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

Paul J. Dolder<sup>a,b,\*</sup>, Cóilín Minto<sup>a</sup>, Jean-Marc Guarini<sup>c</sup>, Jan Jaap Poos<sup>d,e</sup>

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

<sup>c</sup>Sorbonne Université, Faculty of Sciences, 4 Place Jussieu, 75005 Paris, France
 <sup>d</sup>Wageningen Marine Research, Haringkade 1 1976 CP IJmuiden, Netherlands
 <sup>e</sup>Aquaculture and Fisheries Group, Wageningen University & Research, Zodiac Building
 122, De Elst 1, 6708 WD Wageningen, the Netherlands

#### Abstract

To understand how data resolution impacts inference on mixed fisheries interactions, we developed a highly resolved spatiotemporal discrete-event simulation model incorporating: i) delay-difference population dynamics, ii) population movement using Gaussian Random Fields to simulate patchy, heterogeneously distributed populations, and iii) fishery dynamics for multiple fleet characteristics based on species targeting under an explore-exploit strategy. This is implemented via a mix of correlated random walk movement (for exploration) and learned behaviour (for exploitation) phases of the fisheries.

Fifty years of sub-daily fishing was simulated and used to draw inference on the underlying community structures. We compared inferences based on: commercial catch, a simulated fixed-site sampling survey design and the true underlying community. We i) establish the potential limitations of fishery-dependent data in providing a robust picture of spatiotemporal distributions; and then ii) simulated an area closure based on areas defined from the different data sources at a range of temporal and spatial resolutions.

Our framework allows users to explore the assumptions in modelling observational data and evaluate the underlying dynamics of such approaches at a fine

 $Email\ address: \verb"paul.dolder@gmit.ie" (Paul\ J.\ Dolder)$ 

<sup>\*</sup>Corresponding author

spatial and temporal scale. We conclude from our example framework application that commercial data, while containing bias, provide a useful tool for managing catches in mixed fisheries if applied at the correct spatiotemporal scale. [NEED A LITTLE MORE DETAIL OF THE RESULTS HERE - 2 MORE SENTENCES ON KEY TAKE-HOME RESULTS]

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. As
- 4 fishers do not have full control over what species they select in 'mixed fisheries'
- 5 this can result in catch of low quota or protected species. If fishers discard over-
- $_{6}$  quota catch of a species for which they have no quota, it limits our ability to
- control fishing mortality (Alverson et al., 1994; Crowder et al., 1998; Rijnsdorp
- <sub>8</sub> et al., 2007) and the ability to manage fisheries for the biological and economic
- 9 sustainability (Ulrich et al., 2011; Batsleer et al., 2015).

10

There is increasing interest in technical solutions such as gear and spatial clo-

sures as measures to reduce unwanted catch (Kennelly and Broadhurst, 2002;

Catchpole and Revill, 2008; Bellido et al., 2011; Cosgrove et al., 2019) and

adaptive spatial management strategies have been proposed as a way of reduc-

ing over-quota discards (Holmes et al., 2011; Little et al., 2014; Dunn et al.,

6 2014). However, if fisheries are to reduce unwanted catch through spatial avoid-

ance, an in-depth understanding of spatiotemporal fishery dynamics is required.

18

Understanding the correct scale for spatial management measures to be effective is crucial as it enables implementation of effective solutions which minimise economic impact (Dunn et al., 2016). For example, the problem can be to iden-

tify a scale that promotes species avoidance for vulnerable or low quota species while allowing continuance of sustainable fisheries for available quota species.

Identifying the correct spatial scale remains a challenge because data on fish location at high temporal and spatial resolutions is expensive and difficult to collect and proxies are usually inferred from scientific surveys or commercial catches with limited spatial and temporal resolution. Thus, implementation of spatial measures is hampered by a lack of knowledge of fish and fishery spatiotemporal dynamics and understanding of the scale at which these processes become important for management.

31

Identifying appropriate spatial scales for fisheries closures has been a highlighted as crucial to their success (Costello et al., 2010; Dunn et al., 2016).

