Working title: Highly resolved spatiotemporal simulations for exploring mixed fishery dynamics

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Abstract

Most fisheries exploit a variety of spatially and temporally heterogeneous fish populations using species-unselective gear. This can result in unintended, unwanted catch of low quota or protected species and reducing these catches is crucial for biological and economic sustainability of 'mixed fisheries'.

If fisheries are to avoid unwanted catch, a good understanding of spatiotemporal fishery dynamics is required. However, traditional scientific advice is limited by a lack of highly resolved knowledge of population distributions and movement, and how fishers interact with different fish populations. Because data on fish location at high temporal and spatial resolutions is expensive and difficult to collect proxies are usually inferred from scientific surveys or commercial catches with limited spatial and temporal resolution.

To understand how data resolution impacts inference on mixed fisheries interactions, we developed a highly resolved spatiotemporal simulation model incorporating: i) delay-difference population dynamics, ii) population movement using Gaussian Random Fields to simulate patchy, heterogeneously distributed populations, and iii) fishery dynamics for multiple fleet characteristics based on

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species targeting under an explore-exploit strategy. This is implemented via

a mix of correlated random walk movement (for exploration) and learned be-

haviour (for exploitation) phases of the fisheries.

We simulated 50 years of fishing and used the results to draw inference on

the underlying community structures. We compared inference from commercial

catch to a simulated fixed-site sampling design and the true underlying com-

munity. We i) establish the potential limitations of fishery-dependent data in

providing a robust picture of spatiotemporal distributions; and then ii) simu-

lated an area closure based on areas defined from the different data sources at a

range of temporal and spatial resolutions. We assessed the effectiveness of the

closures in reducing catches of a fish population.

Our framework allows users to explore the assumptions in modelling obser-

vational data and evaluate the underlying dynamics of such approaches at a fine

spatial and temporal scale. We conclude from our simulations that commercial

data, while containing bias, provide a useful tool for managing catches in mixed

fisheries if applied at the correct spatiotemporal scale.

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1. Introduction

Fishers exploit a variety of fish populations that are heterogeneously dis-

tributed in space and time, with varying knowledge of species distributions. In

doing so fisheries catch an assemblage of species and may discard over-quota

catch when managed by single species quotas and fishers exhaust one or more

quota. This may lead to overexploitation of fish populations (Ulrich et al.,

2011; Batsleer et al., 2015). Discarding of fish in excess of quota limits the abil-

ity to maintain fishing mortality within sustainable limits (Alverson et al., 1994;

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⁹ Crowder et al., 1998; Rijnsdorp et al., 2007) and the ability to manage for the biological and economic sustainability of fisheries. As such, there is increasing interest in technical solutions such as gear and spatial closures as measures to reduce unwanted catch (Kennelly and Broadhurst, 2002; Catchpole and Revill, 2008; Bellido et al., 2011; Cosgrove et al., 2019).

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Adaptive spatial management strategies have been proposed as a way of reducing over-quota discards (Holmes et al., 2011; Little et al., 2014; Dunn et al., 2014). However, implementation is restricted by lack of knowledge of fish and fishery spatiotemporal dynamics and understanding of the scale at which processes become important for management. Understanding the correct scale for spatial measures is crucial for implementing effective solutions which minimising 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.

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Identifying appropriate spatial scales for fisheries closures has been a chal-26 lenge in the past but is crucial to their success (Costello et al., 2010; Dunn 27 et al., 2016). Inference is hampered where spatial information is coarse due to low resolution reporting of fisheries catch which is aggregated across larger grid-29 ded areas (Branch et al., 2005). Further, if data does not allow identification of spatial features it may lead to poorly sited closures which are ineffectual or have unintended consequences. For example, increased benthic impact on previously 32 unexploited areas from the cod closure in the North Sea were observed without 33 the intended effect of reducing cod exploitation (Rijnsdorp et al., 2001; Dinmore 34 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., 37 2016) and more real-time spatial management has been possible (e.g. Holmes et al., 2011). However, fishers establish favoured fishing grounds through an $_{40}$ explore-exploit strategy (Bailey et al., 2018) where they search for areas with

high catches and then use experience to return to areas where they've experi-

enced high catch in the past. This leads to an inherently biased sampling where

target species are over-represented in catch as fishers exploit areas of high abun-

dance.

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- In order to understand the effect of spatiotemporal aggregation of data and fishery targeting we ask two fundamental questions regarding inference derived
- 48 from observational data:
- 1. How does sampling-derived fisheries data reflects the underlying community structure?
- 2. How does data aggregation and source impact on spatial fisheries management measures?

