MixFishSim: highly resolved spatiotemporal simulations for exploring mixed fishery dynamics

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Abstract

Fishing exploits spatially and temporally hetergenous 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.

To implement effective spatial measures to reduce discards a good understanding of spatiotemporal fishery dynamics is required. However, traditional scientific advice is limited by a lack of highly resolved knowledge of population distribution, movement and how fishers interact with different fish populations. This reflects that data on fish location at high temporal and spatial resolutions is expensive and difficult to collect and therefore proxies inferred from either scientific surveys or commercial catch data are often used to model distributions, often with limited spatial and temporal resolution.

To understand how resolution impacts mixed fisheries inference, we develop a highly resolved spatiotemporal simulation model incorporating: i) delaydifference population dynamics, ii) population movement using Gaussian Ran-

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dom Fields to simulate patchy, hetergenously distributed populations, and iii)

fishery dynamics for multiple fleet characteristics based on targetting via corre-

lated random walk movement and learned behaviour.

We simulate 20 years of exploitation of the fish populations and use the

results from the fishing model 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 un-

derlying population structures input to the simulation, to establish the poten-

tial and limitations of fishery-dependent data - an inherently biased sampling

method due to fisher's targeting- to provide a robust picture of spatiotemporal

distributions. Finally, we simulate an area closure based on areas defined from

commercial 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 not unbiased,

provides a useful tool for managing catches in mixed fisheries if applied at the

correct spatiotemporal scale.

[333 words]

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1. Introduction

Fishers exploit fish populations that are heterogenously distributed in space

and time with verying knowledge of species distributions using species-unselective

fishing gear. Fisheries that catch an assemblage of species, known as mixed fish-

eries, when managed by single-species quotas can end up discarding overquota

catch leading to overexploitation of fish populations. Reducing discarding is

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crucial to ensure biological and economic sustainability of fisheries and implementation of an ecosystem approach to fisheries. As such there is increasing interest in technical solutions such as gear and spatial closures as ways of avoiding discards.

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Use of spatial management as a tool has been proposed as a method to reduce discards. However, its implementation 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 management is crucial in order to implement measures at a resolution that ensures effective management[1] 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.

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Ensuring measures are implemented at an appropriate scale has been a chal-22 lenge in the past that has led to ineffectual measures with unitended conse-23 quences such as limited impact towards the management objective or increased 24 benthic impact on previously unexploited areas (e.g. the cod closure in the 25 North Sea[2, 3]). Since then more refined spatial information has become available through the combination of logbook and Vessel Monitoring System (VMS) 27 data[4, 5, 6, 7] and more real-time spatial management has been possible (e.g. [8]). Such information is, however, patchy and derived from an inherently biased sampling programme (i.e. targeted fishing). Further, fishers generally only 30 recorded landings (not catch) on a daily basis. This leads to questions about 31 the validity of inference that can be drawn from landings data assigned to VMS 32 activity pings.

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In order to understand challenges that face 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 and are known

rather than inferred from sampling or commercial catches. Population movement is driven by a random (diffusive) and directed (advective) process and we incorporate characterisation of a number of different fisheries exploiting four fish populations with different spatial and population demographics.

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Using our model we simulate 20 years of exploitation of the fish populations and use the results from the fishing model to draw inference on the underlying population structures. We compare this inference to: i) a stratified fixed-site sampling survey design commonly used for fisheries monitoring purposes, otherwise know as a fisheries-independent survey, and ii) the underlying population structures input to the simulation.

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We simulate a fishery closure to protect one species based on the fisherydependent inferred distributions at a spatial and temporal scale typical in fisheries management, and assess a theoretical "benefit" to the population, and
effect on the other three populations. Further, we extend our analysis to a
range of spatial and temporal scales to assess the impact of these processes on
the success of the management measure.