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

13

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). However, fishers establish favoured fishing grounds through an exploreexploit strategy (Rijnsdorp et al., 2011; 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. This leads to an inherently biased
sampling where target species are over-represented in the catch as fishers exploit

areas of high abundance. There is a need to understand the influence of these biases on any spatial management measures which are implemented based on inference from commercial landings or catch data.

56

- To understand the effect of spatiotemporal aggregation of data and fishery targeting on our perception of spatial abundance of different fish populations we ask two fundamental questions regarding inference derived from observational data:
- 1. Do different source of sampling-derived fisheries data reflects the underlying community structure?
- 2. How does data aggregation and data source impact on the success of spatial fisheries management measures?

To answer these questions we i) develop a simulation model where population dynamics are highly-resolved in space and time, using a Gaussian spatial process to define suitable habitat for different populations. As the precise locations of the fish are known directly rather than inferred from sampling or commercial catch, we can use the population model to validate how inference from fisheries-dependent and fisheries independent sampling relates to the real community structure in a way we could not with real data. We ii) compare, at different spatial and temporal aggregations, the real (simulated) population distributions to samples from fisheries-dependent and fisheries independent 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.

77

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

# 2. Materials and Methods

A Discrete-event simulation (DES) model of a hypothetical fishery was developed as a software package (*MixFishSim*). The modular approach enabled efficient computation by allowing for sub-modules implemented on time-scales appropriate to capture the 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.

8

Population dynamics operate on a daily time-step, while population movement occurs on a weekly time-step, with the fishing module operating on a tow-by-tow basis (i.e. multiple events a day).

#### 92 2.1. Population dynamics

The basic population level processes were simulated using a modified two-93 stage Deriso-Schnute delay difference model which models the fish populations in 94 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 bi-97 ologically relevant and computationally tractable timescale. Population biomass growth was modelled as a function of previous recruited biomass, intrinsic pop-99 ulation growth and recruitment functionally linked to the adult population size. 100 Biomass for each cell c was incremented each day d as follows (the full parameter 10: list is detailed in Table 1): 102

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

where  $\rho$  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.  $\alpha_d$  represents the proportion of fish recruited during that day for the year, while  $R_{c,\tilde{y},d}$  is the annual recruits in year y and day d for cell c.

108

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

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

where  $C_{c,d}$  is the summed catch from the fishing model across all fleets and vessels in cell c for the population during the day d, and  $B_{c,d}$  the daily biomass for the population in the cell. Here, catch is the sum of those across all fleets and vessels,  $C_{c,d} = \sum_{fl=1}^{fl} \sum_{v=1}^{v} E_{fl,v,c,d} \cdot Q_{fl} \cdot D_{c,d}$  with fl and v the fleet and vessel respectively and  $E_{fl,v,c,d}$  and  $Q_{fl}$  fishing effort and catchability of the gear, and  $D_{c,d}$  is the density of the population at the location fished.

119

120

#### 2.2. Recruitment dynamics

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

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

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

Where  $\alpha$  is the maximum recruitment rate,  $\beta$  the spawning stock biomass (SSB) required to produce half the maximum stock size, S current stock size and  $\sigma^2$ the variability in the recruitment due to stochastic processes, the stochastic Ricker form (Ricker, 1954):

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

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

where  $\alpha$  is the maximum productivity per spawner and  $\beta$  the density dependent reduction in productivity as the SSB increases.

#### 2.3. Population movement dynamics

Population movement is a combination of directed (advective) movement where at certain times of year the population moves towards spawning grounds by increasing the probabilities of moving into the spawning grounds from adjacent cells, and random (diffusive) movement, governed by a stochastic process where movement between adjacent cells is described by a set of probabilities.