To answer these questions we i) develop a simulation model where population dynamics are highly-resolved in space and time by use of a Gaussian spatial process to define suitable habitat for different populations. Precise locations of the fish being 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 population' distributions to samples from fisheries-dependent and fisheries 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.

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

2. Materials and Methods

An event-based simulation 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 characteristic of the different processes (Figure 1). The following sub-modules were included to capture the full system: 1) Population dynamics, 2) Recruitment dynamics, 3) Population movement, 4) fishery dynamics.

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Population dynamics operate on a daily time-step, 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).

80 2.1. Population dynamics

The basic population level processes were simulated using a modified twostage Deriso-Schnute delay difference model 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 (the full parameter list is detailed in Table 1):

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

where ρ is Brody's coefficient, shown to be equal to e^{-K} when K is the growth rate from a von Bertalanffy logistic growth model (Schnute, 1985). Wt_{R-1} is

the average weight of fish prior to recruitment, while Wt_R is the average recruited weight. α_d represents the proportion of fish recruited during that day for the year, while $R_{c,\tilde{y}}$ is the annual recruits in cell c for year y.

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

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

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

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2.2. Recruitment dynamics

Recruitment is modelled through a function relating to adult biomass. In

MixFishSim, it can be either as a stochastic Beverton-Holt stock-recruit form

(Beverton and Holt, 1957):

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

$$R_{c,d} \sim \log N[(\log(\bar{R}_{c,d}), \sigma^2)]$$
(3)

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

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

$$R_{c,d} \sim \log N[(\log(\bar{R}_{c,d}), \log(\sigma^2))]$$
(4)

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

2.3. Population movement dynamics

Population movement is a combination of random (diffusive) movement, 120 governed by a stochastic process where movement between adjacent cells is 121 described by a set of probabilities, and directed (advective) movement where 122 at certain times of year the population moves towards spawning grounds by 123 increasing the probabilities of moving into the spawning grounds from adjacent 124 cells. We incorporate characterisation of a number of different fishing fleet dynamics exploiting four fish populations with different spatial and population demographics. The following describes the implementation of each of the sub-127 modules. 128

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 133 for any set of cells c_1, \ldots, c_n , the joint distribution of $S = \{S(c_1), \ldots, S(c_n)\}$ is 134 multivariate Gaussian with a $Mat\'{e}rn$ covariance structure, where the correlation strength weakens with distance. This enables us to model the spatial autocor-136 relation observed in animal populations where density is more similar in nearby 137 locations (Tobler, 1970; F. Dormann et al., 2007) and we change the parameters 138 to implement different spatial structures for the different populations using the RandomFields R package (Schlater et al., 2015). We define a stationary habitat 140 field and combine with a temporally dynamic thermal tolerance field to imitate 141

two key drivers of population dynamics. Each population was initialised at a

single location, and subsequently moved according to a probabilistic distribution based on habitat suitability (represented by the normalised values from the GRFs), temperature and distance from current cell:

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

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

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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. In the simulations the populations move towards these cells in the weeks prior to spawning, resulting in directional movement towards the spawning grounds.

An advection-diffusion process controls population movement, with a time-varying temperature covariate used to change 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 variance, σ_p^2 so that each cell and population temperature suitability is defined that:

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

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

The final combined process results in a population structure and movement pattern unique to each species, 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 and Rijnsdorp, 2007b). Therefore this process approximated the demographic shifts in fish populations throughout a year with seasonal spawning patterns (Figure S5).

2.4. Fleet dynamics

The fleet dynamics can be broadly categorised into three components; fleet 174 targeting - that determined the fleet catch efficiency and preference towards a particular species; trip-level decisions, that determined the initial location 176 to be fished at the beginning of a trip; and within-trip decisions, that deter-177 mined movement from one fishing spot to another within a trip. Together, 178 these elements implemented an explore-exploit type strategy for individual ves-179 sels to maximise their catch from an unknown resource distribution (Bailey et al., 2018). The decision to use an individual based model for fishing vessels 181 was taken because fishers are heterogeneous in their location choice behaviour 182 due to different objectives, risk preference and targeting preference (Van Putten 183 et al., 2012). Therefore in the simulations fleet dynamics are the productive of individual experiences rather than pre-defined group dynamics.

2.4.1. Fleet targeting

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

194 2.4.2. Trip-level decisions

Several studies (e.g. Hutton et al., 2004; Tidd et al., 2012; Girardin et al., 2015) have confirmed past activity and past catch rates are strong predictors of fishing location choice. For this reason, the fleet dynamics sub-model included a

learning component, where a vessel's initial fishing location in a trip was based on selecting from previously successful fishing locations. This was achieved by calculating an expected revenue based on the catches from locations fished in the preceding trip as well as the same month periods in previous years and the travel costs from the port to the fishing grounds, and choosing randomly from the top 75 % of fishing events as defined by the expected profit, that has a seasonal component.