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57 2. Materials and Methods

We develop a simulation model with a modular event-based approach, where modules are implemented on independent time-scales appropriate to capture the characteristic of the process modelled (Figure 1). The fishing model operated on a tow-by-tow basis, while population dynamics (fishing and natural mortality, growth) operate on a daily time-step. Population movement occurs on a weekly time-step, while recruitment occurs periodcally each year for a set time period (e.g. 3 weeks) at at specified point individual to a species. The simulation framework is implemented in the statistical software package R [9]; available as an R package from the authors github (www.github.com/pdolder/MixFishSim).

Here we describe each of the model components; 1) Population dynamics, 2)
Recruitment dynamics, 3) Population movement, 4) fishery dynamics.

70 2.1. Population dynamics

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The basic population level processes are simulated using a modified twostage Deriso-Schnute delay difference model [10, 11, 12] occurring at a daily time-step. Here, population biomass growth and depletion for pre-recruits and fish recruited to the fishery are modelled separately as a function of previous recruited biomass, intrinsic population growth and recruitment:

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

where ρ is Brody's coefficient, shown to be approximately equal to exp(-K),
where K is the growth rate from a von bertalanffy logistic growth model [11]. 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 $R_{\tilde{y}}$ is the annual recruits.

Mortality Z can be decomposed to natural mortality, M, and fishing mortality, F, where both M and F are instantaneous rates with M fixed and F calculated by solving the Baranov catch equation [13] for F:

$$C_d = \frac{F_d}{F_d + M_d} * (1 - e^{-(F_d + M_d)}) * B$$

where C is the summed catch from the fishing model across all fleets and vessels for the population during the day, and B the daily biomass for the species. [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!) -

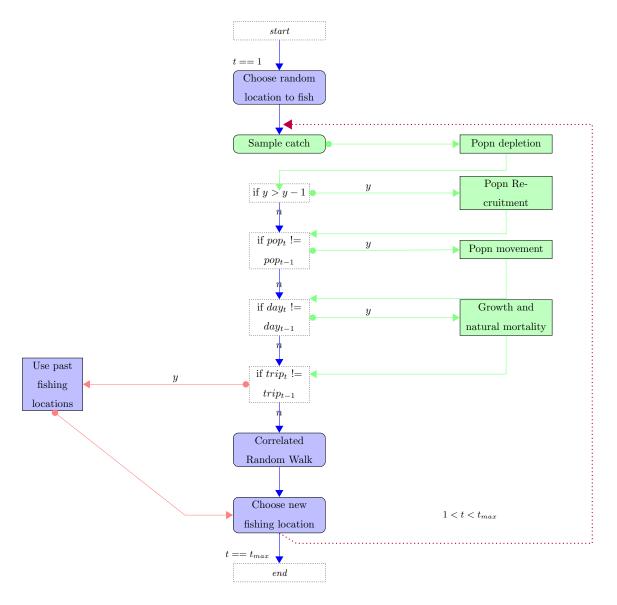


Figure 1: Overview Schematic of simulation model. The blue boxes indicate fleet dynamics processes, the green boxes population dynamics processes while the white boxes are the timesteps at which processes occur; t = tow, tmax is the total number of tows, y = year, pop_t is time of population movement, day is a day timestep, trip is a trip time step.

- catch for a vessel is a product of catchability and biomass, i.e. C = qB, but this
- ocatch is summed to solve for F. So its both really]

2.2. Recruitment dynamics

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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 ([14]):

$$\bar{R} = \frac{(\alpha * B)}{(\beta + B)}$$

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

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 [15]

$$\bar{R} = B * e^{(\alpha - \beta * B)}$$

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

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

2.3. Population movement

To simulate how fish populations might be distributed in space and time,
we employed a Gaussian spatial process to model habitat suitability for each of
the populations, with an advection-diffusion process to control how the populations moved over time with a moving temperature covariate to capture temporal
dependencies. This was intended to balance realism in population movement,
capturing the main directed and random processes, and practicality of modelling the population rather than individual fish.

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For the habitat we define a Gaussian random field process, $\{S(x): x \in \mathbb{R}^2\}$, that is a stochastic process where any collection of locations x_1, \ldots, x_n where for each $x_i \in \mathbb{R}^2$, the joint distribution of $S = \{S(x1), \ldots S(x_n)\}$ is multivariate Gaussian. The distribution is specified by its mean function, $\mu(x) = E[S(x)]$ and its covariance function, $\gamma(x, x') = Cov\{S(x), S(x')\}$ [16].