136 137

132

133

134

135

To simulate fish population distribution in space and time a Gaussian spatial process was employed to model habitat suitability for each of the popula-139 tions on a 2d grid. We first defined a Gaussian random field process,  $\{S(c):$ 140  $c \in \mathbb{R}^2$ , where for any set of cells  $c_1, \ldots, c_n$ , the joint distribution of S =141  $\{S(c1), \ldots S(c_n)\}\$  is multivariate Gaussian with a *Matérn* covariance structure, 143 where the correlation strength weakens with distance. This enables us to model the spatial autocorrelation observed in animal populations where density is more 144 similar in nearby locations (Tobler, 1970; F. Dormann et al., 2007; Poos and 145 Rijnsdorp, 2007b) and we change the parameters to implement different spa-146 tial structures for the different populations using the RandomFields R package 147 (Schlater et al., 2015). We define a stationary habitat field and combine it 148 with a temporally dynamic thermal tolerance field to imitate two key drivers of 149 population dynamics. Each population was initialised at a single location, and 150 subsequently moved across the entire space according to a probabilistic distribution based on habitat suitability (represented by the normalised values from 152

the GRFs), temperature and distance from current cell:

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

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

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

A time-varying temperature covariate changes the interaction between time and suitable habitat on a weekly time-step. Each population p was assigned a thermal tolerance with mean,  $\mu_p$  and variance,  $\sigma_p^2$  so that each cell and population temperature suitability is defined that:

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

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

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

throughout a year with seasonal spawning patterns (Figure S5).

#### 180 2.4. Fleet dynamics

Fleet dynamics can be broadly categorised into three components: fleet tar-181 geting - that determined the fleet catch efficiency and preference towards a 182 particular species; trip-level decisions, that determines the initial location to 183 be fished at the beginning of a trip; and within-trip decisions, that determines 184 movement from one fishing spot to another within a trip. An explore-exploit type strategy was implemented in the model that combined these three compo-186 nents for individual vessels to maximise their catch from an unknown resource 187 distribution (Bailey et al., 2018). The decision to use an individual based model 188 for fishing vessels was taken because fishers are heterogeneous in their location 189 choice behaviour due to different objectives, risk preference and targeting preference (Van Putten et al., 2012; Boonstra and Hentati-Sundberg, 2015). Therefore 191 fleet dynamics are emergent from individual dynamics rather than pre-defined 192 group dynamics. 193

#### 194 2.4.1. Fleet targeting

Each fleet of n vessels was characterised by both a general efficiency,  $Q_{fl}$ , and a population specific efficiency,  $Q_{fl,p}$  which are each bound by [0,1]. The product of these parameters  $[Q_{fl} \cdot Q_{fl,p}]$  affects the overall catch rates for the fleet and the preferential targeting of one 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.

#### 202 2.4.2. Decision about where to fish at the start of the trip

Several studies (Girardin et al., 2016, for a review) 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 209 from the port to the fishing grounds. Then a vessel chooses randomly from the top 75 % of fishing events as defined by the expected profit, that has a seasonal 21 component. 212

#### 2.4.3. Decision about where to fish within the trip

213

214

221

224

228

229

230

23

233

Fishing locations within a trip are initially determined by a modified random walk process. As the simulation progresses the within-trip decision become 215 gradually more influenced by experience gained from past fishing locations (as 216 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 218 process as it is the simplest assumption commonly used in ecology to describe 219 optimal animal search strategy for exploiting heterogeneously distributed prey 220 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 223 some other functional form. The direction of the random walk was also correlated (known as 'persistence') providing some overall directional movement 225 (Codling et al., 2008). 226

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

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

where  $L_{c,d,p}$  is landings of a population p, and  $Pr_p$  price of a population. All species prices were kept the same across fleets and seasons. Here, when fishing is successful vessels remain in a similar location and continue to exploit the local fishing grounds. When unsuccessful, they move some distance away from the current fishing location. The movement distance retains some degree of stochasticity, that can be controlled separately, but is determined by the relationship:

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

Where  $\beta_1$ ,  $\beta_2$  and  $\beta_3$  are parameters determining the shape of the step function in its relation to revenue, so that, a step from (x1,y1) to (x2, y2) is defined by:

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

$$y1 + Le \cdot \sin\left(\frac{\pi \cdot Br}{180}\right)$$

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

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

$$(9)$$

where Le is the step length, k the concentration parameter from the von Mises distribution that we correlate with the revenue so that  $k = (Rev + 1/RefRev) \cdot max_k$ , where  $max_k$  is the maximum concentration value, k, and RefRev is parametrised as for  $\beta_3$  in the step length function.