205 2.4.3. Within-trip decisions

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

We use a *Lévy flight* which is a particular form of random walk characterised by a heavy-tailed distribution of step-length. The Lévy flight has received a lot of attention in ecological theory in recent years as having shown to have very similar characteristics as those observed by animals in nature, and being a near optimum searching strategy for predators pursuing patchily distributed prey (Viswanathan et al., 1999; Bartumeus et al., 2005; Sims et al., 2008). Bertrand et al. (2007) showed that Peruvian anchovy fishermen have a stochastic search pattern similar to that observed with a lévy flight. However,

it remains a subject of debate (e.g. see Edwards et al., 2011; Reynolds, 2015), with the contention that search patterns may be more simply characterised as random walks (Sakiyama and Gunji, 2013) with specific patterns related to the characteristics of the prey field (Sims et al., 2012).

For our implementation of a random walk directional change is based on a negatively correlated circular distribution where a favourable fishing ground is likely to be "fished back over" by the vessel returning in the direction it came from. The step length (i.e. the distance travelled from the current to the

next fishing location) is determined by recent fishing success, measured as the

summed value of fish caught (revenue, Rev),

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

where L_p is landings of a population p, and Pr_p price of a population. All species 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:

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

Where β_1 , β_2 and β_3 are parameters determining the shape of the step function in its relation to revenue, so that, a step from (x1,y1) to (x2, y2) is defined by:

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

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

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

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

$$(9)$$

where k the concentration parameter from the von Mises distribution that we correlate with the revenue so that $k = (Rev + 1/RefRev) * max_k$, where max_k

is the maximum concentration value, k, and RefRev is parametrised as for β_3 in the step length function. A realised example of the step length and turning 251 angle relationships to revenue can be seen at Figure S12.

2.4.4. Local population depletion 253

Where several fishing vessels exploit the same fish population competition 254 is known to play an important role in local distribution of fishing effort (Gillis 255 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). In order 258 to account for this behaviour, the fishing sub-model operates spatially on a 259 daily time-step so that for future days the biomass available to the fishery is 260 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 262 will be experienced. 263

2.5. Fisheries independent survey

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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 268 on population dynamics). This provides a fishery independent snapshot of the populations at a regular spatial intervals each year, similar to scientific surveys 270 undertaken by fisheries research agencies. 271

2.6. Software: R-package development 273

The simulation framework is implemented in the statistical software package 274 R (R Core Team, 2017) and available as an R package from the authors github 275 site (www.github.com/pdolder/MixFishSim). 276

3. Parameterisation

3.1. Population models

We parametrised the simulation model for four populations with different de-280 mographics; growth rates, natural mortality and recruitment parameters (Table 283 4). Habitat preference (Figure S1) and temperature tolerances (Figures S3, S4) 282 were defined to be unique to each population resulting in differently weekly 283 distribution patterns (Figures S5-S7). In addition, each of the populations was 284 assumed to have two defined spawning areas that result in the populations mov-285 ing towards these areas in pre-defined weeks (Figure S2) with population-specific 286 movement rates (Table 4). In such a configuration, the individual habitat preferences and thermal tolerances result in different spatial habitat use for each 288 population (Figure 2) and consequently different seasonal exploitation patterns 289 (Fishing mortality in Figure 3). 290

291 3.2. Fleet parametrisation

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The fleets were parametrised to reflect five different characteristic fisheries 292 with unique exploitation dynamics (Table 5). By setting different catchability 293 parameters $(Q_{fl,p})$ we create different targeting preferences between the fleets 294 and hence spatial dynamics. The random walk process implies that within a fleet different vessels have different spatial distributions based on individual 296 experience. The step function was parametrised dynamically within the simu-297 lations as the maximum revenue obtainable was not known beforehand. This 298 was implemented so that vessels take smaller steps when fishing at a location 299 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). 301

With increasing probability throughout the simulation, fishing locations were chosen based on experience of profitable catches built up in the same month from previous years and from the previous trip. 'Profitable' in this context was defined as the locations where the top 70~% of expected profit would be found

given 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 growth rate that ensures
the upper asymptote (where decisions are mainly based on past knowledge) is
reached approximately halfway through the simulation.

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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 parameters for all populations ($Q_p = 1$). 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.

