Highly resolved spatiotemporal simulations for exploring mixed fishery dynamics

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Abstract

To understand how data resolution impacts inference on mixed fisheries interactions we developed a highly resolved spatiotemporal discrete-event simulation model ('MixFishSim')[CM: I think *MixFishSim* is more effective] incorporating: i) delay-difference population dynamics, ii) population movement using Gaussian Random Fields to simulate patchy, heterogeneously distributed and moving fish populations, and iii) fishery dynamics for multiple fleet characteristics based on population targeting under an explore-exploit strategy.~~ This is implemented via a mix of correlated random walk movement (for exploration) and learned behaviour (for exploitation) phases of the fisheries. Fifty years of sub-daily fishing activity was simulated and used to draw inference on the underlying community structures. W~~We applied 'MixFishSim' to~~drawcompared~~ infer~~ences on~~community structure when using data generated from: ~~based on~~commercial catch, a~~simulated~~ fixed-site sampling survey design and the true (simulated) underlying populations. ~~WIn doing so w~~We thereby ~~i)~~establish the potential limitations of fishery-dependent data in providing a robust characterisation~~picture~~ of spatiotemporal distributions.~~; and then ii) simulated an area closure based on~~

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~~areas defined from the different data sources at a range of temporal and spatial resolutions.Our framework allows users to explore the assumptions in modelling observational data and evaluate the underlying dynamics of such approaches at a fine spatial and temporal scale. In application to a mixed fishery exploiting four different populations w~~ ~~We found d~~Different spatial patterns were evident and ~~that~~ the effectiveness of the spatial closure reduced when data were aggregated across larger spatial areas. ~~; and then ii)We then simulated an area closure based on areas defined from the dif~~ A simulated area closure showed that a~~A~~ggregation across time periods has less of a negative impact on the closure success than aggregation over space. ~~ and w~~While not as effective as when based on on the true population, closures based on high catch rates observed in commercial data were still able to reduce fishing on a protected species.

MixFishSim~~Our framework~~ allows users to explore the assumptions in modelling ======= resolutions. Aggregation across time periods has less of a negative impact on the closure success than over space. ~~ and w~~While not as effective as when based on on the true population, closures based on high catch rates observed in commercial data were still able to reduce fishing on a protected species.
Our framework allows users to explore the assumptions in modelling ¿¿¿¿¿¿¿ f5e5489e3bc3778abecffc1d0c3d90fdb3592e8b observational data and evaluate the underlying dynamics of such approaches at a fine spatial and temporal scale. From our application w~~W~~e conclude that commercial data, while containing bias, provide a useful tool for managing catches in mixed fisheries if applied at the correct spatiotemporal scale.

Keywords: spatiotemporal, mixed fisheries, individual based, spatial management, heterogeneity, bycatch avoidance
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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. As fishers do not have full control over what species they select when fishing in 'mixed fisheries' it can result in catch of low quota or protected species. If over-quota catch of a species for which they have no quota is discarded without being accounted for it limits our ability to control fishing mortality (Alverson et al., 1994; Crowder et al., 1998; Rijnsdorp et al., 2007) and the ability to manage fisheries for the biological and economic sustainability (Ulrich et al., 2011; Batsleer et al., 2015).

There is increasing interest in technical solutions such as gear and spatial closures as measures to reduce unwanted catch which is often discarded (Kennelly and Broadhurst, 2002; Catchpole and Revill, 2008; Bellido et al., 2011; Cosgrove et al., 2019). A~~ and a~~daptive spatial management strategies have been proposed as a way of reducing over-quota discards (Holmes et al., 2011; Little et al., 2015; Dunn et al., 2014). However, if fisheries are to reduce unwanted catch through spatial avoidance, an in-depth understanding of spatiotemporal fishery dynamics is required.

Understanding the correct scale for spatial management measures to be effective is crucial as it enables implementation of effective solutions which minimise economic impact (Dunn et al., 2016). For example, the problem can be to identify a scale that promotes species avoidance for vulnerable or low quota species while allowing continuance of sustainable fisheries for available quota species. Identifying the correct spatial scale remains a challenge because data on fish location at high temporal and spatial resolutions is expensive and difficult to collect and proxies are usually inferred from scientific surveys or commercial catches with limited spatial and temporal resolution. Thus, implementation of spatial measures is hampered by a lack of knowledge of fish and fishery spatiotemporal dynamics and understanding of the scale at which these processes become important for management.

Identifying appropriate spatial scales for fisheries closures ~~has been a highlighted~~ ~~a~~is crucial to their success (Costello et al., 2010; Dunn et al., 2016). Inference on fisheries spatial dynamics is hampered where spatial information is coarse due to low resolution reporting of fisheries catch which is aggregated across larger gridded areas (Branch et al., 2005). Further, if data does not allow identification of spatial features it may lead to poorly sited closures that~~which~~ are ineffectual or have unintended consequences. For example, increased benthic impact on previously unexploited areas from the cod closure in the North Sea were observed without the intended effect of reducing cod exploitation (Rijnsdorp et al., 2001; Dinmore et al., 2003)).

More refined spatiotemporal 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., 2017) and more real-time spatial management has been possible (e.g. Holmes et al., 2011). However, fishers establish favoured fishing grounds through an explore-exploit strategy (Rijnsdorp et al., 2011; Bailey et al., 2019) where they search for areas with high catches and then use experience to return to areas where they have experienced high catch in the past. This leads to an inherently biased sampling where target species are over-represented in the catch as fishers exploit areas of high abundance. There is a need to understand the influence of these biases on any spatial management measures which are implemented based on inference from commercial landings or catch data.

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

1. Do different sources of sampling-derived fisheries data reflect~~s~~ the underlying community structure?

2. How do~~es~~ data aggregation and data source impact on the success of spatial fisheries management measures?

To answer these questions we i) develop a simulation model where population dynamics are highly-resolved in space and time, using a Gaussian spatial process to define suitable habitat for different populations. As the precise locations of the fish are known directly rather than inferred from sampling or commercial catch, we can use the population model to validate how inference from fisheries-dependent and fisheries independent sampling relates to the real community structure in a way we could not with real data. We ii) compare, at different spatial and temporal aggregations, the real (simulated) population distributions to samples from fisheries-dependent and fisheries independent [CM: hyphenate or don't both, i.e., fishery-independent] catches to test if these are a true reflection of the relative density of the populations. We then iii) simulate a fishery closure to protect a species based on different spatial and temporal data aggregations.

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

2. Materials and Methods

A Discrete-event simulation (DES) model of a hypothetical fishery was developed as a software package (*MixFishSim*). The modular approach enabled efficient computation by allowing for sub-modules implemented on time-scales appropriate to capture ~~the~~ characteristics of the different processes (Figure 1). S~~The following s~~ub-modules ~~were included~~ to capture the full system comprised: 1) p~~P~~opulation dynamics, 2) r~~R~~ecruitment dynamics, 3) p~~P~~opulation movement,

4) fishery dynamics.

