MixFishSim: highly resolved spatiotemporal simulations for exploring mixed fishery dynamics

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Abstract

Most fisheries exploit a variety of spatially and temporally heterogeneous fish populations using species-unselective gear that can result in unintended, unwanted catch of low quota or protected species. Reducing these unwanted catches is crucial for biological and economic sustainability of 'mixed fisheries' and implementation of an ecosystem approach to fishing.

If fisheries are to avoid unwanted catch, a good understanding of spatiotemporal fishery dynamics is required. However, traditional scientific advice is limited by a lack of highly resolved knowledge of population distributions, population movement and how fishers interact with different fish populations. This reflects the fact that data on fish location at high temporal and spatial resolutions is expensive and difficult to collect. Proxies inferred from either scientific surveys or commercial catch data are often used to model distributions, usually with sparse data at 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

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using Gaussian Random Fields to simulate patchy, heterogeneously distributed populations, and iii) fishery dynamics for multiple fleet characteristics based on species targeting under an explore-exploit strategy via a mix of correlated random walk movement (for exploration) and learned behaviour (for exploitation) phases of the fisheries.

We simulated 50 years of fishing and used the results from the fisheries catch to draw inference on the underlying community structures. We compared this inference to a simulated fixed-site sampling design commonly used for fisheries monitoring purposes and the true underlying community structure. We i) used the results to establish the potential and limitations of fishery-dependent data in providing a robust picture of spatiotemporal distributions; and ii) simulated an area closure based on areas defined from the different data sources at a range of temporal and spatial resolutions to assess their effectiveness on reducing catches of a fish population.

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. 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 distributed 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 ability to maintain fishing mortality within sustainable limits (Alverson et al., 1994; Crowder et al., 1998; Rijnsdorp et al., 2007) and the ability to manage for the biological and economic sustainability of fisheries. As such, there is increasing interest in technical solutions such as gear and spatial closures as measures to reduce unwanted catch (Kennelly and Broadhurst, 2002; Catchpole and Revill, 2008; Bellido et al., 2011; Cosgrove et al., 2019).

Adaptive spatial management strategies have been proposed as a way of reducing discards (Holmes et al., 2011; Little et al., 2014; Dunn et al., 2014). Implementation of avoidance measures is, however, restricted by lack of knowledge of fish and fishery spatiotemporal dynamics and understanding of the scale at which processes become important for management. Understanding the correct scale for spatial measures is crucial for implementing solutions at a resolution that ensures effective management (Dunn et al., 2016) while minimising economic impact. 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 appropriate spatial scales for fisheries closures has been a challenge in the past but identified as crucial to its success (Costello et al., 2010; Dunn et al., 2016). Further, poorly sited closures have led to ineffectual measures with unintended consequences. For example, increased benthic impact on previously unexploited areas was observed from the cod closure in the North Sea with a lack of observed intended effect in 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., 2016) and more real-time spatial management has been possible (e.g. Holmes et al., 2011). Such information is, however, derived from an inherently biased sampling programme, targeted fishing, where fishers establish favoured fishing grounds through an 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 experienced high catch in the past.

In order to understand the effect of spatiotemporal aggregation of data we ask two fundamental questions regarding inference derived from observational data:

1. How does sampling-derived 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. Precise locations 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. We use these evaluations to draw inference on the utility of commercial data in supporting management decisions.

2. Materials and Methods

A simulation model that is modular and discrete-event based was developed. This approach enables 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.

Population dynamics (fishing and natural mortality which are instantaneous rates, growth of the population biomass) operate on a daily time-step, while population movement occurs on a weekly time-step. Recruitment takes place periodically each year for a set time duration specified for each population, while the fishing module operates on a tow-by-tow basis (i.e. multiple events a day).

Population movement is a combination of random (diffusive) movement, governed by a stochastic process where movement between adjacent cells is described by a set of probabilities, and 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. 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-modules.

2.1. Population dynamics

The basic population level processes were simulated using a modified two-stage 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 and depletion for pre-recruits and recruited fish were modelled separately 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):

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

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

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

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

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 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.

2.2. Recruitment dynamics

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

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

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

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

where α is the maximum productivity per spawner and β the density dependent reduction in productivity as the SSB increases. In our example application the Beverton-Holt form of stock recruit relationship was used for all populations though either functional form can be chosen.

2.3. Population movement dynamics

To simulate fish population distribution in space and time a Gaussian spatial process was employed to model habitat suitability for each of the populations on a 2d grid. JM: MENTION IN THE INTRODUCTION

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. This enables us to model the spatial autocorrelation observed in animal populations where density is more similar in nearby locations (Tobler, 1970; F. Dormann et al., 2007) and we change the parameters to implement different spatial structures for the populations.

The habitat for each of the populations was generated with the *RFSimulate* function of the *RandomFields* R package (Schlater et al., 2015), that simulates a Gaussian Random Field process given a user defined error model and correlation structure. We define a stationary habitat field and combine with a temporally dynamic thermal tolerance field to imitate 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:

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

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).