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

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The following steps are undertaken to determine closures:

- 1. Extract data source
- 2. Aggregate according to desired spatial and temporal resolution

- 33. Interpolate across entire area at desired resolution using simple bivariate
 336 interpolation using the *interp* function from the R package akima (Akima,
 337 2006). This is intended to represent a naive spatial model of catch rates,
 338 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 'real population',
- temporal resolutions: weekly, monthly and yearly closures,
- spatial resolutions: 1 x 1 grid, 5 x 5 grid, 10 x 10 grid and 20 x 20 grid,
 - closure basis: highest 5 % of catch rates for the protected species
- Survey closures were on an annual basis only, as this was the most temporally resolved survey data available.

⁷ 4. Results

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3 4.1. Simulation dynamics

It can be seen from a single vessels movements during a trip that the vessel exploits four different fishing grounds, three of them multiple times (Figure S9), while across several trips fishing grounds that are further apart are fished (Figure S10). These different locations relate to areas where the highest revenue were experienced, as shown by Figure 4, where several trips for the vessel overlaid on the revenue field, i.e.

$$\sum_{c=1}^{c} \sum_{s=1}^{s} B_{s,c} \cdot Q_{s,c}$$

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 explore phase of the fishery (Figure S11). 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 S12).

355 4.2. How does sampling-derived fisheries data reflect the underlying population 356 structure?

In order to answer this question we compare different spatial and temporal aggregations of the 'real population' distributions to:

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

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

Figure 5 shows the aggregated catch composition from each of the data 364 sources over a ten-year period (to average seasonal patterns) at different spatial resolutions. The finer spatial grid for the real population (top left) and commercial data (top middle) show visually similar patterns, though there are 367 large unsampled areas in the commercial data from a lack of fishing activity 368 (particularly in the lower left part of the sampling domain). The survey data at 369 this spatial resolution displays very sparse information about the spatial distri-370 butions of the populations. The slightly aggregated data on a 5 x 5 grid shows 371 similar patterns and, while losing some of the spatial detail, there remains good 372 consistency between the 'real population' and the commercial data. Survey data 373 starts to pick out some of the similar patterns as the other data sources, but 374 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 resolu-376 tions for all data sources, and some differences between the survey, commercial 377 and 'real population' data emerge. 378

Figure 6 shows the consequences of different temporal aggregations of the data over a ten-year period, with weekly (top), monthly (middle) and yearly (bottom) catch compositions from across an aggregated 20 x 20 area. In the 'real population', the monthly aggregation captures the major patterns of composition seen in the weekly data with similar mean and standard deviations. In

the weekly data species 1 = 9.36 (3.99), species 2 = 83.2 (5.60), species 3 = 3.57 (1.23), species 4 = 3.91 (1.59); in the monthly data species 1 = 9.23 (3.87), species 2 = 83.3 (5.52), species 3 = 3.62 (1.15), species 4 = 3.86 (1.52). While means were similar some of the variation was lost when aggregated to an annual level; species 1 = 9.90 (0.173), species 2 = 82.2 (0.308), species 3 = 3.82 (0.119), species 4 = 4.03 (0.0502).

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The commercial data on a weekly basis shows some of the same patterns as the 'real population', though the species 1 (in red) is less well represented and some weeks are missing catches from the area. Here, weekly and monthly compositions were nearly identical, with monthly composition of species $1 = 0.0472 \ (0.0139)$, species $2 = 94.4 \ (1.47)$, species $3 = 3.12 \ (1.47)$, species $4 = 2.40 \ (0.444)$. Again, yearly values head a similar mean but smaller standard deviation.

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The survey data was only available on an annual basis, and showed again a slightly different composition; species $1=0.372\ (0.00473)$, species 2=87.7 (0.193), species $3=0.729\ (0.0200)$, species $4=11.2\ (0.172)$.

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

The trend in fishing mortality for each species show that in most cases the fishery closure was successful in reducing fishing mortality on the species of interest (species 3; Figure 7), though interestingly the largest reductions in fishing mortality happened immediately after the closures, following which the fisheries "adapted" to the closures and fishing mortality increased again somewhat. The

exception to the success was the closures implemented based on the coarsest spatial (20 x 20) and temporal resolution (yearly) that was ineffective 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.

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A regression tree (using the R package REEMtree (Sela and Simonoff, 2012)) 423 highlights that the factor most contributing to differences in fishing mortality 424 before and after the closure was the population (72 % showing that the closures 425 were effective for population 3), followed by data resolution (21 %), data type 426 (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 428 for population 3 after the closures (Figure 8). The notable outliers are the com-429 mercial data at the coarsest spatial resolution (20 x 20) at a yearly and weekly 430 timescale, where closures were nearly as effective as the fine-scale resolution. In 431 this case the closures were sufficiently large to protect a core are of the habitat 432 for the population, but this was achieved in a fairly crude manner by closing a 433 large area - including area where the species was not found (Figure 9) that may 434 have consequences in terms of restricting the fishery in a much larger area than 435 necessary.