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

2.1. Population dynamics

The basic population level processes were simulated using a modified two-stage Deriso-Schnute delay difference model that~~which~~ models the fish populations in terms of aggregate biomass of recruits and mature components rather than keeping track of individuals (Deriso, 1980; Schnute, 1985; Dichmont et al., 2003). A daily time-step was chosen to discretise continuous population processes on a biologically relevant and computationally tractable timescale. Population biomass growth was modelled as a function of previous recruited biomass, intrinsic population growth and recruitment functionally linked to the adult population size. Biomass for each cell c was incremented each day d as follows (see~~the full parameter list is detailed in~~ Table 1 for all parameter details):

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

where ρ is Brody's coefficient, shown to be equal to e^{-K} when K is the ~~growth~~ rate at which the asymptote is approached 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 [CM: do we need Wt or can we just use W? Use mass instead of weight?]. α_d represents the proportion of fish recruited during that day for the year, while $R_{c,\tilde{y}(c)}$ is the annual recruits in year y for cell c.

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 $F_{c,d}$:

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

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 is the sum of those across all fleets and vessels, $C_{c,d} = \sum_{fl=1}^{FL} \sum_{v=1}^{V} E_{fl,v,c,d} \cdot Q_{fl} \cdot D_{c,d}$ with fl and FL the fleet and total number of fleets, v and V the vessel and total number of vessels respectively [CM: do we want to allow for different numbers of vessels per fleet? If so, use V_{fl} for the upper limit] and $E_{fl,v,c,d}$ and Q_{fl} fishing effort and catchability of the gear, and $D_{c,d}$ is the density of the population at the location fished.

2.2. Recruitment dynamics

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

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

[CM: Do we include a bias correction? If not the first term is the median, which is fine, just not the mean] 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. The stochastic Ricker form (Ricker, 1954) is [CM: edit as above]:

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

where α is the maximum productivity per spawner and β the density dependent[CM: hyphenate?] reduction in productivity as the SSB increases.

2.3. Population movement dynamics

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

The combined process results in a population structure and movement pattern unique to each population, with population movement occurring on a weekly basis. M~~The decision to mo~~deling population movement on a weekly timescale~~ was to~~ reflects that fish tend to aggregate in species-specific locations ~~that have been~~ observed to last between~~around~~ one and~~to~~ two weeks (Poos and Rijnsdorp, 2007b). Therefore this process approximated the demographic shifts in fish populations throughout a year with seasonal spawning patterns (Figure S7)[CM: shouldn't it be S1 so that the they follow the main ms? Maybe not . . .].

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. 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 with a *Matérn* covariance structure, where the correlation strength weakens with distance controlled by two parameters, with ν a scale parameter in the units of distance and κ a shape parameter which determines the smoothness of the process. We use the most commonly used Matérn covariance structure as it is a flexible form that contains the~~under certain conditions is of the same form as an~~ exponential and double exponential as special cases~~ function~~ and it~~This~~ enables us to model the spatial autocorrelation observed in animal populations where density is more similar in nearby locations~~, but that correlation decreases non-linearly~~ (Tobler, 1970; F. Dormann et al., 2007; Poos and Rijnsdorp, 2007b). We change the parameters to implement different spatial structures for the different populations using the *RandomFields* R package (Schlather et al., 2015). We define a stationary habitat field with an anisotropic pattern (to simulate a depth gradient) and combine it with a temporally dynamic thermal tolerance field to imitate two key drivers of population dynamics without modelling the processes explicitly. Each population was initialised at a single location, and subsequently moved across the entire space according to a probabilistic distribution based on habitat suitability (represented by the normalised values from the GRFs), temperature tolerance and distance from current cell:

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

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

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

A time-varying temperature covariate changes the ~~interaction between time and~~ suitable habitat on a weekly time-step. Each population p was assigned a thermal tolerance with mean, μ_p and standard deviation, σ_p so that each cell and population temperature tolerance is defined as~~that~~:

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

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 the mean and standard deviation of the population temperature tolerance (see Table 2 for variable descriptions).~~. The variables, their meaning and units for population movement is provided in Table 2~~.

~~The final combined process results in a population structure and movement pattern unique to each population, with population movement occurring on a weekly basis. The decision to model population movement on a weekly timescale was to reflect that fish tend to aggregate in species specific locations that have been observed to last around one to two weeks (Poos et al 2007). Therefore this process approximated the demographic shifts in fish populations throughout a year with seasonal spawning patterns (Figure S7).~~

2.4. Fleet dynamics

Fleet dynamics were~~can be~~ broadly categorised into three components. *Fleet targeting* determined~~determines~~ the fleet catch efficiency and preference towards a particular population; *trip-level decisions* determined~~that determines~~ the initial location to be fished at the beginning of a trip; and *within-trip decisions* determined fishing locations~~, that determines movement from one fishing spot to another~~ within a trip. This results in an explore-exploit strategy ~~was implemented in the model that combined these three components~~ for individual vessels to maximise their catch from an unknown resource distribution (Bailey et al., 2019). The decision to use an individual based model for fishing vessels was taken because fishers are heterogeneous in their location choice behaviour due to different objectives, risk preference and targeting preference (Van Putten et al., 2012; Boonstra and Hentati-Sundberg, 2016). Therefore fleet dynamics are emergent from individual dynamics rather than pre-defined group dynamics.

2.4.1. Fleet targeting

Each fleet of n ([CM: can the n's vary by fleet? If so write n_{fl}]) vessels was characterised by both a general efficiency, Q_{fl}, and a population specific efficiency, $Q_{fl,p}$ which are each bound by [0,1]. 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 species 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.

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

Several studies (for a review see Girardin et al., 2017) have confirmed past activity and past catch rates are strong predictors of fishing location choice. For this reason, the fleet dynamics sub-model included a learning component, where a vessel's initial fishing location in a trip was based on selecting from previously successful fishing locations. This was achieved by calculating an expected revenue based on the catches from locations fished in the preceding trip as well as the same month periods in previous years and the travel costs from the port to the fishing grounds. Then a vessel chooses randomly from the top 70 % of fishing events (defined as the 'threshold') in terms of expected profit within that season.

2.4.3. Decision about where to fish within a trip

Fishing locations within a trip are initially determined by a modified random walk process. As the simulation progresses the within-trip decision become gradually more influenced by experience gained from past fishing locations (as per the initial trip-level location choice), moving location choice towards areas of higher perceived profit. A random walk was chosen for the exploratory fishing process as it is the simplest assumption commonly used in ecology to describe optimal animal search strategy for exploiting heterogeneously distributed prey about which there is uncertain knowledge (Viswanathan et al., 1999). In a random walk, movement is a stochastic process through a series of steps. These steps have a length, and a direction that can either be equal in length or take some other functional form. The direction of the random walk was also correlated (known as 'persistence') providing some overall directional movement (Codling et al., 2008).

