MixFishSim: highly resolved spatiotemporal simulations for exploring mixed fishery dynamics

Paul J. Dolder^{a,b,*}, Cóilín Minto^a, Jean-Marc Guarini^c, Jan Jaap Poos^d

^a Galway-Mayo Institute of Technology (GMIT), Dublin Road, Galway, Ireland
^b Centre for Environment, Fisheries and Aquaculture Science (Cefas), Pakefield Road,
Lowestoft, UK

^cSorbonne Université, Faculty of Sciences, 4 Place Jussieu, 75005 Paris, France ^dWageningen Marine Research, Haringkade 1 1976 CP IJmuiden, Netherlands

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 develop a highly resolved spatiotemporal simulation model incorporating: i) delay-difference population dynamics, ii) population movement

*Corresponding author

Email address: paul.dolder@gmit.ie (Paul J. Dolder)

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 ran-

dom walk movement (for exploration) and learned behaviour (for exploitation)

phases of the fisheries.

We simulate 50 years of fishing and use the results from the fisheries catch

to draw inference on the underlying population structures. We compare this

inference to a simulated fixed-site sampling design commonly used for fisheries

monitoring purposes and the true underlying population structures. We i) use

the results to establish the potential and limitations of fishery-dependent data

in providing a robust picture of spatiotemporal distributions; and ii) simulate an

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

of temporal and spatial resolutions and assess their effectiveness on reducing

catches of a fish population.

We conclude from our simulations that commercial data, while containing

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

the correct spatiotemporal scale.

[333 words]

Keywords: Some, keywords, here. Max 6

2010 MSC: 00-01, 99-00

1. Introduction

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

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

using species non-selective fishing gear. 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 overexploita-

2

tion 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).

.4

Changes to spatial fishing patterns have been proposed as a method to reduce discards (Holmes et al., 2011; Little et al., 2014; Dunn et al., 2014). 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 implementation at a resolution that ensures effective management (Dunn et al., 2016) while minimising economic impact. For example, a scale that promotes species avoidance for vulnerable or low quota species while allowing continuance of sustainable fisheries for available quota species.

25

Identifying an appropriate scale has been a challenge in the past that has led to ineffectual measures with unintended consequences such as limited impact 27 towards the management objective or increased benthic impact on previously unexploited areas (e.g. the cod closure in the North Sea (Rijnsdorp et al., 2001; Dinmore et al., 2003)). More refined spatial information has since become available through the combination of logbook and Vessel Monitoring System (VMS) 31 data (Lee et al., 2010; Bastardie et al., 2010; Gerritsen et al., 2012; Mateo et al., 32 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 35 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.

39

We ask two fundamental questions regarding spatiotemporal inference derived from observational data:

1. How does sampling-derived data reflects the underlying population structures?

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. Being known directly rather 47 than inferred from sampling or commercial catch, we can use the population 48 model to validate how inference from fisheries-dependent and fisheries independent sampling relates to the real population structure in a way we could not 50 with real data. We ii) compare, at different spatial and temporal aggregations, the simulated population distributions to samples from fisheries-dependent and fisheries independent catches to test if these are a true reflection of the relative 53 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 55 evaluations to draw inference on the utility of commercial data in supporting management decisions.

58

• [We find..]

2. Materials and Methods

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

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

This comes as a surprise: I thought this was going to be about discardsAgree, have removed this to avoid confusion

If the paper has two goals this should be clear from the start, but may be bet ter over 2 MSsI would like to keep both parts but have made clearer in how its set out. The closure scenarios form validation of the data aggregation. rather than effectiveness of the closures themselves - so its a continuation of the same question in my

movement, 4) fishery dynamics.

67

Population dynamics (fishing and natural mortality, growth) operate on a daily time-step, while population movement occurs on a weekly time-step. Recruitment takes place 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).

In the model system population movement is driven by random (diffusive) and directed (advective) processes and we incorporate characterisation of a number of different fishing fleet dynamics exploiting four fish populations with different spatial and population demographics. The following describes the implementation of each of the sub-modules.



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.