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5. Discussion

Our study evaluates 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 444 due to species targeting in fisheries resulting in preferential sampling (Martínez-445 Minaya et al., 2018). Often data are aggregated or extrapolated which requires assumptions about the spatial and temporal scale of processes. Our study ex-447 plores the assumptions behind such aggregation and preferential sampling to 448 identify potential impacts on management advice. With modern management 449 approaches increasingly employing more nuanced spatiotemporal approaches in 450 order to maximise productivity while taking account of both the biological and 451 human processes operating on different time-frames (Dunn et al., 2016), un-452 derstanding assumptions behind the data used - increasingly a combination of 453 logbook and positional information from vessel monitoring systems - is vital to 454 ensure measures are effective. 455

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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.

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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 465 and thus not usually considered in fisheries simulations. While other simulation 466 frameworks seek to model individual vessel dynamics based on inferred dynam-467 ics from VMS and logbook records (Bastardie et al., 2010), or as a system to 468 identify measures to meet particular management goals (Bailey et al., 2018), our framework allows users to explore the assumptions in modelling observational 470 data and evaluate the underlying dynamics of such approaches at a fine spatial 471 and temporal scale. This offers the advantage that larger scale fishery patterns 472 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 and realising catch distributions that may differ from the underlying populations. 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., 2018).

5.2. How does sampling-derived fisheries data reflect the underlying population 505 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.

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 capture some of the same spatial patterns as the 'real population', but missed others due to gaps between survey stations limiting spatial and temporal coverage. 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 individual locations over the course of the year (Figure 2).

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 species 2 - 4, though species 1 remains under-represented. On an annual basis, interestingly the commercial data under represents the first species (in red) while the survey over represents species 1. This is likely due to the biases in commercial sampling, with the fisheries not targeting the areas where species 1 are present and the survey sampling areas where species 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 reduced fishing mortality. The likely cost of poor spatial and temporal resolution is associated with reduced effectiveness and potentially closing fishing opportunities for other fisheries.

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 significantly (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 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 model 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 have 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 S1, S3). Our assumptions in parametrising 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 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., 2014; 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, 2013); 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. (2016); 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. 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 hypothesis 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.

651 Abbreviations

Detail any unusual ones used.

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659 Appendices

Table 1: Description of	of variables fo	r nonulation	dynamics sub-modu	le-

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}						
ho	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						
$lpha_d$	Proportion of annually recruited fish recruited during	-						
	$\mathrm{day}\ d$							
Baranov catch equation								
$C_{c,d}$	Catch from cell c for day d	kg						
$F_{c,d}$	Instantaneous rate of fishing mortality in cell \boldsymbol{c} on	-						
	$\mathrm{day}\ d$							
$M_{c,d}$	Instantaneous rate of natural mortality in cell \boldsymbol{c} on	-						
	$\operatorname{day} d$							
$B_{c,d}$	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}						
$S_{c,d}$	is the stock size in cell c for day d	d^{-1}						
α	the maximum recruitment rate	kg						
β	the stock size required to produce half the maximum	kg						
	rate of recruitment							

Table 2: Description of variables for population movement sub-module								
Variable	Meaning	Units						
	Population movement dynamics							
Habitat me	Habitat model							
a	b	с						
Thermal to	olerance							
$T_{c,wk}$	Temperature for cell in week	$^{\circ}\mathrm{C}$						
μ_p	Mean of the thermal tolerance for population	$^{\circ}\mathrm{C}$						
σ_p^2	Standard deviation of thermal tolerance for the pop-	$^{\circ}\mathrm{C}$						
	ulation							
Population	n movement model							
λ	decay rate for population movement	-						
$Hab_{c,p}^2$	Square of habitat suitability for cell \boldsymbol{c} and population	-						
	p							
$Tol_{c,p,wk}$	Thermal tolerance for population p in cell c at week	-						
	wk							
d_{IJ}	euclidean distance between cell I and cell J	-						

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

Variable	Meaning	Units					
Short-term fleet dynamics							
Rev	Revenue from fishing tow	€					
L_p	Landings of population p	kg					
Pr_p	Average price of population p	$\in \ \mathrm{kg}^{-1}$					
StepL	Step length for vessel	euclidean					
		distance					
Br	Bearing	degrees					
k	Concentration parameter for Von mises distribution	-					
β_1	shape parameter for step function	-					
eta_2	shape parameter for step function	-					
β_3	shape parameter for step function	-					