# 2.4.4. Local population depletion

240

Where several fishing vessels exploit the same fish population competition is 248 known to play an important role in local distribution of fishing effort (Gillis and 249 Peterman, 1998). If several vessels are fishing on the same patch of fish, local 250 depletion and interference competition will affect fishing location choice of the 25 fleet as a whole (Rijnsdorp, 2000; Poos and Rijnsdorp, 2007a). To account for this behaviour, the fishing sub-model operates spatially on a daily time-step so 253 that for future days the biomass available to the fishery is reduced in the areas 254 fished. The cumulative effect is to make heavily fished areas less attractive as a 255 future fishing location choice as reduced catch rates will be experienced.

#### 2.5. Fisheries independent survey

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

265

#### 66 2.6. Software: R-package development

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

270

#### 271 3. Parameterisation

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

#### 3.1. Population models

We parametrised the simulation model for four example populations with different demographics, growth rates, natural mortality and recruitment parameters (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).

#### 3.2. Fleet parametrisation

The fleets were parametrised to reflect five different characteristic fisheries 284 with unique exploitation dynamics (Table 5). By setting different catchability 285 parameters  $(Q_{fl,p})$  we create different targeting preferences between the fleets and hence spatial dynamics. The learned random walk process implies that 287 within a fleet different vessels have different spatial distributions based on indi-288 vidual experience. The step function was parametrised dynamically within the 289 simulations as the maximum revenue obtainable was not known beforehand. This was implemented so that vessels take smaller steps when fishing at a loca-29: tion that yields landings value in the top 90th percentile of the value experienced 292 in that year so far (as defined per fleet in Table 5). 293

294

297

298

299

301

302

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

303

305

#### 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  $100 \times 100$  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.

319

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

322

325

326

327

328

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.

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.

334

336

The following steps are undertaken to determine closures:

- 1. Extract data source (real population, commercial or survey),
- 2. Aggregate according to desired spatial and temporal resolution,

- 338 3. Interpolate across entire area at desired resolution using simple bivariate
  339 interpolation using the *interp* function from the R package akima (Akima,
  340 2006). This is intended to represent a naive spatial model of catch rates,
  341 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.

#### 350 4. Results

346

351 4.1. Emergent simulation dynamics

Individual habitat preferences and thermal tolerances result in different spatial habitat use for each population (Figure 2) and consequently different seasonal exploitation patterns (Figure 3).

It can be seen from a single vessels movements during a trip that the vessel exploits three different fishing grounds, each of them multiple times (Figure 4(A)), while across several trips fishing grounds that are further apart are fished (Figure 4 (B)). These different locations relate to areas where the highest revenue were experienced, as shown by Figure 4 (D), where several vessels tracks are 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 exploratory phase of the fishery (Figure 4 (C)). This results from the randomness in the correlated random walk step function, with distance moved during the exploitation phase and the direction stochastically related to the revenue experienced on the fishing ground (Figure 4 (D)).

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

The aggregated catch composition from each of the data sources over a ten-363 year period (which shows average seasonal patterns) at different spatial resolu-364 tions highlights different patterns in perceived community structure depending on the data source and aggregation level (Figure 5). The finer spatial grid for 366 the real population (top left) and commercial data (top middle) show visually 367 similar patterns, though there are large unsampled areas in the commercial data 368 from a lack of fishing activity (particularly in the lower left part of the sam-369 pling domain). The survey data at this spatial resolution displays very sparse 370 information about the spatial distributions of the populations. The slightly ag-371 gregated data on a 5 x 5 grid shows similar patterns and, while losing some of 372 the spatial detail, there remains good consistency between the real population 373 and the commercial data. Survey data starts to pick out some of the similar 374 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 376 of information about the spatial resolutions for all data sources, and some dif-377 ferences between the survey, commercial and real population data emerge. 378