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

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

where $L_{c,d,p}$ is landings of a population p, and Pr_p price of a population. All population prices were kept the same across fleets and seasons. Here, when fishing is successful vessels remain in a similar location and continue to exploit the local fishing grounds. When unsuccessful, they move some distance away from the current fishing location. The movement distance retains some degree of stochasticity, that can be controlled separately, but is determined by the relationship: ([CM: use ln where we use the natural logarithm. Double-check this equation is right as per the code. As it looks different here: `https://github.com/pdolder/MixFishSim/blob/master/R/step_length.R`]. There it looks to simplify to $b_2(b_1/b_2)^{Rev/b_3}$, assuming parameters are positive.)

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

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 (x_t, y_t) to (x_{t+1}, y_{t+1}) is defined by:

$$\begin{aligned}(x_{t+1}, y_{t+1}) =& x_t + Le \cdot \cos\left(\frac{\pi \cdot Br_{t+1}}{180}\right), \\ & y_t + Le \cdot \sin\left(\frac{\pi \cdot Br_{t+1}}{180}\right) \\ when \quad & Br_t < 180, Br_{t+1} = 180 + \sim vm[(0,360), k] \\ & Br_t > 180, Br_{t+1} = 180 - \sim vm[(0,360), k]\end{aligned} \tag{9}$$

where Le is the step length, Br_t is the bearing at time t, k the concentration parameter from the von Mises distribution that we correlate with the revenue so that $k = (Rev + 1/RefRev) \cdot max_k$, where max_k is the maximum concentration value, k, and $RefRev$ is parametrised as for β_3 in the step length function. Details of the variables, meaning and units for fleet dynamics are provided in Table 3.

2.4.4. Local population depletion

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

2.5. Fisheries independent survey

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

2.6. Software: R-package development

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

3. Model calibration

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

3.1. Population models

We calibrated the simulation model for four example populations with different demographics, growth rates, natural mortality and recruitment (Table 4). Habitat preference (Figure S3) and temperature (Figures S5, with temperature tolerance S6) defined to be unique to each population resulting in differently weekly distribution patterns (Figures S7-S9). In addition, each of the populations was assumed to have two defined spawning areas that result in the populations moving towards these areas in pre-defined weeks (Figure S4) with population-specific movement rates (Table 4). The population demographics were defined to broadly represent three mobile low-medium value groundfish species and one high value species with low mobility, with the dynamics hypothetical but ~~as you~~ might be expected ~~to find~~ in a typical demersal fishery.

3.2. Fleet calibration

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

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

3.3. Survey settings

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

3.4. Example research question

To illustrate the capabilities of *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.

How does sampling-derived fisheries data reflect the underlying population structure?

To answer this question we compare different spatial and temporal aggregations of the true population distributions to:

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

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

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 true population) used at different spatial and temporal scales.

The following steps are undertaken to determine closures:

1. Extract data source (true population, commercial or survey),

2. Aggregate according to desired spatial and temporal resolution,

3. Interpolate across entire area at desired resolution using simple bivariate interpolation using the *interp* function from the R package akima (Akima and Gebhardt, 2016). This is intended to represent a naive spatial model of catch rates, without knowledge of the spatial population dynamics.

4. Close area covering top 5 % of catch rates.

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

- **data types:** commercial logbook data, survey data and true 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:** highest 5 % of catch rates for the protected population ([CM: do we need this as it's common to all scenarios and is above?])

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

4. Results

4.1. Emergent simulation dynamics

Individual habitat preferences and thermal tolerances result in different spatial habitat use for each population (Figure S1) and consequently different seasonal exploitation patterns (Figure S2).

It can be seen from a single vessels movements during a trip that the vessel exploits three different fishing grounds, each of them multiple times (Figure 2(A))([CM: I'd drop the sub-figure parentheses: Figure 2A]), while across several trips fishing grounds that are further apart are fished (Figure 2 (B)). These different locations relate to areas where the highest revenue were experienced, as shown by Figure 2 (D), where several vessels tracks are overlaid on the revenue field, i.e. ([CM: do we need this equation as we have a revenue equation above?])

$$Rev_c = \sum_{p=1}^{P} B_{c,p} \cdot Q_{fl,p} \cdot Pr_p$$

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

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

~~The aggregated C~~Catch composition aggregated at different spatial resolutions from each of the data sources (~~which shows~~ average seasonal patterns over a ten-year period) highlights different patterns in perceived community structure depending on the data source and aggregation level (Figure 3). The finer spatial grid for the true 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). S~~The s~~urvey 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 true population and the commercial data. Survey data starts to pick out some of the similar patterns as the other data sources, but lacks spatiotemporal coverage. The spatial catch information on a 10 x 10 and 20 x 20 grid lose a significant amount of information about the spatial resolutions for all data sources, and some differences between the survey, commercial and true population data emerge.

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

Weekly~~The~~ commercial data ~~on a weekly basis~~ shows some of the same patterns as the true population, though ~~the~~ population 1 ~~(in red)~~ is less well represented and some weeks are missing catches from the area. Here, weekly and monthly compositions were nearly identical (Figure 4; Table 7). ~~Again, y~~Yearly values h~~e~~ad a similar mean but smaller standard deviation.

The survey data was only available on an annual basis, and showed again a slightly different composition from the true population and the commercial data; in particular a greater proportion of population 4 (Figure 4).

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

~~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 population 3, given availability of data and its use at different resolutions in order to evaluate the trade-offs in data sources.~~

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

The factor most contributing to differences in fishing mortality before and after the closure was the population (72 % showing that the closures were effective for population 3), followed by spatial data resolution (21 %), data type (7 %) with the least important factor the timescale (< 1 %). In general the finer the spatial resolution of the data used the greater reduction in fishing mortality for population 3 after the closures (Figure 6). The notable outliers are the commercial data at the coarsest spatial resolution (20 x 20) at a yearly and weekly timescale, where closures were nearly as effective as the fine-scale resolution. In this case the closures were sufficiently large to protect a core area of the habitat for the population, but this was achieved in a fairly crude manner by closing a large area - including area where the species was not found (Figure 7) that may have consequences in terms of restricting the fishery in a much larger area than necessary. We found that these trade-offs existed, with high catches maintained with an effective closure when the highest resolution data was used, with the effect being linear when the true population distribution was known and also persisting for closures based on commercial information (Figure 8).