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.

JM: WHAT ABOUT INDIVIDUAL INTERACTIONS:w

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:

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

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

The final process 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 (e.g. Figure S5).

2.4. Fleet dynamics

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

2.4.2. Trip-level decisions

Several studies (e.g. Hutton et al., 2004; Tidd et al., 2012; Girardin et al., 2015) have confirmed past activity and past catch rates are strong predictors of fishing location choice. For this reason, the fleet dynamics sub-model included a learning component, where a vessel's initial fishing location in a trip was based on selecting from previously successful fishing locations. This was achieved by calculating an expected revenue based on the catches from locations fished in the preceding trip as well as the same month periods in previous years and the travel costs from the port to the fishing grounds, and choosing randomly from the top 75 % of fishing events as defined by the expected profit, that has a seasonal component.

2.4.3. Within-trip decisions

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

We use a *Lévy flight* which is a particular form of random walk characterised by a heavy-tailed distribution of step-length. The Lévy flight has received a lot of attention in ecological theory in recent years as having shown to have very similar characteristics as those observed by animals in nature, and being a near optimum searching strategy for predators pursuing patchily distributed prey (Viswanathan et al., 1999; Bartumeus et al., 2005; Sims et al., 2008). Bertrand et al. (2007) showed that Peruvian anchovy fishermen have a stochastic search pattern similar to that observed with a lévy flight. However, it remains a subject of debate (e.g. see Edwards et al., 2011; Reynolds, 2015), with the contention that search patterns may be more simply characterised as random walks (Sakiyama and Gunji, 2013) with specific patterns related to the characteristics of the prey field (Sims et al., 2012).

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

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

where L_p is landings of a population p, and Pr_p price of a population. Here, when fishing is successful vessels remain in a similar location and continue to exploit the local fishing grounds. When unsuccessful, they move some distance away from the current fishing location. The movement distance retains some degree of stochasticity, that can be controlled separately, but is determined by the relationship:

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

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

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

where k the concentration parameter from the von Mises distribution 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 angle relationships to revenue can be seen at Figure S15.

2.4.4. Local population depletion

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

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 authors github site (`www.github.com/pdolder/MixFishSim`).

3. Parameterisation

3.1. Population models

We parametrised the simulation model for four populations with different demographics; growth rates, natural mortality and recruitment functions (Table 4). Habitat preference (Figure S1) and temperature tolerances (Figures S3, S4) were defined to be unique to each population resulting in differently weekly distribution patterns (Figures S5-S7). 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 S2) with population-specific movement rates (Table 4). In such a configuration, the individual habitat preferences and thermal tolerances result in different spatial habitat use for each population (Figure S9) and consequently different seasonal exploitation patterns (Fishing mortality in Figure S10).

3.2. Fleet parametrisation

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

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

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.

The following steps are undertaken to determine closures:

1. Extract data source
2. Aggregate according to desired spatial and temporal resolution
3. Interpolate across entire area at desired resolution using simple bivariate kriging using the *interp* function from the R package akima (Akima, 2006). 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 '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.

4. Results

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 S11), while across several trips fishing grounds that are further apart are fished (Figure S12). These different locations relate to areas where the highest revenue were experienced, as shown by Figure S13, 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 S14). 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 S15).

4.2. How does sampling-derived data reflect the underlying population 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;

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

Figure 2 shows the aggregated catch composition from each of the data sources over a ten-year period (to average seasonal patterns) at different spatial resolutions. The finer spatial grid for the real population (top left) and commercial data (top middle) show visually similar patterns, though there are large unsampled areas in the commercial data from a lack of fishing activity (particularly in the lower left part of the sampling domain). The survey data at this spatial resolution displays very sparse information about the spatial distributions of the populations. The slightly aggregated data on a 5 x 5 grid shows similar patterns and, while losing some of the spatial detail, there remains good consistency between the ‘real population’ and the commercial data. Survey data starts to pick out some of the similar patterns as the other data sources, but lacks 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 ’real population’ data emerge.

Figure 3 shows the consequences of different temporal aggregations of the data over a ten-year period, with weekly (top), monthly (middle) and yearly (bottom) catch compositions from across an aggregated 20 x 20 area. By comparison to the ’real population’, the monthly aggregation captures the major patterns seen in the weekly data, albeit missing more subtle differences. The yearly data 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 commercial data on a weekly basis shows some of the same patterns as the ’real population’, though the first species (in red) is less well represented and some weeks are missing catches from the area. The monthly data shows some consistency between the ’real population’ and commercial data for species 2 - 4, though species 1 remains under-represented. On an annual basis, interestingly the commercial data under represents the first species (in red) while the survey over represents species 1. This is likely due to the biases in commercial sampling, with the fisheries not targeting the areas where species 1 are present and the survey sampling areas where species 1 is more abundant than on average.