2.1. Population dynamics

The basic population level processes are simulated using a modified two-stage Deriso-Schnute delay difference model (Deriso, 1980; Schnute, 1985; Dichmont et al., 2003) occurring at a daily time-step. A daily time-step was chosen to discretise continuous population processes on a biologically relevant and computationally tractable timescale. Under the population dynamics module population biomass growth and depletion for pre-recruits and recruited fish are modelled separately as a function of previous recruited biomass, intrinsic population growth and recruitment functionally linked to the adult population size. Biomass for each cell c is 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.

84

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

$$C_{c,d} = \frac{F_{c,d}}{F_{c,d} + M_{c,d}} * (1 - e^{-(F_{c,d} + M_{c,d})}) * B_{c,d}$$
 (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 $F_{fl,v,c,d,p} = E_{fl,v,c,d} \cdot Q_{fl,p} \cdot B_{c,d,p}$ with
- fl, v and p the fleet, vessel and population respectively and E and Q fishing
- effort and catchability.

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):

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

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

> $\bar{R}_{c,d} = B_{c,d} * e^{(\alpha - \beta * B_{c,d})}$ (4) $R_{c,d} \sim \log N[(\log(\bar{R}_{c,d}), \log(\sigma^2))]$

- where α is the maximum productivity per spawner and β the density dependent
- reduction in productivity as the SSB increases. In 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 97
- To simulate fish population distribution in space and time a Gaussian spatial 98
- process was employed to model habitat suitability for each of the populations
- on a 2d grid. 100

101

102 for any set of cells c_1,\dots,c_n , the joint distribution of $S=\{S(c1),\dots S(c_n)\}$

We first defined a Gaussian random field process, $\{S(c): c \in \mathbb{R}^2\}$, where

ity - as I think an emergent property of the fleets rather than something we solve for (I could be wrong though!) catch for a vessel is a product of catchability and biomass, i.e. C = qB, but this catch is summed to solve for F. So its both really]

[link F to effort

and catchabil-

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

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.

108 109

105

106

107

The habitat for each of the populations was generated with the *RFSimulate* function of the *RandomFields* R package (Schlater et al., 2015). Each population was initialised at a single location, and subsequently moved according to a probabilistic distribution based on habitat suitability (represented by the normalised values from the GRFs), temperature and distance from current cell:

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

114

116

117

118

119

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

120

An advection-diffusion process controls population movement, with a timevarying 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 What does it mean concisely? Areas are assigned? Yes, the areas are pre-defined - I have amended to reflect and tried to clarify

What have a temperature covariate? Could just use time-Was intended as some biological meaning - species thermal tolerances load onto the

temperature ef-

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.

124

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 and range within a week is fairly limited [REF!!]. 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 - which determined the fleet catch efficiency and preference towards a 134 particular species; trip-level decisions, which determined the initial location to 135 be fished at the beginning of a trip; and within-trip decisions, determining move-136 ment from one fishing spot to another within a trip. Together, these element 137 implement 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 140 fishers as a group tend to show heterogeneity and individual rather than group 141 dynamics [REF!]. Thus this was the fleet dynamics is the productive of individual experiences rather than pre-ordained 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., 153 2015) have confirmed past activity and past catch rates are strong predictors of 154 fishing location choice. For this reason, the fleet dynamics sub-model included a 155 learning component, where a vessel's initial fishing location in a trip was based 156 on selecting from previously successful fishing locations. This was achieved by 157 calculating an expected revenue based on the catches from locations fished in 158 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 160 the top 75 % of fishing events as defined by the expected profit, which has a 161 seasonal component. 162

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 165 gradually more influenced by experience gained from past fishing locations (as 166 per the initial trip-level location choice), moving location choice towards areas 167 of higher perceived profit. A random walk was chosen for the exploratory fishing 168 process as it is the simplest assumption commonly used in ecology to describe optimal animal search strategy for exploiting homogeneously distributed prey 170 about which there is uncertain knowledge (Viswanathan et al., 1999). In a ran-171 dom walk, movement is a stochastic process through a series of steps. These 172 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 cor-174 related (known as 'persistence') providing some overall directional movement 175 (Codling et al., 2008).