5. Discussion

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

5.1. Simulation dynamics

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

Our approach is unique in that it captures fine scale population and fishery dynamics and their interaction in a way not usually possible with real data and thus not usually considered in fisheries simulations. While other simulation frameworks seek to model individual vessel dynamics based on inferred dynamics from VMS and logbook records (Bastardie et al., 2010), or as a system to identify measures to meet particular management goals (Bailey et al., 2019), our framework allows users to explore ~~the~~ assumptions in modelling observational data and to evaluate the underlying dynamics of such approaches at ~~a~~ fine spatial and temporal scales. This offers the advantage that larger scale fishery patterns are emergent properties of the system and results can be compared to those obtained under a statistical modelling framework.

Typically, simulation models that treat fish as individuals are focussed on exploring the inter- and intra- specific interactions among fish populations (e.g. OSMOSE; Shin et al. (2004)) in order to understand how they vary over space and time. Our focus was on understanding the strengths and limitations of inference from catch data obtained through commercial fishing activity with fleets exploiting multiple fish populations. This shows how ~~and~~ realised~~ing~~ catch distributions ~~that~~ may differ from the underlying populations, as identified by Gillis et al. (2008). As such, we favoured a minimum realistic model of the fish populations (Plagányi et al., 2014) taking account of environmental but not demographic stochasticity, while incorporating detailed fishing dynamics that take account of different drivers in a mechanistic way.

Demographic stochasticity arises due to individual-level variability in time to reproduction and death. This form of stochasticity is often modelled by drawing random time intervals from a given distribution (Gillespie, 1977). The impact of demographic stochasticity depends on the population size, with the effects expected to decrease with increasing population size (Lande et al., 2010). This contrasts with environmental stochasticity, which affects all population sizes and is present at the population level in our model by variability in recruitment.

We take account of heterogeneity in fleet dynamics due to different preferences and drivers similarly to other approaches (Fulton et al., 2011), but at an individual vessel rather than fleet level. We do not explicitly define fleets as rational profit maximisers at the outset, but consider there are several stages to development of the fishery; information gathering through search where the resource location is not known, followed by individual learnt behaviour of profitable locations. This provides a realistic model of how fishing patterns are established and maintained to exploit an uncertain resource through an explore-exploit strategy (Mangel and Clark, 1983; Bailey et al., 2019).

5.2. How does sampling-derived fisheries data reflect the underlying population structure?

Our results demonstrate the importance of considering data scale and resolution when using observational data to support management measures. We find that understanding of the community composition dynamics will depend on the level of data aggregation and its important to consider the scale of processes; including population movement rates, habitat uniformity and fishing targeting practices if potential biases in data are to be understood and taken into account (Figures 2 and S1).

Our simulation shows that, despite biases introduced through the fishing process, the commercially derived data could still inform on the key spatial patterns in the community structures where the fisheries occurred, which was spatially limited due to the "hotspots" of commercially valuable species being fished. Similarly, despite ~~the~~ even spatial coverage the survey ~~was able to~~ captured some of the same spatial patterns as the true population, but missed others due to gaps between survey stations limiting spatial and temporal coverage (Figure 3). This provides a challenge when modelling unsampled areas in inferring species distribution maps, though these limitations may be overcome by understanding the relationship between the species and habitat covariates where these are known at unsampled locations (Robinson et al., 2011).

5.3. How does data aggregation and source impact on spatial fisheries management measures?

From our simulations spatial disaggregation was more important than the temporal disaggregation of the commercial data. This reflects the fact that there was greater spatial heterogeneity over the spatial domain than experienced in given~~individual~~ locations over the course of the year (Figure S1).

The yearly data assumes the same proportion of each population caught at any time of the year due to the data aggregation. This assumption introduces ‘aggregation bias’ as the data may only be representative of some point (or no point) in time. The monthly data shows some consistency between the real population and commercial data for population 2 - 4, though population 1 remains under-represented. On an annual basis, interestingly the commercial data under represents the first species (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 population 1 are present and the survey sampling areas where population 1 is more abundant than on average. This indicates that fixed closures, at the right resolution, when based on commercially derived data have the potential to reduce~~d~~ fishing mortality. The likely cost of poor spatial and temporal resolution is associated with reduced effectiveness and potentially closing fishing opportunities for other fisheries (Figure 8).

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

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

5.4. Model assumptions and caveats

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

Fish populations in our simulations move in pre-defined timescales and according to fixed habitat preferences and temperature gradients (Figures S3, S5). Our assumptions in calibrating the model (movement rates, temperature tolerances) will have a direct impact on our conclusions on the relative importance of spatial and temporal processes. These assumptions could be explored in a future study by varying the parameters and assessing the robustness of our conclusions. For our example application we have chosen movement rates to reflect aggregation periods observed in past studies (Poos and Rijnsdorp, 2007b).

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

5.5. Future applications of MixFishSim

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

Other novel applications of our framework could be: testing different survey designs given multiple species and data generating assumptions (Xu et al., 2015); commercial index standardisation methods and approaches and understanding of appropriate scales and data aggregations and non-proportionality in catch rate and abundance (Harley et al., 2001; Maunder and Punt, 2004); exploring assumptions about the distribution of natural mortality and fishing mortality throughout the year and importance of capturing in-year dynamics in estimating stock status (Liu and Heino, 2014); at-sea sampling scheme designs to deliver unbiased estimates of population parameters (Cotter and Pilling, 2007; Kimura and Somerton, 2006); adaptive management (Walters, 2007; Dunn et al., 2016); testing the ability of commonly employed fleet dynamics models such as Random Utility Models to capture fine scale dynamics and understand their importance (Girardin et al., 2017); and as a detailed operating model in a management strategy evaluation (Mahévas and Pelletier, 2004).

6. Conclusions

MixFishSim provides a detailed simulation framework to explore the interaction of multiple fisheries exploiting different fish populations. The framework enables users to evaluate assumptions in modelling commercially derived data through comparison to the true underlying dynamics at a fine spatial and temporal scale. Understanding these dynamics, the limitations of the data and any potential biases that may be introduced when making inference on spatiotemporal interactions will enable users to identify weaknesses in modelling approaches and identity where data collection is needed to strengthen inference.

Our application shows that inference on community dynamics may change depending on the scale of data aggregation. There is an important balance in ensuring that the data are sufficiently spatially and temporally disaggregated that the main features of the data are captured, yet maintaining enough data coverage that the features can be distinguished. We found ~~in our application~~ that there was greater spatial heterogeneity than temporal heterogeneity and that when using aggregated data to define spatial closures coarser temporal resolution (months instead of weeks) could still achieve the same results in reducing exploitation rates of a vulnerable species at the highest temporal resolution data ([CM: reduce the length of this sentence or break it up - it reads well but is a bit long.]). Conversely, reducing the spatial resolution had a negative effect on the effectiveness of the measures ~~(~~though, importantly, there was still some benefit even with coarse spatial resolution~~)~~.