Different perceptions of the proportion of each stock in an area are seen when we aggregate the data over a smaller geographical region at different timescales, with weekly (top), monthly (middle) and yearly (bottom) catch compositions from across an aggregated 20 x 20 area (Figure 6). In the real population, the

379

381

382

383

monthly aggregation captures the major patterns of composition seen in the

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

392

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

400

406

407

408

409

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

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

We implemented a spatial closure using the different data sources and spatial and temporal aggregations as outlined in the protocol in Section 3.4. We used this to assess the efficacy of a closure in reducing fishing mortality on species 3, given availability of data and its use at different resolutions in order to evaluate the trade-offs in data sources.

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

"adapted" to the closures and fishing mortality increased again somewhat. The 415 exception to the success was the closures implemented based on the coarsest 416 spatial (20 x 20) and temporal resolution (yearly) that was ineffective with all 417 data sources. As expected, closures based on the "known" population distribu-418 tion were most effective, with differing degrees of success using the commercial 419 data. Fishing mortality rates on the other species changed in different propor-420 tions, depending on whether the displaced fishing effort moved to areas where 421 the populations were found in greater or lesser density. 422

423

A regression tree (using the R package REEMtree (Sela and Simonoff, 2012)) 424 highlights that the factor most contributing to differences in fishing mortality 425 before and after the closure was the population (72 % showing that the closures 426 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 428 the spatial resolution of the data used the greater reduction in fishing mortality 429 for population 3 after the closures (Figure 8). The notable outliers are the com-430 mercial data at the coarsest spatial resolution (20 x 20) at a yearly and weekly 431 timescale, where closures were nearly as effective as the fine-scale resolution. In 432 this case the closures were sufficiently large to protect a core area of the habitat 433 for the population, but this was achieved in a fairly crude manner by closing a 434 large area - including area where the species was not found (Figure 9) that may 435 have consequences in terms of restricting the fishery in a much larger area than necessary. 437

438

#### 5. Discussion

Our study presents a new highly resolved fisheries simulation framework, 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 hetero-

geneously distributed fish populations with different catch limits or conservation 444 status requires detailed understanding of the overlap of resources; this is difficult 445 to achieve using conventional modelling approaches due to species targeting in fisheries resulting in preferential sampling (Martínez-Minaya et al., 2018). Of-447 ten data are aggregated or extrapolated which requires assumptions about the 448 spatial and temporal scale of processes. Our study explores the assumptions 449 behind such aggregation and preferential sampling to identify potential impacts 450 on management advice. With modern management approaches increasingly 451 employing more nuanced spatiotemporal approaches to maximise productivity 452 while taking account of both the biological and human processes operating on 453 different time-frames (Dunn et al., 2016), understanding assumptions behind 454 the data used - increasingly a combination of logbook and positional information from vessel monitoring systems - is vital to ensure measures are effective.

457

458

459

460

461

462

#### 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.

463

467

468

Our approach is unique in that it captures fine scale population and fish-465 ery dynamics and their interaction in a way not usually possible with real data 466 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 470 framework allows users to explore the assumptions in modelling observational 471 data and evaluate the underlying dynamics of such approaches at a fine spatial 472 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 identified by Gillis et al. (2008). As such, we favoured a minimum realistic model of the fish populations (Plagányi et al., 2014) taking account of environmental but not demographic stochasticity, while incorporating detailed fishing dynamics that take account of different drivers in a mechanistic way.

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

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

exploit strategy (Mangel and Clark, 1983; Bailey et al., 2018).

5.2. How does sampling-derived fisheries data reflect the underlying population 507 structure?

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

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 (Figures X,Y,Z). This provides a challenge when modelling unsampled areas in inferring species distribution maps, though these limitations may be overcome by understanding the relationship between the species and habitat covariates where these are known at unsampled locations (Robinson et al., 2011).