177

180

181

184

We use a Lévy flight which is a particular form of random walk charac-178 terised by a heavy-tailed distribution of step-length. The Lévy flight has re-179 ceived 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 dis-182 tributed prey (Viswanathan et al., 1999; Bartumeus et al., 2005; Sims et al., 183 2008). Bertrand et al. (2007) showed that Peruvian anchovy fishermen have a stochastic search pattern similar to that observed with a lévy flight. However, 185 it remains a subject of debate (e.g. see Edwards et al., 2011; Reynolds, 2015), 186 with the contention that search patterns may be more simply characterised as 187 random walks (Sakiyama and Gunji, 2013) with specific patterns related to the characteristics of the prey field (Sims et al., 2012).

190

188

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, which can be controlled separately, but is determined by the relationship:

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

Where β_1 , β_2 and β_3 are parameters determining the shape of the step function

So step length increases with increasingly enue?No, the opposite

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 which we correlate with the revenue so that $k = (Rev + 1/RefRev) * max_k$, where max_k is the maximum concentration value, k, and RefRev is parametrised as for β_3 in the step length function. A realised example of the step length and turning angle relationships to revenue can be seen at Figure S15.

2.4.4. Local population depletion

Where several fishing vessels 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, 199 local depletion and interference competition will affect fishing location choice 200 of the fleet as a whole (Rijnsdorp, 2000; Poos and Rijnsdorp, 2007). In order 201 to account for this behaviour, the fishing sub-model operates spatially on a 202 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 204 areas less attractive as a future fishing location choice as reduced catch rates 205 will be experienced. 206

207 2.5. Fisheries independent survey

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

213 surveys undertaken by fisheries research agencies.

214

215

2.6. Software

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).

219

221

220 3. Parameterisation

3.1. Population models

We parametrised the simulation model for four populations with different 222 demographics; growth rates, natural mortality and recruitment functions (Table 223 4). Habitat preference (Figure S1) and temperature tolerances (Figures S3, 224 S4) were unique to each population resulting in differently weekly distribution patterns (Figures S5-S7). In addition, each of the populations has two defined 226 spawning areas which result in the populations moving towards these areas in 227 pre-defined weeks (Figure S2) with population-specific movement rates (Table 228 4). The individual habitat preferences and thermal tolerances result in different spatial habitat use for each population (Figure S9) and consequently different 230 seasonal exploitation patterns (Fishing mortality in Figure S10). 231

3.2. Fleet parametrisation

The fleets were parametrised to reflect five different characteristic fisheries with unique exploitation dynamics (Table 5). By setting different catchability parameters $(Q_{fl,p})$ we create different targeting preferences between the fleets and hence spatial dynamics. The stochasticity in the random walk process ensures that within a fleet different vessels have slightly different spatial distributions based on individual experience. The step function was parametrised dynamically within the simulations as the maximum revenue obtainable was

not known beforehand. This was implemented so that vessels take smaller steps
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).

243

245

248

249

250

25

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 previous trips revenue and cost of movement to the new fishing location. This probability was based on a logistic sigmoid function with a lower asymptote of 0 and upper asymptote of 0.95, and a growth rate which ensures the upper asymptote (where decisions are mainly based on past knowledge) is reached approximately halfway through the simulation.

253

3.3. Survey settings

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

260 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

272

275

- 2. Aggregate according to desired spatial and temporal resolution
- 3. Interpolate across entire area at desired resolution using simple kriging using the *interp* function from the R package akima [REF!].
- 4. Close area covering top 5 % of catch rates
- 279 In total 28 closure scenarios were run which represent combinations of:
- data types: commercial logbook data, survey data and 'real population',
- temporal resolutions: weekly, monthly and yearly closures,
- spatial resolutions: 1 x 1 grid, 5 x 5 grid, 10 x 10 grid and 20 x 20 grid,
- closure basis: 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.

286 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

Is there equilibrium after 5 years or still some trend in B? I have rerun to ensure some steady state dy-

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

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) exploit similar but slightly different fishing grounds depending on their own personal experience during the explore phase of the fishery (Figure S14), which is the result of 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).