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 4), 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.

A regression tree (using the R package REEMtree (Sela and Simonoff, 2012)) highlights that 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 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 5). 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 are 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 S17) that may have consequences in terms of restricting the fishery in a much larger area than necessary.

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 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 in order to maximise productivity while taking account of both the biological and human processes operating on different time-frames (Dunn et al., 2016), understanding assumptions behind the data used - increasingly a combination of logbook and positional information from vessel monitoring systems - is vital to ensure measures are effective.

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., 2018), 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. 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 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), while incorporating detailed fishing dynamics that take account of different drivers in a mechanistic way. In this way 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 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.

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 S9). 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.

Abbreviations

Detail any unusual ones used.

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Appendices

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

Variable	Meaning	Units
	Population dynamics	
Delay-difference model		
$B_{c,d}$	Biomass in cell c and day d	kg
$Z_{c,d}$	Total mortality in cell c for day d	-
$R_{c,\tilde{y}}$	Annualy recruited fish in cell	yr^{-1}
ρ	Brody's growth coefficient	yr^{-1}
Wt_R	Weight of a fully recruited fish	kg
Wt_{R-1}	Weight of a pre-recruit fish	kg
α_d	Proportion of annually recruited fish recruited during day d	-
Baranov catch equation		
$C_{c,d}$	Catch from cell c for day d	kg
$F_{c,d}$	Instantaneous rate of fishing mortality in cell c on day d	-
$M_{c,d}$	Instantaneous rate of natural mortality in cell c on day d	-
$B_{c,d}$	Biomass in cell c on day d	kg
	Recruitment dynamics	
$\tilde{R}_{c,d}$	is the recruitment in cell c for day d	d^{-1}
$S_{c,d}$	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 rate of recruitment	kg

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

Variable	Meaning	Units
	Population movement dynamics	
Habitat model		
a	b	c
Thermal tolerance		
$T_{c,wk}$	Temperature for cell in week	°C
μ_p	Mean of the thermal tolerance for population	°C
σ_p^2	Standard deviation of thermal tolerance for the population	°C
Population movement model		
λ	decay rate for population movement	-
$Hab_{c,p}^2$	Square of habitat suitability for cell c and population p	-
$Tol_{c,p,wk}$	Thermal tolerance for population p in cell c at week wk	-
d_{IJ}	euclidean distance between cell I and cell J	-

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

Variable	Meaning	Units
	Short-term fleet dynamics	
Rev	Revenue from fishing tow	€
L_p	Landings of population p	kg
Pr_p	Average price of population p	€ kg^{-1}
StepL	Step length for vessel	euclidean distance
Br	Bearing	degrees
k	Concentration parameter for Von mises distribution	-
β_1	shape parameter for step function	-
β_2	shape parameter for step function	-
β_3	shape parameter for step function	-

Table 4: Population dynamics and movement parameter setting

Parameter	Pop 1	Pop 2	Pop 3	Pop 4
Habitat quality				
Matérn ν	1/0.015	1/0.05	1/0.01	1/0.005
Matérn κ	1	2	1	1
Anisotropy	1.5,3,-3,4	1,2,-1,2	2.5,1,-1,2	0.1,2,-1,0.2
Spawning areas (bound box)	40,50,40,50; 80,90,60,70	50,60,30,40; 80,90,90,90	30,34,10,20; 60,70,20,30	50,55,80,85; 30,40,30,40
Spawning multiplier	10	10	10	10
Movement λ	0.1	0.1	0.1	0.1
Population dynamics				
Starting Biomass	1e5	2e5	1e5	1e4
Beverton-Holt Recruit 'a'	6	27	18	0.3
Beverton-Holt Recruit 'b'	4	4	11	0.5
Beverton-Holt Recruit σ^2	0.7	0.6	0.7	0.6
Recruit week	13-16	12-16	14-16	16-20
Spawn week	16-18	16-19	16-18	18-20
K	0.3	0.3	0.3	0.3
wt	1	1	1	1
wt_{d-1}	0.1	0.1	0.1	0.1
M (annual)	0.2	0.1	0.2	0.1
Movement dynamics				
μ	12	15	17	14
σ^2	8	9	7	10

Table 5: Fleet dynamics parameter setting

Parameter	Fleet 1	Fleet 2	Fleet 3	Fleet 4	Fleet 5
Targeting preferences	pop 2/4	pop 1/3	-	pop 4	pop 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	T	T	T	T	T
Past Year & Month	T	T	T	T	T
Past Trip	T	T	T	T	T
Threshold	0.7	0.7	0.7	0.7	0.7
Fuel Cost	3	2	5	2	1