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

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

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Appendices

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

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}
$B_{c,d}$	biomass in cell c for day d	d^{-1}
α	the maximum recruitment rate (Beverton Holt) or maximum productivity per spawner (Ricker)	kg
β	the stock size required to produce half the maximum rate of recruitment (Beverton Holt) or density dependent reduction in productivity per capita of SSB	kg

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

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

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

Variable	Meaning	Units
Rev	Revenue from fishing tow	€
L_p	Landings of population p	kg
Pr_p	Average price of population p	€ kg^{-1}
Le	Step length for vessel	-
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 settings.

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				
Movement $\lambda = 0.1$				
Population dynamics				
Starting Biomass	1e5	2e5	1e5	1e4
Beverton-Holt Recruit α	6	27	18	0.3
Beverton-Holt Recruit β	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
$K = 0.3$				
$wt = 1$				
$wt_{d-1} = 0.1$				
M (annual)	0.2	0.1	0.2	0.1
Movement dynamics				
μ_p	12	15	17	14
σ_p^2	8	9	7	10

Table 5: Fleet dynamics parameter setting.

Parameter	Fleet 1	Fleet 2	Fleet 3	Fleet 4	Fleet 5
Targeting preferences	pop 2/4	pop 1/3	-	pop 4	pop 2/3
Price $Pr_p1 = 100$					
Price $Pr_p2 = 200$					
Price $Pr_p3 = 350$					
Price $Pr_p4 = 600$					
Q_p	0.01	0.02	0.02	0.01	0.01
Q_p	0.02	0.01	0.02	0.01	0.03
Q_p	0.01	0.02	0.02	0.01	0.02
Q_p	0.02	0.01	0.02	0.05	0.01
Exploitation dynamics					
step function β_1	1	2	1	2	3
step function β_2	10	15	8	12	7
step function β_3, the landings value nth quantile	90	90	85	90	80
step function $rate$	20	30	25	35	20
Past Knowledge = TRUE					
Threshold	0.7	0.7	0.7	0.7	0.7
Fuel Cost	3	2	5	2	1

Table 6: Fishing mortality effects of the closure scenarios on population 3 (ordered by most effective first). The fishing mortality rate before the closure was 1.08.

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

53	1.06	-1.64	true Population	yearly	20.00
49	1.07	-1.01	survey	yearly	20.00

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

Data type	Timescale	Population 1	Population 2	Population 3	Population 4
commercial	monthly	0.047(0.014)	94.435(1.47)	3.122(1.468)	2.396(0.444)
commercial	weekly	0.047(0.016)	94.426(1.514)	3.117(1.563)	2.411(0.498)
commercial	yearly	0.051(0.001)	94.388(0.205)	3.021(0.175)	2.539(0.046)
True Population	monthly	9.225(3.872)	83.287(5.522)	3.624(1.151)	3.864(1.519)
True Population	weekly	9.358(3.992)	83.165(5.596)	3.567(1.233)	3.91(1.592)
True Population	yearly	9.899(0.173)	82.25(0.308)	3.821(0.119)	4.031(0.05)
survey	yearly	0.372(0.005)	87.667(0.193)	0.729(0.02)	11.232(0.172)

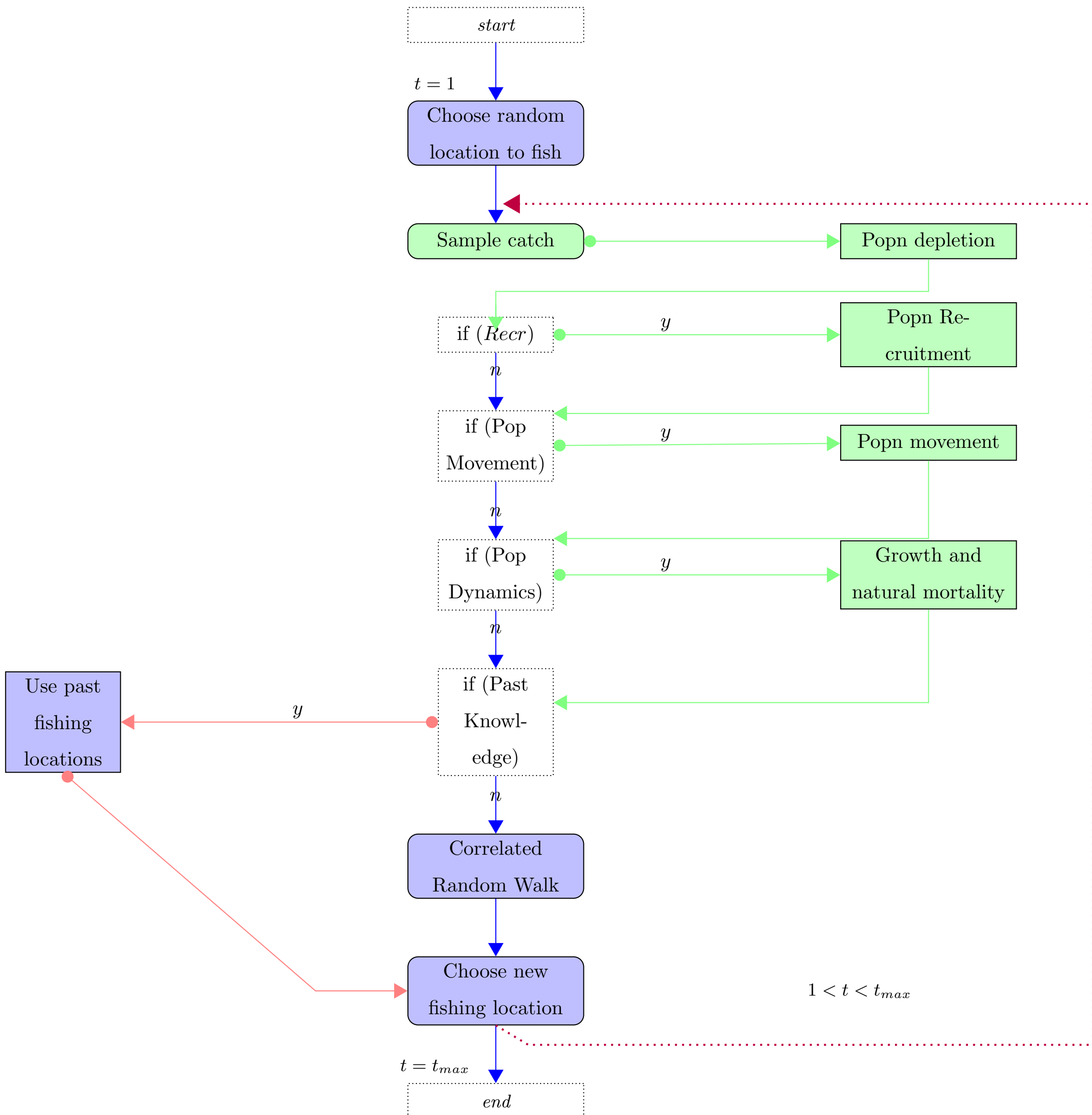

Figure 1: Schematic overview of the simulation model. Blue boxes indicate fleet dynamics processes, the green boxes population dynamics processes while the white boxes are the time steps at which processes occur; t = tow, $tmax$ is the total number of tows; (Recr), (Pop Movement), (Pop Dynamics) logic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