289

290

291

293

296

297

298

301

302

303

304

307

308

309

311

312

Move some of the supplementary figures to the manuscript

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 simulated 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 which 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 coverage. The spatial catch information on a 10×10 and 20×20 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.

317

332

333

341

Figure 3 shows the consequences of different temporal aggregations of the 318 data over a ten-year period, with weekly (top), monthly (middle) and yearly 319 (bottom) catch compositions from across an aggregated 20 x 20 area. As can be seen by comparison to the 'real population', the monthly aggregation captures 321 the major patterns seen in the weekly data, albeit missing more subtle differ-322 ences. The yearly data results in a constant catch pattern due to the aggregation 323 process (sometimes known as an aggregation bias). The commercial data on a 324 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 326 catches from the area. The monthly data shows some consistency between the 327 'real population' and commercial data for species 2 - 4, though species 1 remains 328 under-represented. On an annual basis, interestingly the commercial data under 329 represents the first species (in red) while the survey over represents species 1. 330 This is likely due to the biases in commercial sampling, with the fisheries not 331

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

sampling from over representation of the spatial distribution.

targeting the areas where species 1 are present, and the biases in the survey

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 in-

terest (species 3; Figure 4), though interestingly the largest reductions in fishing 343 mortality happened immediately after the closures, following which the fisheries 344 "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) which were ineffective with all 347 data sources. As expected, closures based on the "known" population distribu-348 tion 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 351 the populations were found in greater or lesser density. 352

353

A regression tree (using the R package REEMtree [ref]) highlights that the 354 factor most contributing to differences in fishing mortality before and after the closure was the population (72 % showing that the closures were effective for 356 population 3), followed by data resolution (21 %), data type (7 %) with the least 357 important factor the timescale (< 1 %). In general the finer the spatial resolu-358 tion of the data used the greater reduction in fishing mortality for population 3 359 after the closures (Figure 5). The notable outliers are the commercial data at 360 the coarsest spatial resolution (20 x 20) at a yearly and weekly timescale, where 361 closures were nearly as effective as the fine-scale resolution. In this case the 362 closures were sufficiently large to protect the population (and was as effective as 363 when the closure was based on the "real population"; CHECK THIS, COULD PLOT ACTUAL CLOSURE LOCATIONS??) but this may have consequences in terms of restricting a much larger area than necessary. 366

367

5. Discussion

Our study evaluates the importance of data scaling and considers potential bias introduced through data aggregation when using commercial fisheries data to infer spatio-temporal dynamics in fisheries. Understanding how fish-

ers exploit multiple heterogeneously distributed fish populations with different 372 catch limits or conservation status requires detailed understanding of the overlap 373 of resources; this is difficult to achieve using conventional modelling approaches due to species targeting in fisheries resulting in preferential sampling (Martínez-375 Minaya et al., 2018). Often data is aggregated or extrapolated which requires 376 assumptions about the spatial and temporal scale of processes. Our study ex-377 plores the assumptions behind such aggregation and preferential sampling to 378 identify potential impacts on management advice. With modern management 379 approaches increasingly employing more nuanced spatio-temporal approaches 380 in order to maximise productivity while taking account of both the biological 381 and human processes operating on different time-frames (Dunn et al., 2016), 382 understanding assumptions behind the data used - increasingly a combination 383 of logbook and positional information from vessel monitoring systems - is vital to ensure measures are effective. 385

386 387

388

389

390

391

392

We employ a simulation approach to model each of the population and fishery processes in a hypothetical 'mixed fishery', allowing us to i) evaluate the consequences of different aggregation assumptions on our understanding of the spatio-temporal distribution of the underlying fish populations, and ii) evaluate the effectiveness of a spatial closure given those assumptions. Our approach captures fine scale population and fishery dynamics not usually considered (although see Bastardie et al. (2010); Bailey et al. (2018)) which offers the advantage that larger scale fishery patterns are emergent properties of the system rather than the result of a statistical modelling framework.

396 397

395

Our results show commercial data can provide at right scale and resolution - depends on scale of process: pop movement etc... Important to consider how fishers interact / adapt to changes with the resource and mgmt.