Table 6: Fishing mortality effects of the closure scenarios. 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	spp_3	1.08	0.61	-43.20	monthly	high_pop	real_pop	5.00
3	F	spp_3	1.08	0.64	-40.82	yearly	high_pop	commercial	1.00
25	F	spp_3	1.08	0.65	-39.94	yearly	high_pop	real_pop	5.00
17	F	spp_3	1.08	0.67	-38.11	yearly	high_pop	commercial	5.00
15	F	spp_3	1.08	0.71	-34.38	weekly	high_pop	commercial	5.00
43	F	spp_3	1.08	0.71	-34.31	weekly	high_pop	commercial	20.00
16	F	spp_3	1.08	0.73	-32.58	monthly	high_pop	commercial	5.00
51	F	spp_3	1.08	0.78	-27.92	weekly	high_pop	real_pop	20.00
37	F	spp_3	1.08	0.78	-27.76	weekly	high_pop	real_pop	10.00
39	F	spp_3	1.08	0.79	-26.98	yearly	high_pop	real_pop	10.00
38	F	spp_3	1.08	0.81	-25.47	monthly	high_pop	real_pop	10.00
21	F	spp_3	1.08	0.81	-25.21	yearly	high_pop	survey	5.00
35	F	spp_3	1.08	0.81	-25.05	yearly	high_pop	survey	10.00
44	F	spp_3	1.08	0.87	-19.91	monthly	high_pop	commercial	20.00
52	F	spp_3	1.08	0.88	-18.39	monthly	high_pop	real_pop	20.00
30	F	spp_3	1.08	0.96	-11.06	monthly	high_pop	commercial	10.00
29	F	spp_3	1.08	0.98	-9.80	weekly	high_pop	commercial	10.00
31	F	spp_3	1.08	1.03	-4.36	yearly	high_pop	commercial	10.00
53	F	spp_3	1.08	1.06	-1.64	yearly	high_pop	real_pop	20.00
49	F	spp_3	1.08	1.07	-1.01	yearly	high_pop	survey	20.00