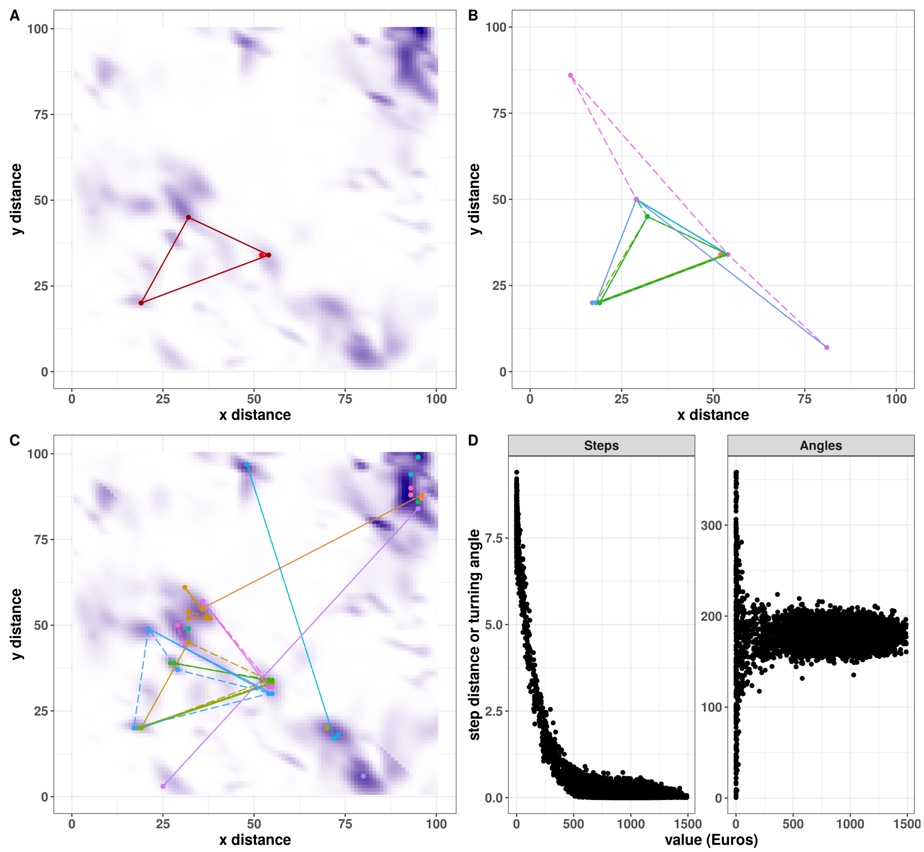

Figure 2: (A) The fishing locations (points) and movements (lines) of a single vessel during a trip overlaid on the revenue of a fishing site (landings x price; darker purple = higher revenue); (B) the fishing locations of the vessel over several trips (value field changes over the period so not shown). Note that movements are a mixture of correlated random walk (solid lines) and experience-based (dashed lines), and that the field is wrapped on a torus so that opposite sides of the spatial domain are considered spatially close; (C) the locations of multiple vessels from the same fleet overlaid on the value field, (D) the realised step distance and turning angles for a single vessel over the simulation.

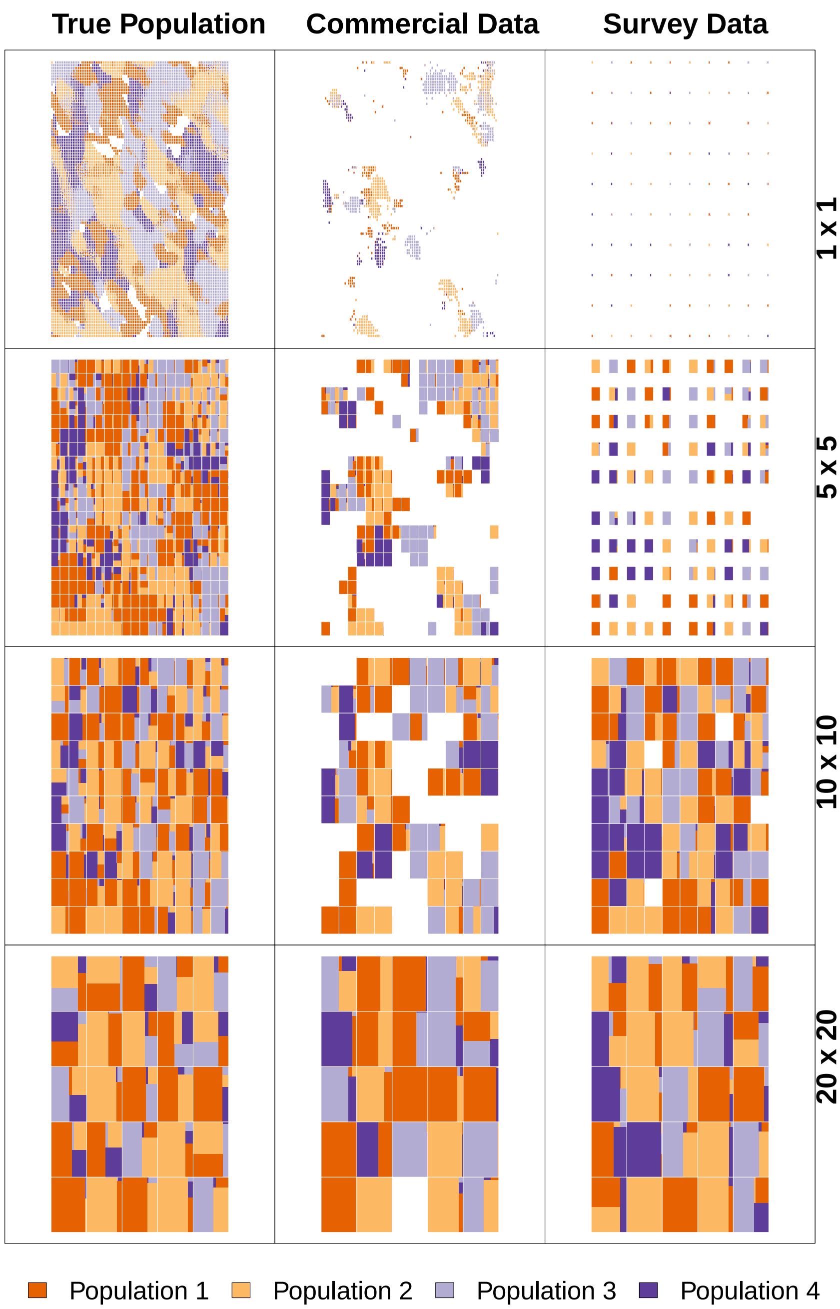

Figure 3: [Colour] Data aggregation at different spatial resolutions over a ten year period. The figure shows catch composition at each spatial unit represented by a square pie chart of the four populations. The area of each colour is proportional to the weight of each population caught in that unit.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