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

From our simulations spatial disaggregation was more important than the temporal disaggregation of the commercial data. This reflects the fact that there was greater spatial heterogeneity over the spatial domain than experienced in individual locations over the course of the year (Figure 2).

The yearly data assumes the same proportion of each population caught at any time of the year due to the data aggregation. This assumption introduces 'aggregation bias' as the data may only be representative of some point (or no point) in time. The monthly data shows some consistency between the real population and commercial data for species 2 - 4, though species 1 remains under-represented. On an annual basis, interestingly the commercial data under represents the first species (in red) while the survey over represents species 1. This is likely due to the biases in commercial sampling, with the fisheries not targeting the areas where species 1 are present and the survey sampling areas where species 1 is more abundant than on average. This indicates that fixed closures, at the right resolution, when based on commercially derived data have the potential to reduced fishing mortality. The likely cost of poor spatial and temporal resolution is associated with reduced effectiveness and potentially closing fishing opportunities for other fisheries.

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

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

#### 5.4. Model assumptions and caveats

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

Fish populations in our simulations move in pre-defined timescales and according to fixed habitat preferences and temperature gradients (Figures S1, S3). Our assumptions in parameterising 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)).

600

Other novel applications of our framework could be: testing different sur-601 vey designs given multiple species and data generating assumptions (Xu et al., 602 2015); commercial index standardisation methods and approaches and under-603 standing of appropriate scales and data aggregations and non-proportionality 604 in catch rate and abundance (Harley et al., 2001; Maunder and Punt, 2004); exploring assumptions about the distribution of natural mortality and fishing 606 mortality throughout the year and importance of capturing in-year dynamics 607 in estimating stock status (Liu and Heino, 2013); at sea sampling scheme de-608 signs to deliver unbiased estimates of population parameters (Cotter and Pilling, 609 2007; Kimura and Somerton, 2006); adaptive management (Walters, 2007; Dunn 610 et al., 2016); testing the ability of commonly employed fleet dynamics models 611 such as Random Utility Models to capture fine scale dynamics and understand 612 their importance (Girardin et al., 2016); and as a detailed operating model in a 613 management strategy evaluation (Mahévas and Pelletier, 2004).

615

617

618

619

621

# 616 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.

# 653 Abbreviations

Detail any unusual ones used.

# 655 Acknowledgements

those providing help during the research..

# Funding

This work was supported by the MARES doctoral training program (MARES\_14\_15)

and the Centre for Environment, Fisheries and Aquaculture Science seedcorn

program (DP227AC).

# 661 Appendices

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

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

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

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 $p$	$\in \ \mathrm{kg}^{-1}$						
Le	Step length for vessel	euclidean						
		distance						
$\operatorname{Br}$	Bearing	degrees						
k	Concentration parameter for Von mises distribution	-						
$\beta_1$	shape parameter for step function	-						
$eta_2$	shape parameter for step function	-						
$\beta_3$	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 $\nu$	1/0.015	1/0.05	1/0.01	1/0.005
Matérn $\kappa$	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 $\lambda$	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 $\sigma^2$	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				
$\mu$	12	15	17	14
$\sigma^2$	8	9	7	10

