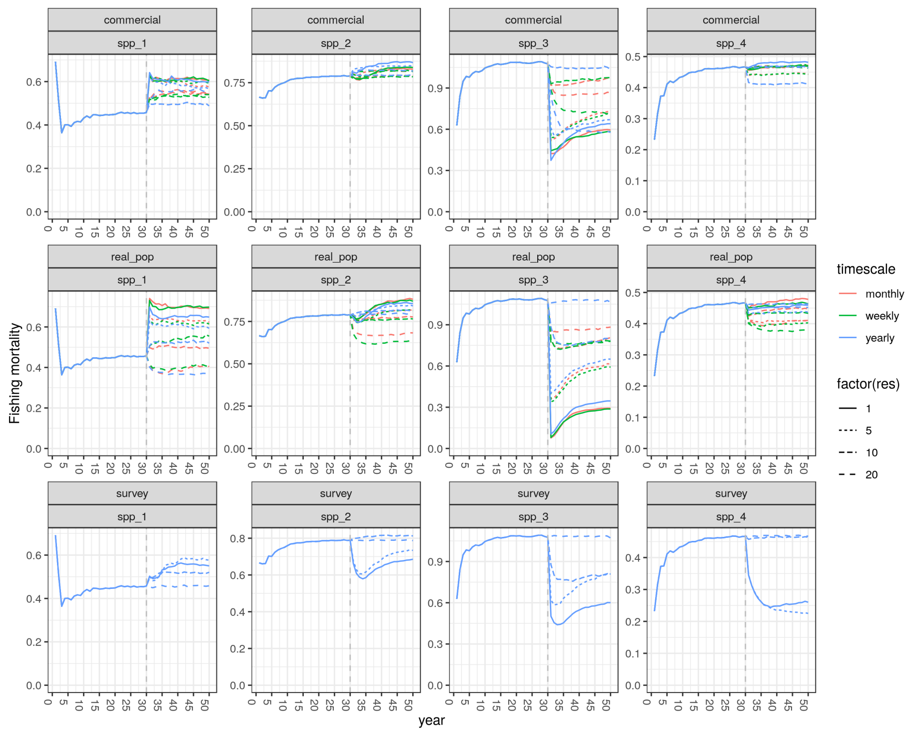

Figure 4: Comparison of closure scenarios - F trends

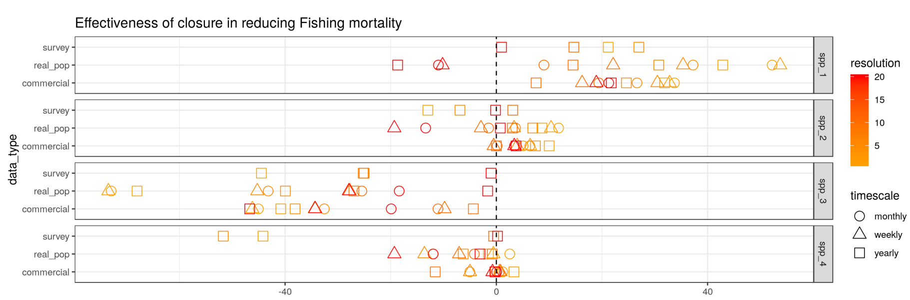

Figure 5: Comparison of closure scenarios

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.

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.