Table 4: Population dynamics and movement parameter setting

Parameter	Pop 1	Pop 2	Pop 3	Pop 4
Habitat quality				
Matérn ν	1/0.015	1/0.05	1/0.01	1/0.005
Matérn κ	1	2	1	1
Anisotropy	1.5, 3, -3, 4	1,2,-1,2	2.5,1,-1,2	0.1,2,-1,0.2
Spawning areas (bound	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	0.1	0.1	0.1	0.1
Population dynamics				
Starting Biomass	1e5	2e5	1e5	1e4
Beverton-Holt Recruit 'a'	6	27	18	0.3
Beverton-Holt Recruit 'b'	4	4	11	0.5
Beverton-Holt Recruit σ^2	0.7	0.6	0.7	0.6
Recruit week	13-16	12-16	14-16	16-20
Spawn week	16-18	16-19	16-18	18-20
K	0.3	0.3	0.3	0.3
wt	1	1	1	1
wt_{d-1}	0.1	0.1	0.1	0.1
M (annual)	0.2	0.1	0.2	0.1
Movement dynamics				
μ	12	15	17	14
σ^2	8	9	7	10

Table 5: Fleet dynamics parameter setting								
Parameter	Fleet	Fleet	Fleet	Fleet	Fleet			
	1	2	3	4	5			
Targeting preferences	pop	pop	-	pop 4	pop			
	2/4	1/3			2/3			
Price Pop1	100	100	100	100	100			
Price Pop2	200	200	200	200	200			
Price Pop3	350	350	350	350	350			
Price Pop4	600	600	600	600	600			
Q Pop1	0.01	0.02	0.02	0.01	0.01			
Q Pop2	0.02	0.01	0.02	0.01	0.03			
Q Pop3	0.01	0.02	0.02	0.01	0.02			
Q Pop4	0.02	0.01	0.02	0.05	0.01			
Exploitation dynamics								
step function β_1	1	2	1	2	3			
step function β_2	10	15	8	12	7			
step function β_3	Q90	Q90	Q85	Q90	Q80			
step function rate	20	30	25	35	20			
Past Knowledge	${ m T}$	${ m T}$	${ m T}$	${ m T}$	T			
Past Year & Month	${f T}$	${ m T}$	${ m T}$	T	T			
Past Trip	${ m T}$	Τ	Τ	T	T			
Threshold	0.7	0.7	0.7	0.7	0.7			
Fuel Cost	3	2	5	2	1			

Table 6: Fishing mortality effects of the closure scenarios. Results show the fishing mortality before the closure (f_before) and after the closure (f_after) and the percentage change in f (f_change). The results are ordered by most effective scenario first, least effective last.)

scenario	metric	pop	f_before	f_after	f_change	timescale	basis	data_type	resolution
9	F	spp_3	1.08	0.29	-73.47	weekly	high_pop	real_pop	1.00
10	F	spp_3	1.08	0.29	-72.94	monthly	high_pop	$real_pop$	1.00
11	F	spp_3	1.08	0.35	-68.04	yearly	high_pop	$real_pop$	1.00
45	F	spp_3	1.08	0.58	-46.70	yearly	high_pop	commercial	20.00
1	F	spp_3	1.08	0.58	-46.21	weekly	high_pop	commercial	1.00
23	F	spp_3	1.08	0.59	-45.27	weekly	high_pop	$real_pop$	5.00
2	F	spp_3	1.08	0.59	-45.06	monthly	high_pop	commercial	1.00
7	F	$spp_{-}3$	1.08	0.60	-44.48	yearly	high_pop	survey	1.00
24	F	${\rm spp_3}$	1.08	0.61	-43.20	monthly	$high_pop$	$real_pop$	5.00
3	F	${\rm spp_3}$	1.08	0.64	-40.82	yearly	$high_pop$	commercial	1.00
25	F	${\rm spp} \text{-} 3$	1.08	0.65	-39.94	yearly	$high_pop$	$real_pop$	5.00
17	F	spp_3	1.08	0.67	-38.11	yearly	$high_pop$	commercial	5.00
15	F	${\rm spp_3}$	1.08	0.71	-34.38	weekly	$high_pop$	commercial	5.00
43	F	${\rm spp} \text{-} 3$	1.08	0.71	-34.31	weekly	$high_pop$	commercial	20.00
16	F	${\rm spp} \text{-} 3$	1.08	0.73	-32.58	monthly	$high_pop$	commercial	5.00
51	F	${\rm spp_3}$	1.08	0.78	-27.92	weekly	$high_pop$	$real_pop$	20.00
37	F	${\rm spp_3}$	1.08	0.78	-27.76	weekly	$high_pop$	$real_pop$	10.00
39	F	${\rm spp} \text{-} 3$	1.08	0.79	-26.98	yearly	$high_pop$	$real_pop$	10.00
38	F	spp_3	1.08	0.81	-25.47	monthly	$high_pop$	$real_pop$	10.00
21	F	${\rm spp_3}$	1.08	0.81	-25.21	yearly	$high_pop$	survey	5.00
35	F	spp3	1.08	0.81	-25.05	yearly	$high_pop$	survey	10.00
44	F	spp3	1.08	0.87	-19.91	monthly	$high_pop$	commercial	20.00
52	F	${\rm spp_3}$	1.08	0.88	-18.39	monthly	$high_pop$	$real_pop$	20.00
30	F	spp_3	1.08	0.96	-11.06	monthly	$high_pop$	commercial	10.00
29	F	${\rm spp_3}$	1.08	0.98	-9.80	weekly	$high_pop$	commercial	10.00
31	F	spp_3	1.08	1.03	-4.36	yearly	high_pop	commercial	10.00
53	F	spp_3	1.08	1.06	-1.64	yearly	high_pop	$real_pop$	20.00
49	F	spp_3	1.08	1.07	-1.01	yearly	high_pop	survey	20.00