The covariance structure affects the smoothness of the surfaces which the process generates, and we used the $Mat\acute{e}rn$ family of covariance structures, one where the correlation strength weakens the further the distance apart (i.e. the correlation between S(x) and S(x') decreases as the distance u = ||x - x'|| increases). The $Mat\acute{e}rn$ 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.

The temperature field is simulated to be 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 cycle to lower temperatures and low temperature areas vice versa. Each population is assigned a thermal tolerance with mean, μ and variance, σ^2 so that each cell and population temperature suitability is defined that:

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

Where $Tol_{c,p}$ is the tolerance of population p in cell c, T_c is the temperature in the cell and μ and σ^2 the mean and standard deviation of the population temperature tolerance.

 In the simulation model, the habitat for each of the populations is generated through the *RFSimulate* function of the *RandomFields* R package [17], implementing different parameter settings to affect the patchiness of the populations. Each population is initialised at a single location, and subsequently moves according to a probabilistic distribtion based on habitat suitability, temperature and distance from current cell.

$$Pr(B|A) = \frac{e^{-\lambda * d_{AB}} \cdot (Hab_B^2 \cdot Tol_{B,wk})}{\sum\limits_{c=1}^{C} e^{-\lambda * d} \cdot (Hab_B^2 \cdot Tol_{B,wk})}$$
(2)

Where d_{AB} is the euclidean distance between cell A and cell B, λ is a given rate of decay, Hab_B^2 is the squared index of habitat suitability for cell B and $Tol_{B,wk}$ the temperature tolerance for the cell in week wk; population index, p has been dropped for simplicity.

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During specified weeks of the year, the habitat quality is modified for spawning habitats, meaning each population has a concentrated area where spawning takes place and the population moves towards this in the weeks prior to spawning.

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2.4. Fleet dynamics

The fleet dynamics can be broadly categorised into three components; fleet targeting - which determines the fleet catch efficiency and preference towards a particular species; trip-level decisions, which determine 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.

2.4.1. Fleet targeting

Each fleet of n vessels is characterised by both a general efficiency, Q, and a population specific efficiency, Q_p . Thus, the product of these parameters 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 (as well as some randomness from the exploratory fishing process) determines the preference of fishing locations for the fleet. All species prices are kept the same, across fleets, though can be made to vary seasonally.

2.4.2. Trip-level decisions

Several studies (e.g.[18, 19, 20]) have confirmed past activity and past catch 170 rates are strong predictors of fishing location choice. For this reason, the fleet 171 dynamics sub-model includes a learning component, where a vessel's initial fishing location in a trip is based on selecting from previously successful fishing 173 locations. This is achieved by sorting all previous fishing events in the previous 174 trip as well as the previous time periods in past years, and choosing randomly 175 from the top x % of fishing events in value. Simulation testing indicated that this learning increased the mean value of catches for the vessels, over just relying 177 on the correlated random walk function. 178

2.4.3. Within-trip decisions

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Fishing locations within a trip are determined by a modified random walk process. A random walk type was chosen as it is the simplest assumption commonly used in ecology to describe animal movement which searching for homogeneously distributed prey about which there is uncertain knowledge. In a random walk, movement is a stochastic process through a series of steps that can either be equal in length or take some other functional form. The direction of the random walk can be correlated, a characteristic known as 'persistence', providing some overall location of directional movement [21] or uncorrelated.

A *lévy walk* is a particular form of random walk characterised by a heavy-tailed distribution of step-length and 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 [22, 23]. [24] showed that

Peruvian anchovy fishermen have a stochastic search pattern similar to that observed with a lévy walk. However, it remains a subject of debate, with the contention that search patterns may be more simply characteristed as random walks [25] with specific patterns related to the characteristics of the prey field [26].