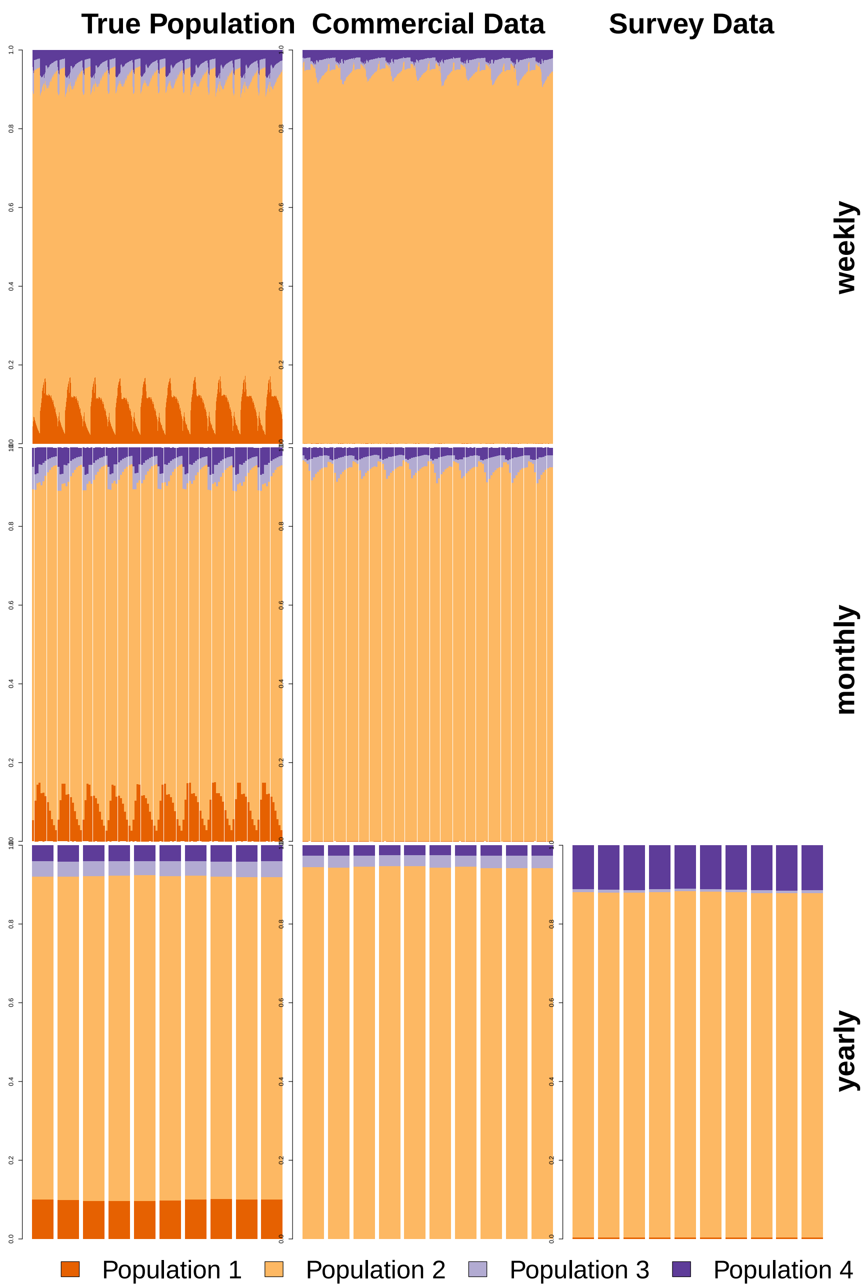

Figure 4: [Colour]Proportion of each population (y axis) for data aggregated at different temporal resolutions. Data is aggregated over a ten-year period for an area 20 x 20. Each bar represents either a week, month or year respectively.

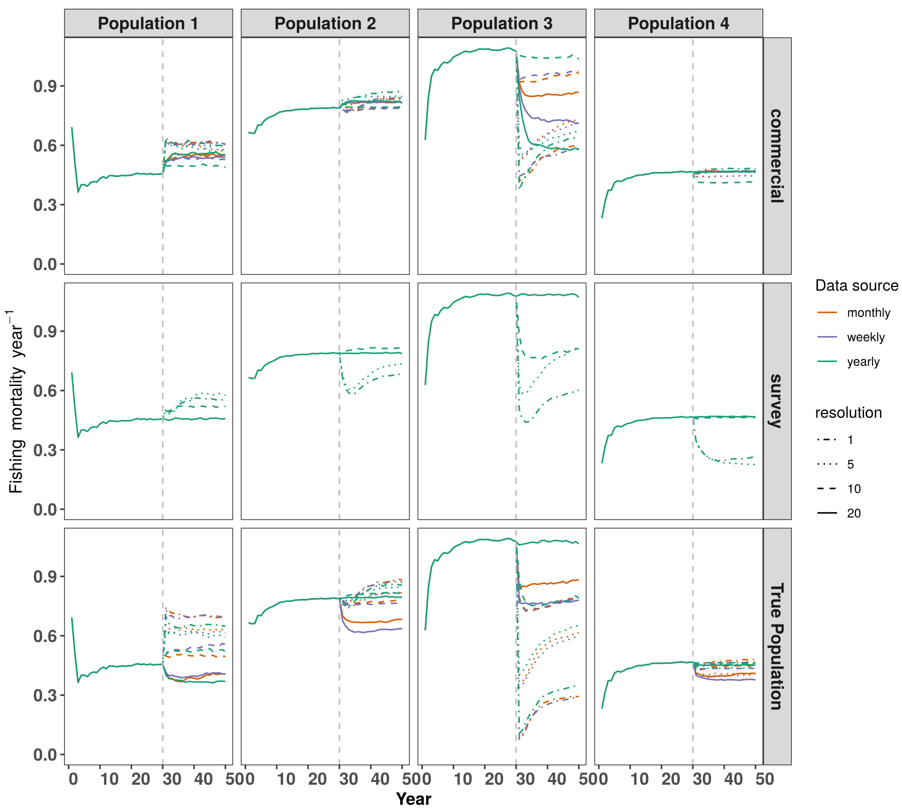

Figure 5: [Colour]Comparison of closure scenarios effect on fishing mortality trends. Line colour denotes timescale, while linestyle denotes spatial resolution. The vertical dashed line indicates the onset of the spatial closures.