Table 7: Proportions of each species at different levels of temporal aggregation

data_type	timescale	spp1	sd_spp1	spp2	sd_spp2	spp3	sd_spp3	spp4	sd_spp4
commercial	monthly	0.047	0.014	94.435	1.470	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
$real_pop$	monthly	9.225	3.872	83.287	5.522	3.624	1.151	3.864	1.519
$real_pop$	weekly	9.358	3.992	83.165	5.596	3.567	1.233	3.910	1.592
real_pop	yearly	9.899	0.173	82.250	0.308	3.821	0.119	4.031	0.050
survey	yearly	0.372	0.005	87.667	0.193	0.729	0.020	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; (Rec), (Pop Movement), (Pop Dynamics) logic gates for recruitment periods, population movement and population dynamics for each of the populations, (Past Knowledge) a switch whether to use a random (exploratory) or past knowledge (exploitation) fishing strategy.

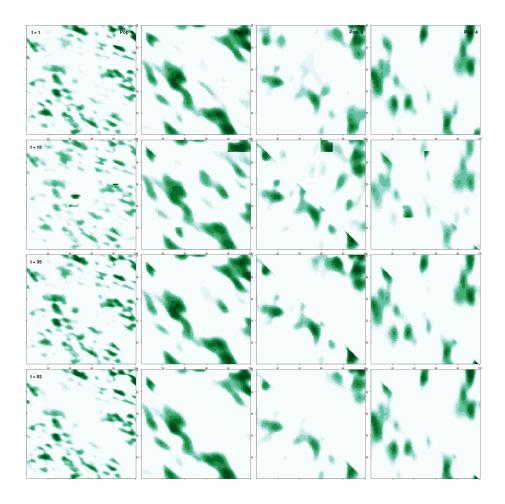


Figure 2: Simulated spatial dynamics - the four populations abundance (log+1) at four time steps.

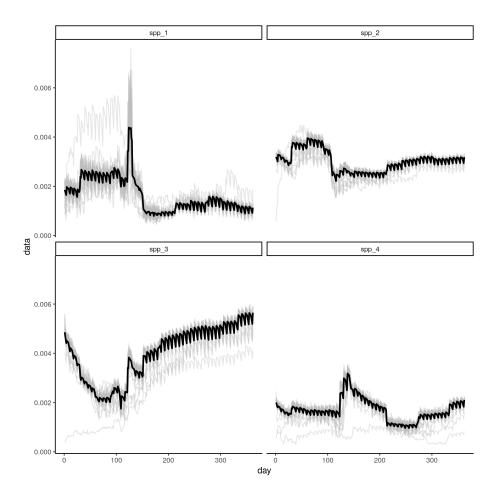


Figure 3: Fishing mortality dynamics - the daily fishing mortalities showing weekly and seasonal patterns in exploitation. Individual years and the light grey lines, the mean of all years the thick black line