400

It seems clear that spatial disaggregation is more important than the temporal disaggregation of the commercial data... WHY

Closure scenarios demonstrate potential tor reduce F - not as high as with real pop, but good. Make link to other studies – read up on these. The what next: Real world spatiotemp closures rarely been able to consider these issues / de-signed with these issues fully in mind - NS cod closures, plaice and trevose box... Use of commercial data increasing - likely to become more important in future. Also collaborative approach with industry, e.g. hotspot mapping, spa-tiotemp advice... Other potential uses of the model Survey design commercial index standardization methods Sampling scheme design Testing fleet dynamics models at an aggregated level Bigger picture stuff:: LO, increasing desire for more nuanced spatiotemp mgmt... Wider applicability: birds, wildlife?? 6. Conclusions Study shows This is important because

How we might apply this in future

433

434 Abbreviations

Detail any unusual ones used.

436 Acknowledgements

those providing help during the research..

438 Funding

- 439 This work was supported by the MARES doctoral training program (MARES_14_15)
- $_{\rm 440}$ $\,$ and the Centre for Environment, Fisheries and Aquaculture Science seedcorn
- program (DP227AC).

442 Appendices

| Table 1: Description of variables for population dynamics sub-module | Table 1: | Description | of variables | for po | pulation | 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} | | | | | | |
| ho | Brody's growth coefficient | ${ m yr}^{-1}$ | | | | | | |
| 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 | - | | | | | | |
| | $\mathrm{day}\ d$ | | | | | | | |
| 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 | - | | | | | | |
| | $\mathrm{day}\ d$ | | | | | | | |
| $B_{c,d}$ | Biomass in cell c on day d | kg | | | | | | |
| Recruitment dynamics | | | | | | | | |
| $\tilde{R}_{c,d}$ | is the recruitment in cell c for day d | d^{-1} | | | | | | |
| $B_{c,d}$ | is the Biomass in cell c for day d | d^{-1} | | | | | | |
| α | the maximum recruitment rate | kg | | | | | | |
| β | the biomass required to produce half the maximum | kg | | | | | | |
| | rate of recruitment | | | | | | | |

| Tal | Table 2: Description of variables for population movement sub-module | | | | | | | |
|----------------|--|----------------------|--|--|--|--|--|--|
| Variable | Meaning | Units | | | | | | |
| | Population movement dynamics | | | | | | | |
| Habitat me | odel | | | | | | | |
| a | b | С | | | | | | |
| Thermal to | plerance | | | | | | | |
| $T_{c,wk}$ | 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 | 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 | - | | | | | |
| eta_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 dyn | amics para | meter setti | ng | |
|-------------------------|--------------|------------|-------------|----------|-------|
| 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 | ${ m T}$ | ${ m T}$ | 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 | 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 | ${\rm spp_3}$ | 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 | $high_pop$ | ${\rm real_pop}$ | 10.00 |
| 39 | F | ${\rm spp_3}$ | 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 | ${\rm spp_3}$ | 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 | ${\rm spp_3}$ | 1.08 | 0.88 | -18.39 | monthly | $high_pop$ | ${\rm real_pop}$ | 20.00 |
| 30 | F | ${\rm spp_3}$ | 1.08 | 0.96 | -11.06 | monthly | $high_pop$ | commercial | 10.00 |
| 29 | \mathbf{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 | ${\rm spp_3}$ | 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 2: Data aggregation at different spatial resolutions over a ten year period

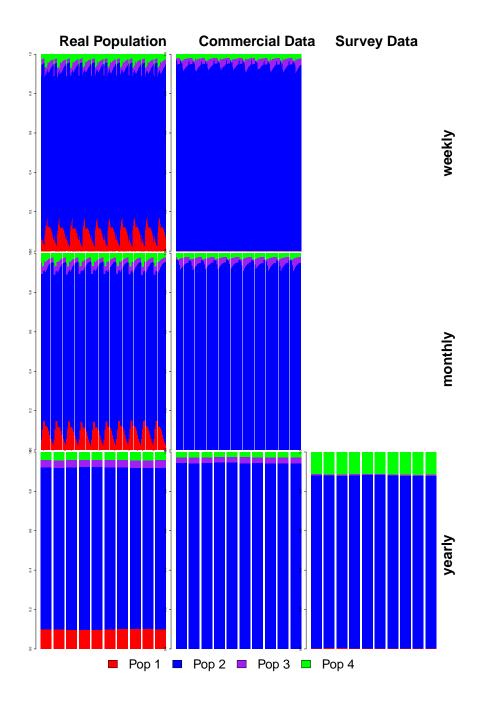


Figure 3: Data aggregation at different temporal resolutions over a ten-year period