Table 5: Fleet dynamics parameter setting								
Parameter	Fleet	Fleet	Fleet	Fleet	Fleet			
	1	2	3	4	5			
Targeting preferences	pop	pop	-	pop 4	pop			
	2/4	1/3			2/3			
Price Pop1	100	100	100	100	100			
Price Pop2	200	200	200	200	200			
Price Pop3	350	350	350	350	350			
Price Pop4	600	600	600	600	600			
Q Pop1	0.01	0.02	0.02	0.01	0.01			
Q Pop2	0.02	0.01	0.02	0.01	0.03			
Q Pop3	0.01	0.02	0.02	0.01	0.02			
Q Pop4	0.02	0.01	0.02	0.05	0.01			
Exploitation dynamics								
step function $\beta_1$	1	2	1	2	3			
step function $\beta_2$	10	15	8	12	7			
step function $\beta_3$	Q90	Q90	Q85	Q90	Q80			
step function rate	20	30	25	35	20			
Past Knowledge	${ m T}$	${ m T}$	${ m T}$	${ m T}$	T			
Past Year & Month	${f T}$	${ m T}$	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	$\mathrm{spp}\_3$	1.08	0.29	-72.94	monthly	high_pop	$real\_pop$	1.00
11	F	$\mathrm{spp}\_3$	1.08	0.35	-68.04	yearly	high_pop	$real\_pop$	1.00
45	F	$\mathrm{spp}\_3$	1.08	0.58	-46.70	yearly	high_pop	commercial	20.00
1	F	$\mathrm{spp}\_3$	1.08	0.58	-46.21	weekly	high_pop	commercial	1.00
23	F	$\mathrm{spp}\_3$	1.08	0.59	-45.27	weekly	high_pop	$real\_pop$	5.00
2	F	$\mathrm{spp}\_3$	1.08	0.59	-45.06	monthly	high_pop	commercial	1.00
7	F	$spp_{-}3$	1.08	0.60	-44.48	yearly	high_pop	survey	1.00
24	F	${\rm spp\_3}$	1.08	0.61	-43.20	monthly	$high\_pop$	$real\_pop$	5.00
3	F	${\rm spp\_3}$	1.08	0.64	-40.82	yearly	$high\_pop$	commercial	1.00
25	F	${\rm spp} \text{-} 3$	1.08	0.65	-39.94	yearly	$high\_pop$	$real\_pop$	5.00
17	F	$spp\_3$	1.08	0.67	-38.11	yearly	$high\_pop$	commercial	5.00
15	F	${\rm spp\_3}$	1.08	0.71	-34.38	weekly	$high\_pop$	commercial	5.00
43	F	${\rm spp} \text{-} 3$	1.08	0.71	-34.31	weekly	$high\_pop$	commercial	20.00
16	F	${\rm spp} \text{-} 3$	1.08	0.73	-32.58	monthly	$high\_pop$	commercial	5.00
51	F	${\rm spp\_3}$	1.08	0.78	-27.92	weekly	$high\_pop$	$real\_pop$	20.00
37	F	${\rm spp\_3}$	1.08	0.78	-27.76	weekly	$high\_pop$	$real\_pop$	10.00
39	F	${\rm spp} \text{-} 3$	1.08	0.79	-26.98	yearly	$high\_pop$	$real\_pop$	10.00
38	F	${\rm spp\_3}$	1.08	0.81	-25.47	monthly	$high\_pop$	$real\_pop$	10.00
21	F	${\rm spp\_3}$	1.08	0.81	-25.21	yearly	$high\_pop$	survey	5.00
35	F	spp3	1.08	0.81	-25.05	yearly	high_pop	survey	10.00
44	F	spp3	1.08	0.87	-19.91	monthly	$high\_pop$	commercial	20.00
52	F	${\rm spp\_3}$	1.08	0.88	-18.39	monthly	$high\_pop$	$real\_pop$	20.00
30	F	$\mathrm{spp}\_3$	1.08	0.96	-11.06	monthly	$high\_pop$	commercial	10.00
29	F	${\rm spp\_3}$	1.08	0.98	-9.80	weekly	$high\_pop$	commercial	10.00
31	F	${\rm spp\_3}$	1.08	1.03	-4.36	yearly	high_pop	commercial	10.00
53	F	$spp_3$	1.08	1.06	-1.64	yearly	high_pop	$real\_pop$	20.00
49	F	$spp_3$	1.08	1.07	-1.01	yearly	high_pop	survey	20.00