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We use a modified random walk where directional change is based on a 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 and step length (i.e. the distance travelled from the current to the next fishing location) is determined by relating recent fishing success, measured as the summed value of fish caught,

$$Rev = \sum_{s=1}^{\infty} C_s \cdot Pr_s$$

where C_s is catch of a species, and Pr_s price of a species, to step distance. 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.

The step function takes the form:

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

So that, a step from (x1,y1) to (x2, y2) is defined by:

$$(x2, y2) = x1 + StepL \cdot \cos(\frac{\pi \cdot Br}{180}),$$

$$y1 + StepL \cdot \sin(\frac{\pi \cdot Br}{180})$$

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

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

with 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 parameterised as for β_3 in the step length function.

2.4.4. Local population depletion

Where several fishing vessels are exploiting the same fish population compe-212 tition is known to play an important role in local distribution of fishing effort 213 [27]. If several vessels are fishing on the same patch of fish, local depletion and 214 interference will affect fishing location choice of the fleet as a whole [28, 29]. In 215 order to account for this behaviour, the fishing sub-model operates spatially on 216 a daily time-step so that for future days the biomass available to the fishery 217 is reduced in the areas fished. The cumulative effect is to make heavily fished 218 areas less attractive as future fishing opportunities. 219

2.20 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 present are recorded but not removed from the population. This provides a fishery independent snapshot of the populations at a regular spatial distribution each year, similar to scientific surveys undertaken by fisheries research agencies.

3. Calculation

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3.1. Population parameterisation

We parameterised the simulation model for four populations with differing
habitat preference and temperature tolerances (Figures S1, S3, S4, S5, S6, S7),
population demographic 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 1). 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.

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3.2. Fleet parameterisation

The fleets were parameterised to reflect five different characteristics based on targeting preference and exploitation dynamics (Table 2). This ensures that different fleets have different spatial dynamics, preferentially targeted different fish populations. The stochasticity in the random walk process ensures that different vessels within a fleet have slightly different spatial distributions based on individual experience, while the step function was parameterised dynamically so that vessels take smaller steps where the fishing location yields in a top quartile of the value available in that year (as defined per fleet in Table 2).

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Each fleet was set so that, after the first year, 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 revenue from was found in previous trips.

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, S13 the vessel movements for some trips overlaid on the value field, S14 shows fishing locations for an entire fleet of 20 vessels for a single trip, while S15 shows an example of the step function realisation and turning angles from the correlated random walk.

258 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 with same catchability parameters for all populations (Q = 1).

2 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 reduc-

tion in catches of a population given spatial closures. To do so, we first set up with simulation to run for 10 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.

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We allow the simulation to run unrestricted for 5 years, and subsequently close areas for the last 5 years of the simulation based on data (either derived from the commercial catches, fisheries-independent survey or the 'real population' - the underlying populations assumed to be known perfectly) used at different spatial and temporal scales.

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- The following steps are undertaken to determine closures:
- 1. Extract data source
- 278 2. Aggregate according to resolution
- 3. Interpolate across entire area at desired resoltion
 - 4. Close top 5 % of areas
- 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.
- Survey closures were on an annual basis only, as this was the most temporally resolved survey data available.

287 4. Results

- The species distribution themselves
- 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 5×5 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 10×10 and 20×20 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 20×20 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 20×20 , 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 \sim 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.

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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

371 Appendices

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372 Abbreviations

Detail any unusual ones used.

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Table 1: Population dynamics and movement parameter setting

Parameter	Pop 1	Pop 2	Pop 3	Pop 4
Habitat quality				
Matérn ν	1/0.15	1/0.05	1/0.55	1/0.05
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	40,50,40,50;	50,60,30,40;	30,34,10,20;	50,55,80,85;
box)	80,90,60,70	80,90,90,90	60,70,20,30	30,40,30,40
Spawning multiplier	10	10	10	10
Movement λ	0.3	0.3	0.3	0.3
Population dynamics				
Starting Biomass	1e5	2e5	1e5	1e4
Beverton-Holt Recruit 'a'	60	100	80	2
Beverton-Holt Recruit 'b'	250	250	200	50
Beverton-Holt Recruit σ^2	0.4	0.3	0.4	0.3
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	0.2	0.2	0.1