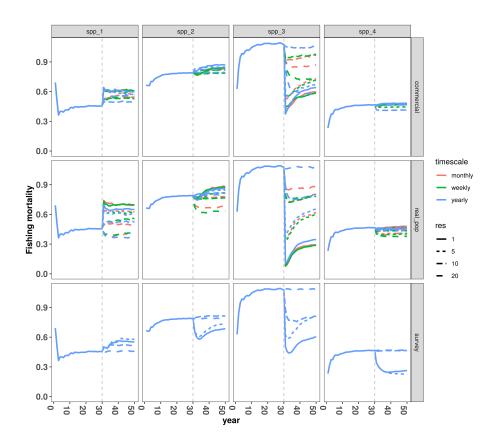


Figure 4: Comparison of closure scenarios effect on fishing mortality trends. Line colour denotes the timescale, while linestyle denotes the spatial resolution.

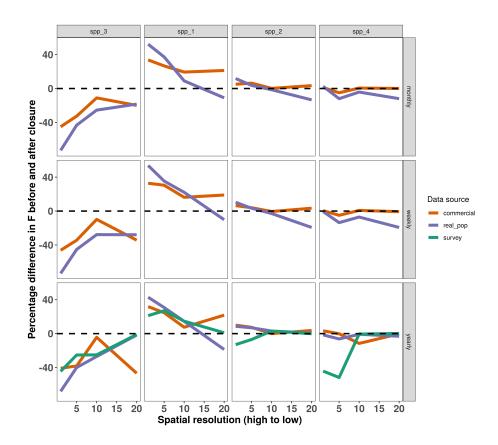


Figure 5: Comparison of closure scenario effectiveness based on different spatial and temporal resolutions.

443 References

- Alverson, D.L., Freeberg, M.H., Murawski, S.A., Pope, J., 1994. A global assessment of fisheries bycatch and discards.
- 446 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.
- 449 Bartumeus, F., Da Luz, M.G.E., Viswanatham, G.M., Catalan, J., 2005. Animal Search
- 450 Strategies: A Quantitative Random Walk Analysis. Ecological Society of America 86,
- 451 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.
- 455 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,
- 457 715-736.
- 458 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
- 460 670, 317–333.
- Bertrand, S., Bertrand, A., Guevara-Carrasco, R., Gerlotto, F., 2007. Scale-invariant move-
- ments of fishermen: The same foraging strategy as natural predators. Ecological Applica-
- tions 17, 331–337.
- Beverton, R.J., Holt, S.J., 1957. On the Dynamics of Exploited Fish Populations , 533.
- 465 Catchpole, T.L., Revill, A.S., 2008. Gear technology in Nephrops trawl fisheries. Reviews in
- Fish Biology and Fisheries 18, 17–31.
- 467 Codling, E.A., Plank, M.J., Benhamou, S., Interface, J.R.S., 2008. Random walk models in
- biology. Journal of the Royal Society, Interface / the Royal Society 5, 813–34.
- Crowder, B.L.B., Murawski, S.a., Crowder, L.B., Murawski, S.a., 1998. Fisheries Bycatch:
- Implications for Management. Fisheries 23, 8–17.
- 471 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.
- 473 7455v3.