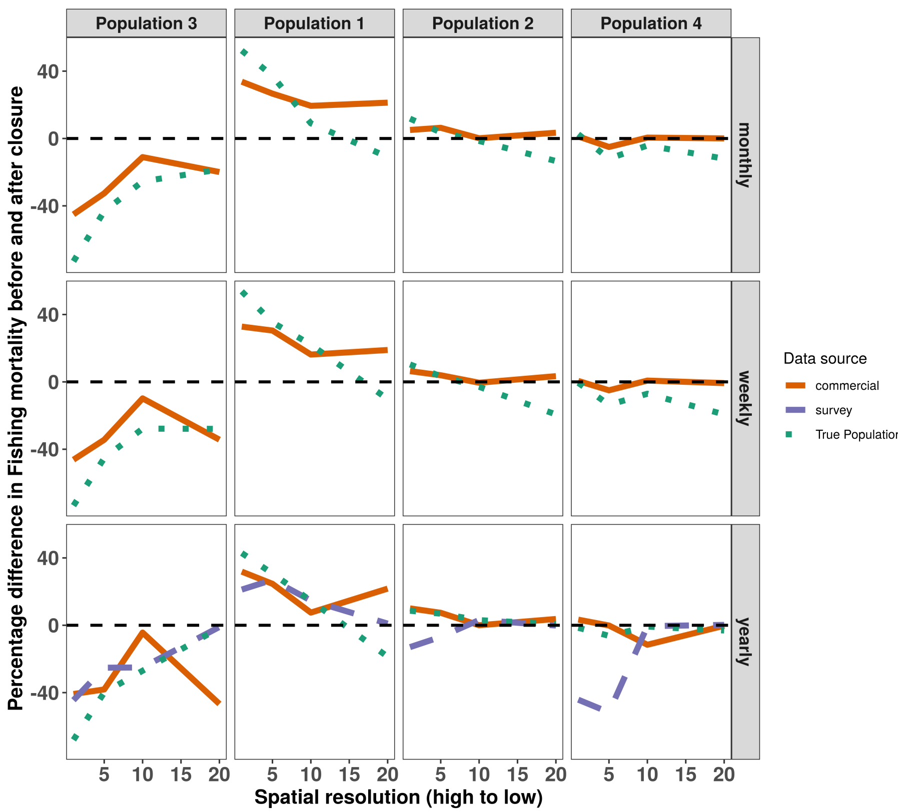

Figure 6: Comparison of closure scenario effectiveness based on different spatial and temporal resolutions.

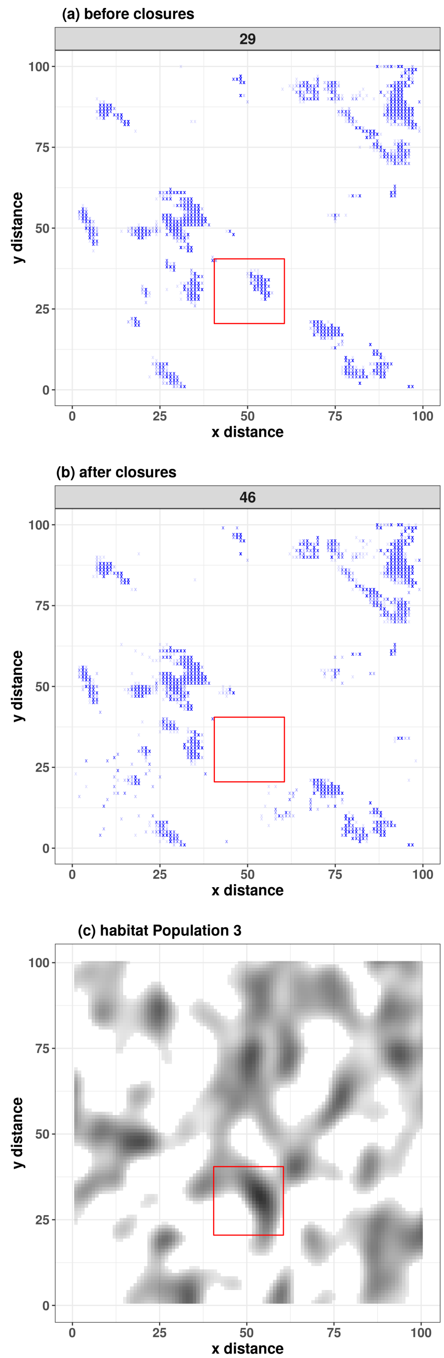

Figure 7: The location of fishing effort, (a) before the spatial closure and (b) after the spatial closure (years in panel), and (c) the suitable habitat for population 3. The site of the closure can be seen in the red box on all three panels.

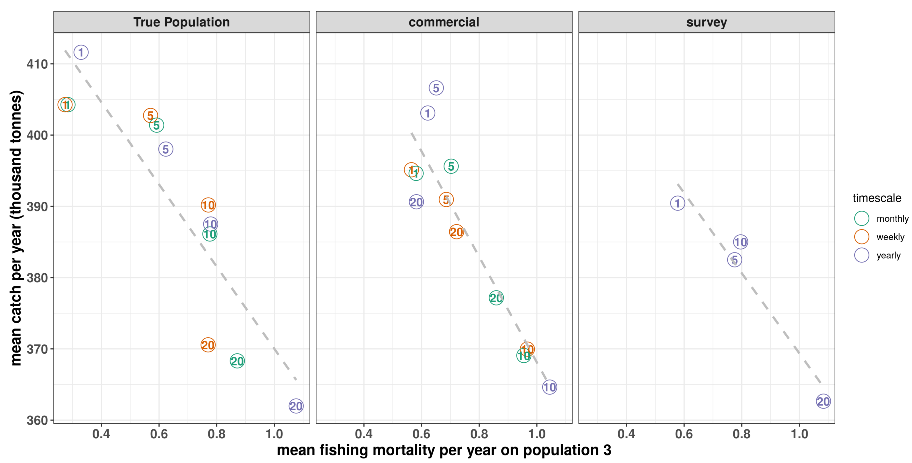

Figure 8: [Colour]Effectiveness of closure with regards to reducing fishing mortality on protected population (further left on x-axis is best) and maintaining high catches in the fishery (highest on y-axis is best). The numbers indicate the spatial resolution of the data, while grey lines indicate the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

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