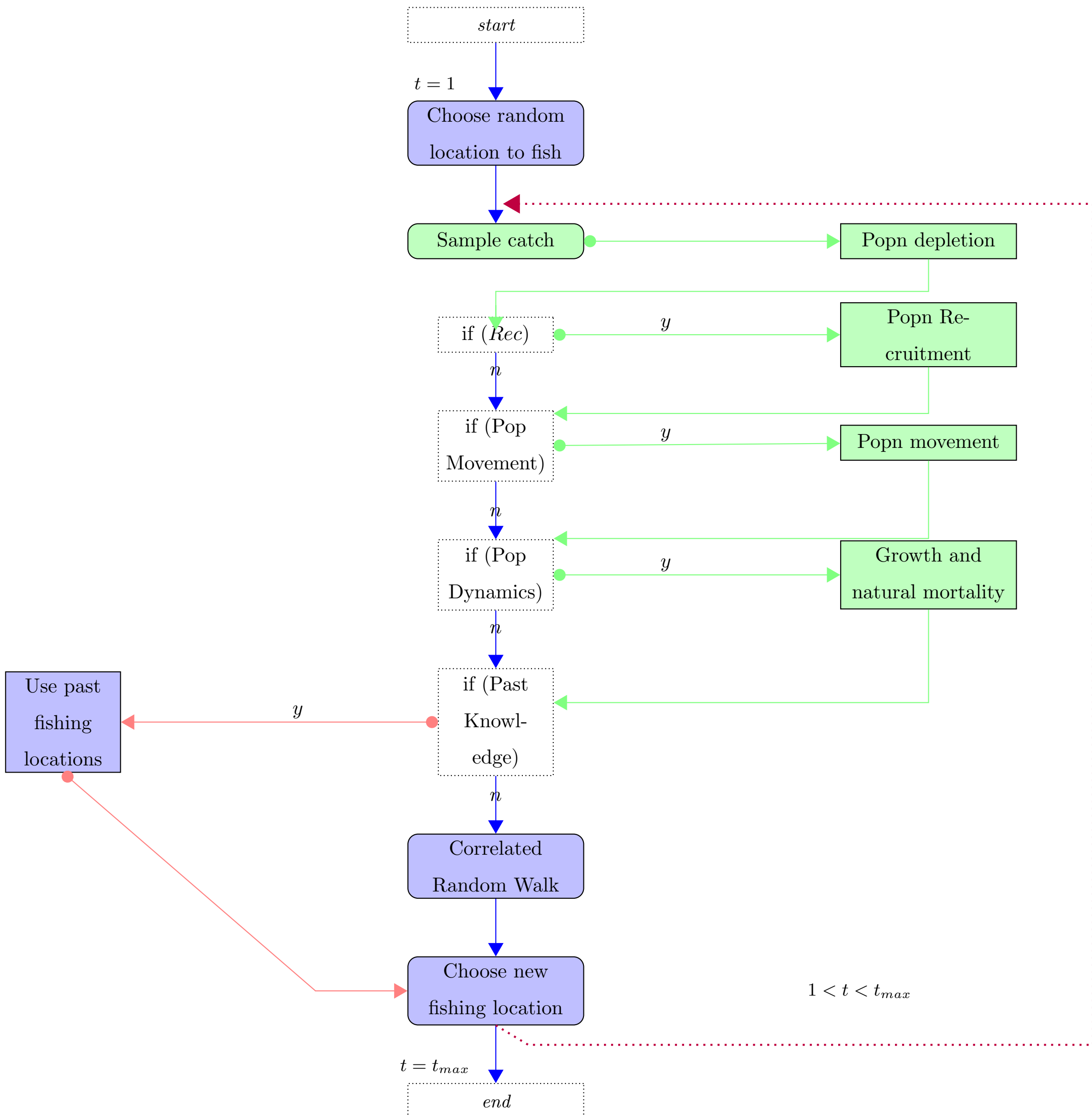

Figure 1: Schematic overview of the simulation model. Blue boxes indicate fleet dynamics processes, the green boxes population dynamics processes while the white boxes are the time steps at which processes occur; t = tow, $tmax$ is the total number of tows; (Rec), (Pop Movement), (Pop Dynamics) logic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

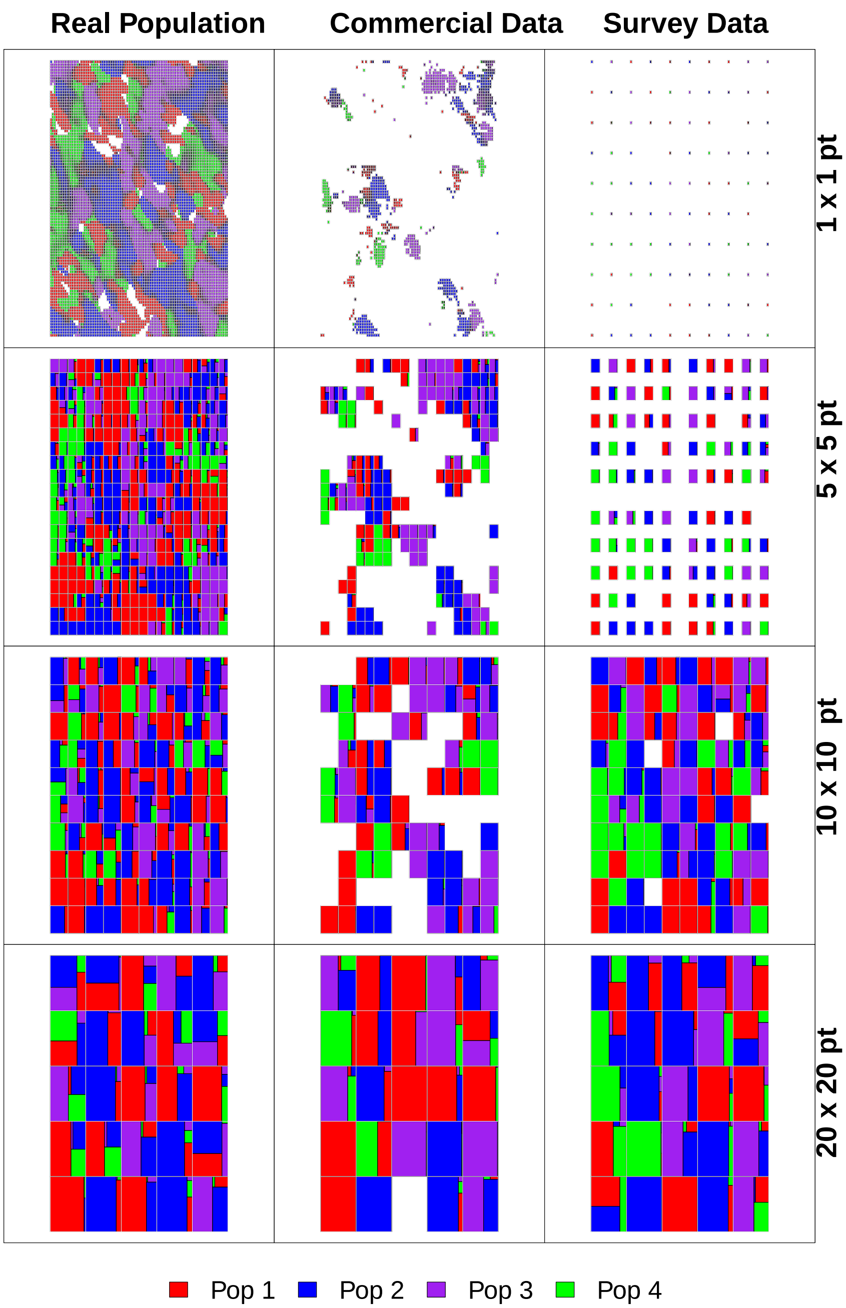

Figure 2: Data aggregation at different spatial resolutions over a ten year period