- 474 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.
- 477 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.
- 480 Dunn, D.C., Boustany, A.M., Roberts, J.J., Brazer, E., Sanderson, M., Gardner, B., Halpin,
- 481 P.N., 2014. Empirical move-on rules to inform fishing strategies: A New England case
- study. Fish and Fisheries 15, 359–375.
- 483 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.
- 486 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.
- 488 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. Ecogra-
- phy 30, 609–628.
- 493 Gerritsen, H.D., Lordan, C., Minto, C., Kraak, S.B.M., 2012. Spatial patterns in the re-
- tained catch composition of Irish demersal otter trawlers: High-resolution fisheries data as
- a management tool. Fisheries Research 129-130, 127–136.
- 496 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.
- 499 Girardin, R., Vermard, Y., Thébaud, O., Tidd, A., Marchal, P., 2015. Predicting fisher
- response to competition for space and resources in a mixed demersal fishery. Ocean &
- Coastal Management 106, 124–135.
- Hilborn, R., Walters, C., 1992. Quantitative fisheries stock assessment: Choice, dynamics and
- uncertainty. volume 2. arXiv:1011.1669v3.
- Holmes, S.J., Bailey, N., Campbell, N., Catarino, R., Barratt, K., Gibb, A., Fernandes, P.G.,
- 505 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
- 507 Science 68, 1679–1688.

- 508 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
- 510 Science 61, 1443–1452.
- Kennelly, S.J., Broadhurst, M.K., 2002. By-catch begone: Changes in the philosophy of fishing technology. Fish and Fisheries 3, 340–355.
- Lee, J., South, A.B., Jennings, S., 2010. Developing reliable, repeatable, and accessible meth-
- ods to provide high-resolution estimates of fishing-effort distributions from vessel monitor-
- ing 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 by catch and discards: experiences from Europe and the
- United States. Fish and Fisheries , n/a-n/a.
- 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.
- Poos, J.J., Rijnsdorp, A.D., 2007. An "experiment" on effort allocation of fishing vessels: the
- role of interference competition and area specialization. Canadian Journal of Fisheries and
- 526 Aquatic Sciences 64, 304–313.
- 527 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.
- 531 Ricker, W.E., 1954. Stock and recruitment. Journal of the Fisheries Research Board of Canada
- 11, 559 623.
- Rijnsdorp, A., 2000. Competitive interactions among beam trawlers exploiting local patches
- of flatfish in the North Sea. ICES Journal of Marine Science 57, 894–902.
- Rijnsdorp, a.D., Daan, N., Dekker, W., Poos, J.J., Van Densen, W.L.T., 2007. Sustainable
- use of flatfish resources: Addressing the credibility crisis in mixed fisheries management.
- Journal of Sea Research 57, 114–125.
- Rijnsdorp, A.D., Piet, G.J., Poos, J.J., 2001. Effort allocation of the Dutch beam trawl fleet
- in response to a temporarily closed area in the North Sea. Ices Cm 2001/N: 01 , 1-17.

- Sakiyama, T., Gunji, Y.P., 2013. Emergence of an optimal search strategy from a simple
 random walk. Journal of the Royal Society, Interface 10, 20130486.
- 542 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.
- 547 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.
- 550 Sims, D.W., Southall, E.J., Humphries, N.E., Hays, G.C., Bradshaw, C.J.A., Pitchford, J.W.,
- James, A., Ahmed, M.Z., Brierley, A.S., Hindell, M.A., Morritt, D., Musyl, M.K., Righton,
- D., Shepard, E.L.C., Wearmouth, V.J., Wilson, R.P., Witt, M.J., Metcalfe, J.D., 2008.
- Scaling laws of marine predator search behaviour. Nature 451, 1098–U5.
- Tidd, A.N., Hutton, T., Kell, L.T., Blanchard, J.L., 2012. Dynamic prediction of effort reallocation in mixed fisheries. Fisheries Research 125-126, 243-253.
- Tobler, W.R., 1970. A Computer Movie Simulating Urban Growth in the Detroit Region.
- 557 Economic Geography 46, 234. arXiv:1011.1669v3.
- Ulrich, C., Reeves, S.a., Vermard, Y., Holmes, S.J., Vanhee, W., 2011. Reconciling single-
- species TACs in the North Sea demersal fisheries using the Fcube mixed-fisheries advice
- framework. ICES Journal of Marine Science 68, 1535–1547.
- Viswanathan, G.M., Buldyrev, S.V., Havlin, S., Da Luz, M.G.E., Raposo, E.P., Stanley, H.E.,
- 1999. Optimizing the success of random searches. Nature 401, 911–914.