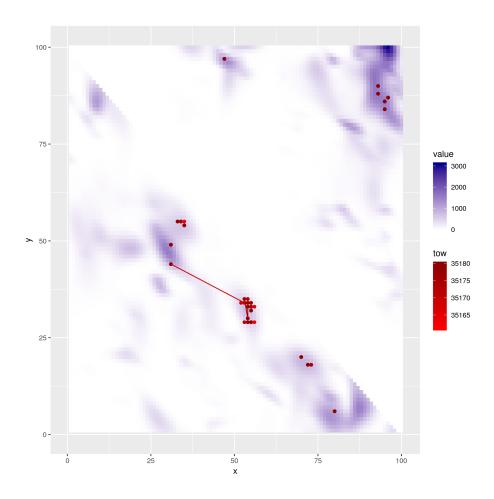


Figure 4: movement of a fleet over a single trip reference overlaid on the value field (i.e. sum of the population abundance ${\bf x}$ catchability ${\bf x}$ value



Figure 5: Data aggregation at different spatial resolutions over a ten year period

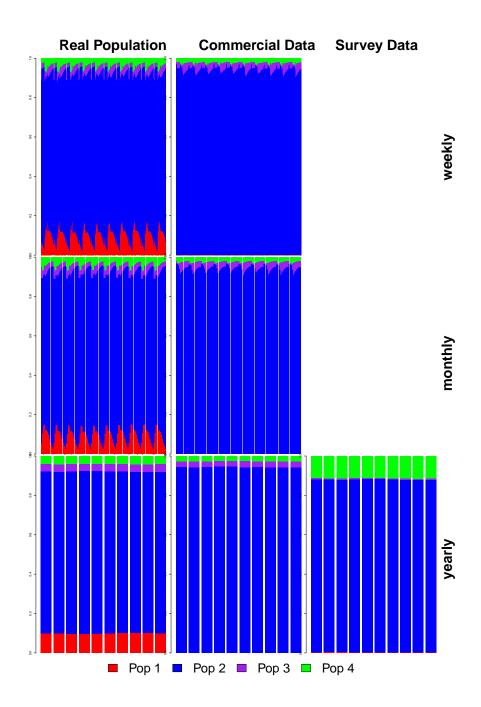


Figure 6: Data aggregation at different temporal resolutions over a ten-year period

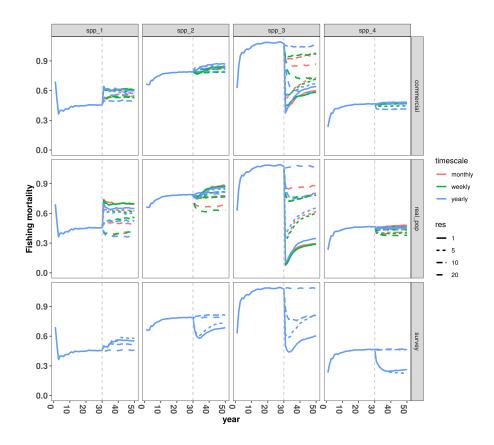


Figure 7: Comparison of closure scenarios effect on fishing mortality trends. Line colour denotes the timescale, while linestyle denotes the spatial resolution.

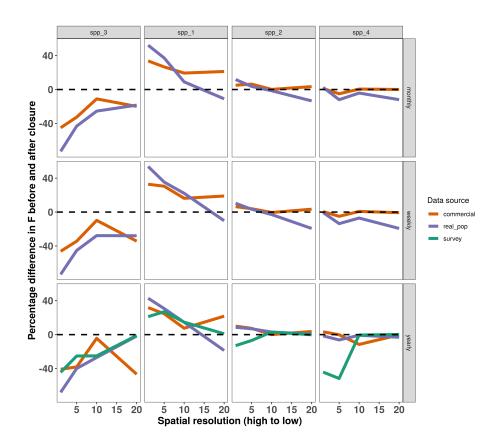


Figure 8: Comparison of closure scenario effectiveness based on different spatial and temporal resolutions.

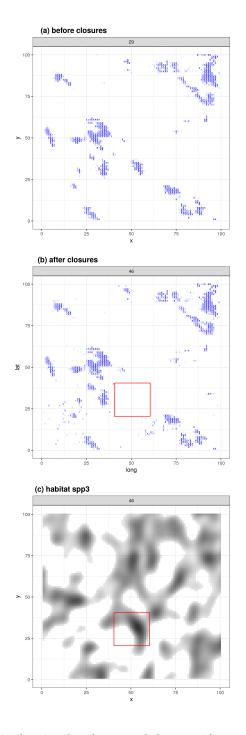


Figure 9: Closure fishing locations based on annual closures with a coarse spatial resolution. Closure location can be seen in red in relation to a) before the closure fishing locations, b) after the closure fishing locations, c) species 3 habitat distribution $42\,$

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