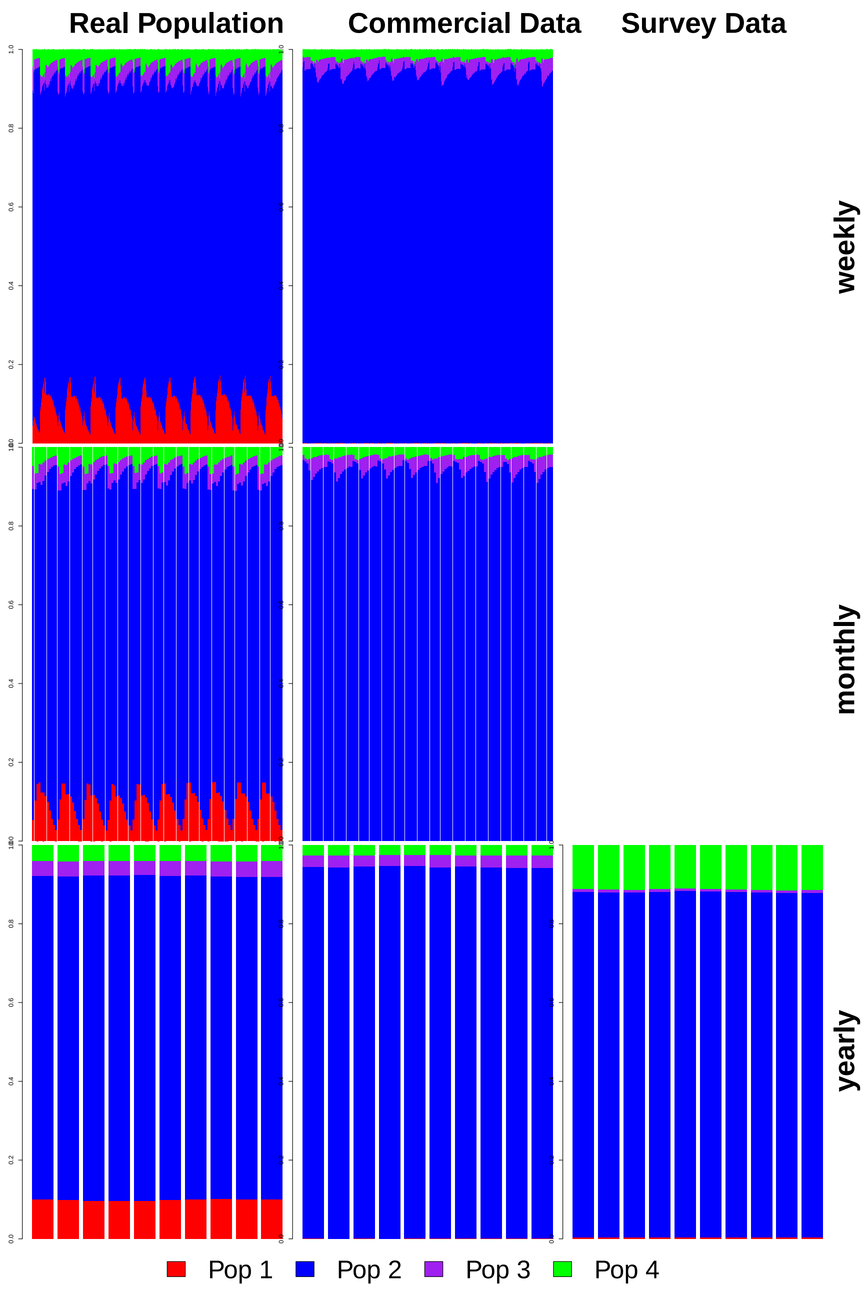

Figure 3: Data aggregation at different temporal resolutions over a ten-year period