Table 2: Fleet dynamics parameter setting							
Parameter	Fleet	Fleet	Fleet	Fleet	Fleet		
	1	2	3	4	5		
Targeting preferences							
Price Pop1	100	100	100	100	100		
Price Pop2	200	200	200	200	200		
Price Pop3	600	600	600	600	600		
Price Pop4	1600	1600	1600	1600	1600		
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	10	8	12	7		
step function β_3	Q90	Q90	Q85	Q90	Q80		
step function $rate$	10	20	15	25	10		
Past Knowledge	${ m T}$	Τ	Τ	Τ	T		
Past Year & Month	${ m T}$	T	T	T	${f T}$		
Past Trip	${ m T}$	${ m T}$	${ m T}$	${ m T}$	T		
Threshold	0.75	0.75	0.75	0.75	0.75		

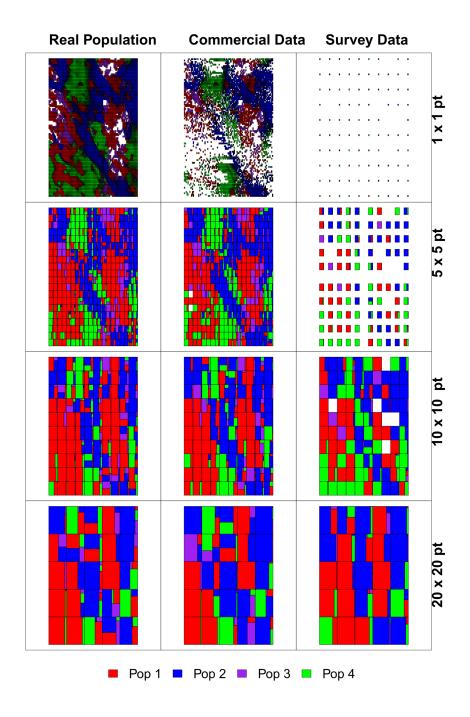


Figure 2: Data aggregation at different spatial resolutions

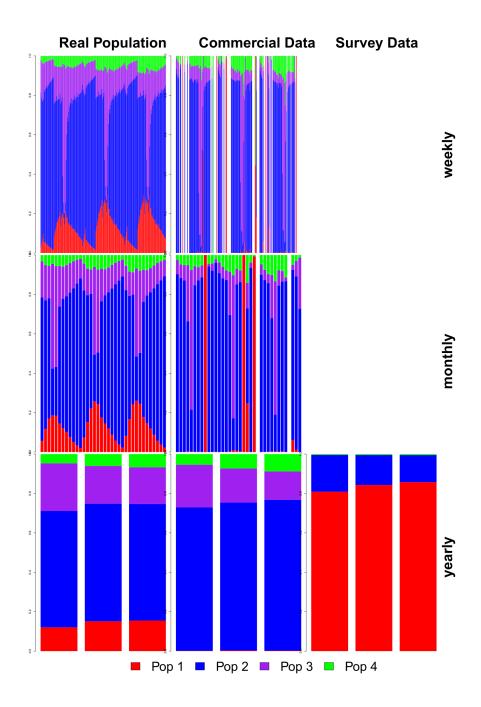


Figure 3: Data aggregation at different temporal resolutions

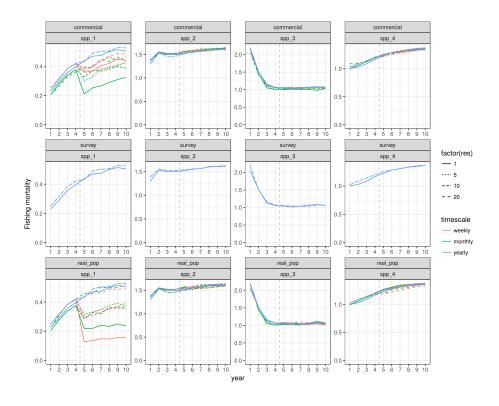


Figure 4: Comparison of closure scenarios - F trends



Figure 5: Comparison of closure scenarios

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