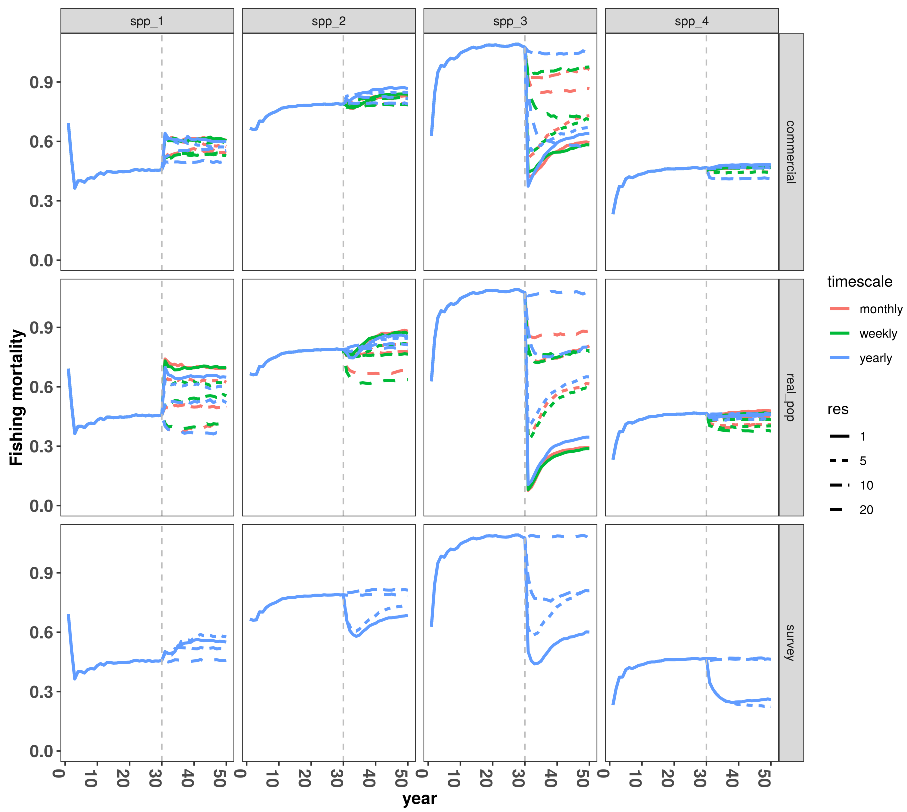

Figure 4: Comparison of closure scenarios effect on fishing mortality trends. Line colour denotes the timescale, while linestyle denotes the spatial resolution.

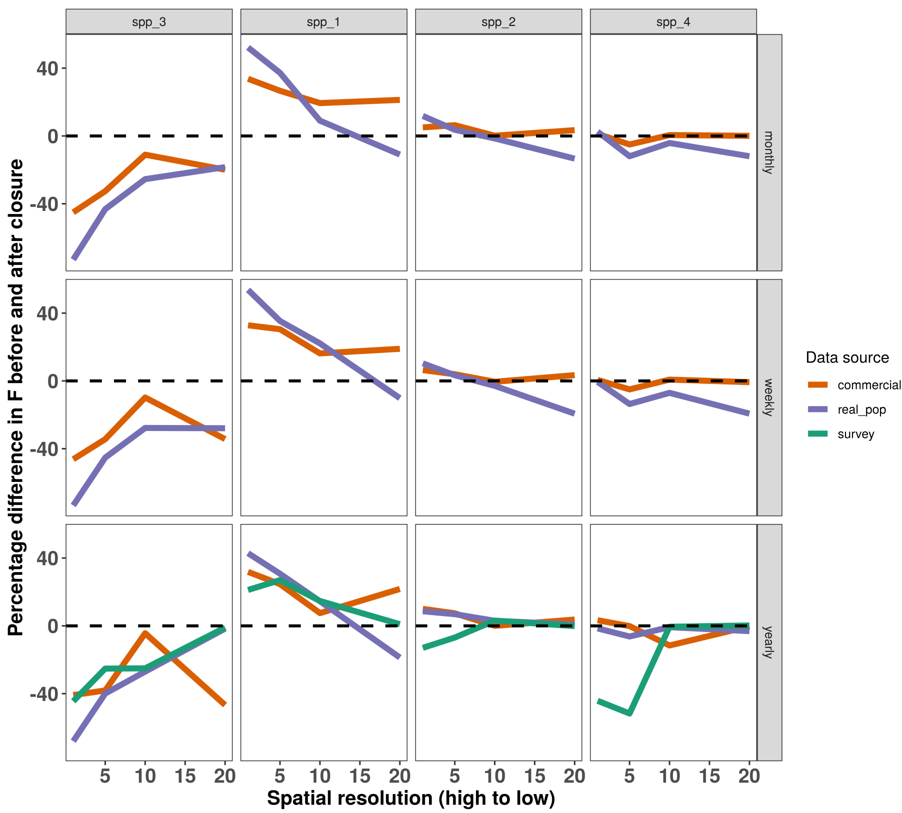

Figure 5: Comparison of closure scenario effectiveness based on different spatial and temporal resolutions.

References

Akima, H., 2006. Interpolation of irregularly spaced data, The akima Package. Interpolation of Irregularly and Regularly Spaced Data .

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

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

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

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

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

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

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

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

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

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

Cosgrove, R., Browne, D., Minto, C., Tyndall, P., Oliver, M., Montgomerie, M., McHugh, M., 2019. A game of two halves: Bycatch reduction in Nephrops mixed fisheries. Fisheries Research 210, 31–40.

Costello, C., Rassweiler, A., Siegel, D., De Leo, G., Micheli, F., Rosenberg, A., 2010. The value of spatial information in MPA network design. Proceedings of the National Academy of Sciences .

Cotter, A.J., Pilling, G.M., 2007. Landings, logbooks and observer surveys: Improving the protocols for sampling commercial fisheries. Fish and Fisheries 8, 123–152.

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

Dedman, S., Officer, R., Brophy, D., Clarke, M., Reid, D.G., 2015. Modelling abundance hotspots for data-poor Irish Sea rays. Ecological Modelling 312, 77–90.

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

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

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

Dolder, P.J., Thorson, J.T., Minto, C., 2018. Spatial separation of catches in highly mixed fisheries. Scientific Reports .

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

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

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

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

Fulton, E.A., Link, J.S., Kaplan, I.C., Savina-Rolland, M., Johnson, P., Ainsworth, C., Horne, P., Gorton, R., Gamble, R.J., Smith, A.D., Smith, D.C., 2011. Lessons in modelling and management of marine ecosystems: The Atlantis experience. Fish and Fisheries .

Gardner, B., Sullivan, P.J., Morreale, S.J., Epperly, S.P., 2008. Spatial and temporal statistical analysis of bycatch data: patterns of sea turtle bycatch in the North Atlantic. Canadian Journal of Fisheries and Aquatic Sciences 65, 2461–2470.

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

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

Girardin, R., Hamon, K.G., Pinnegar, J., Poos, J.J., Thébaud, O., Tidd, A., Vermard, Y., Marchal, P., 2016. Thirty years of fleet dynamics modelling using discrete-choice models: What have we learned? Fish and Fisheries , 1–18.

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

Harley, S.J., Myers, R.A., Dunn, A., 2001. Is catch-per-unit-effort proportional to abundance? Canadian Journal of Fisheries and Aquatic Sciences 58, 1760–1772.

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

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

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

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

Kimura, D.K., Somerton, D.A., 2006. Review of statistical aspects of survey sampling for marine fisheries. Reviews in Fisheries Science 14, 245–283.

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

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

Liu, X., Heino, M., 2013. Overlooked biological and economic implications of within-season fishery dynamics. Canadian Journal of Fisheries and Aquatic Sciences .

Mahévas, S., Pelletier, D., 2004. ISIS-Fish, a generic and spatially explicit simulation tool for evaluating the impact of management measures on fisheries dynamics. Ecological Modelling .

Mangel, M., Clark, C.W., 1983. Uncertainty, search, and information in fisheries. ICES Journal of Marine Science .

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

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

Maunder, M.N., Punt, A.E., 2004. Standardizing catch and effort data: A review of recent approaches. Fisheries Research .

Needle, C.L., Catarino, R., 2011. Evaluating the effect of real-time closures on cod targeting. ICES Journal of Marine Science 68, 1647–1655.

Plagányi, É.E., Punt, A.E., Hillary, R., Morello, E.B., Thébaud, O., Hutton, T., Pillans, R.D., Thorson, J.T., Fulton, E.A., Smith, A.D.M., Smith, F., Bayliss, P., Haywood, M., Lyne, V., Rothlisberg, P.C., 2014. Multispecies fisheries management and conservation: tactical applications using models of intermediate complexity. Fish and Fisheries 15, 1–22.

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

Poos, J.J., Rijnsdorp, A.D., 2007b. The dynamics of small-scale patchiness of plaice and sole as reflected in the catch rates of the Dutch beam trawl fleet and its implications for the fleet dynamics. Journal of Sea Research 58, 100–112.

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

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

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

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

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

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

Robinson, L.M., Elith, J., Hobday, A.J., Pearson, R.G., Kendall, B.E., Possingham, H.P., Richardson, a.J., 2011. Pushing the limits in marine species distribution modelling: Lessons from the land present challenges and opportunities. Global Ecology and Biogeography 20, 789–802.

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

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

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

Sela, R., Simonoff, J., 2012. Package 'REEMtree'.

Shin, Y.J., Shannon, L.J., Cury, P.M., 2004. Simulations of fishing effects on the southern Benguela fish community using an individual-based model: Learning from a comparison with ECOSIM, in: African Journal of Marine Science.

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

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

Stock, B.C., Ward, E.J., Eguchi, T., Jannot, J.E., Thorson, J.T., Feist, B.E., Semmens, B.X., 2019. Comparing predictions of fisheries bycatch using multiple spatiotemporal species distribution model frameworks. Canadian Journal of Fisheries and Aquatic Sciences .

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

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

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

Van Putten, I.E., Kulmala, S., Thébaud, O., Dowling, N., Hamon, K.G., Hutton, T., Pascoe, S., 2012. Theories and behavioural drivers underlying fleet dynamics models. Fish and Fisheries 13, 216–235.

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

Walters, C.J., 2007. Is adaptive management helping to solve fisheries problems? Ambio .

Ward, E.J., Jannot, J.E., Lee, Y.W., Ono, K., Shelton, A.O., Thorson, J.T., 2015. Using spatiotemporal species distribution models to identify temporally evolving hotspots of species co-occurrence. Ecological Applications 25, 2198–2209.

Xu, B., Zhang, C., Xue, Y., Ren, Y., Chen, Y., 2015. Optimization of sampling effort for a fishery-independent survey with multiple goals. Environmental Monitoring and Assessment .