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

data_type	timescale	spp1	sd_spp1	spp2	sd_spp2	spp3	sd_spp3	spp4	sd_spp4
commercial	monthly	0.047	0.014	94.435	1.470	3.122	1.468	2.396	0.444
commercial	weekly	0.047	0.016	94.426	1.514	3.117	1.563	2.411	0.498
commercial	yearly	0.051	0.001	94.388	0.205	3.021	0.175	2.539	0.046
$real\_pop$	monthly	9.225	3.872	83.287	5.522	3.624	1.151	3.864	1.519
$real\_pop$	weekly	9.358	3.992	83.165	5.596	3.567	1.233	3.910	1.592
real_pop	yearly	9.899	0.173	82.250	0.308	3.821	0.119	4.031	0.050
survey	yearly	0.372	0.005	87.667	0.193	0.729	0.020	11.232	0.172



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

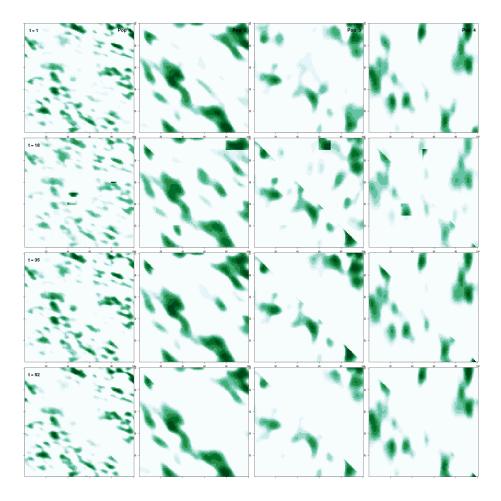


Figure 2: Spatial density (log abundance) for each of the four populations at four time steps. The darker the colour the greater the density of the population. Note that you can see the diagonal isotropic patterns in populations 2 and 3 and concentrated spawning areas in the second row of the panels (t=18)

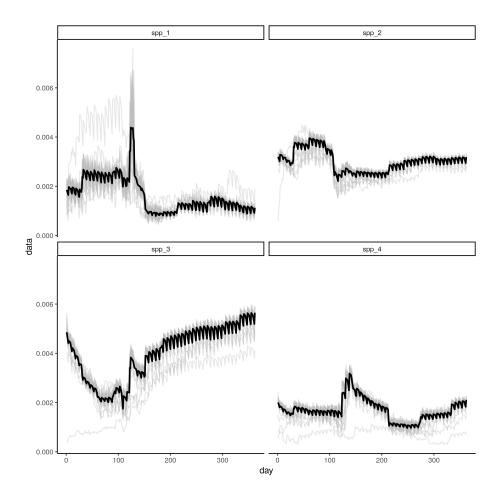


Figure 3: Fishing mortality dynamics - the daily fishing mortalities across the entire spatial domain showing weekly and seasonal patterns in exploitation. Individual years and the light grey lines, the mean of all years the thick black line

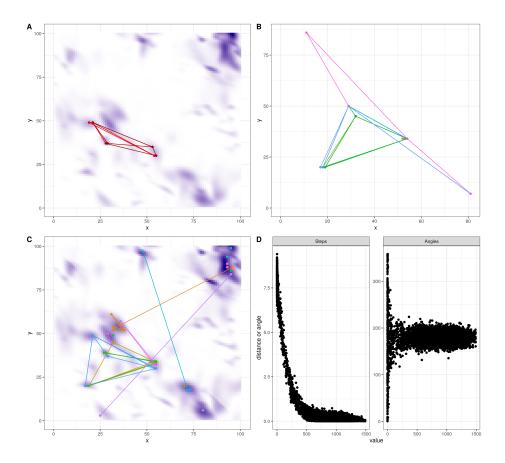


Figure 4: (A) The fishing locations (points) and movements (lines) of a single vessel during a trip overlaid on the relative value of a fishing site; (B) the fishing locations of the vessel over several trips (value field changes over the period so not shown). Note that the field is wrapped on a torus so that distances between opposite side of the spatial domain are considered next to each other, hence apparent large movements; (C) the locations of multiple vessels from the same fleet overlaid on the value field, (D) the realised step distance and turning angles for a single vessel over the simulation

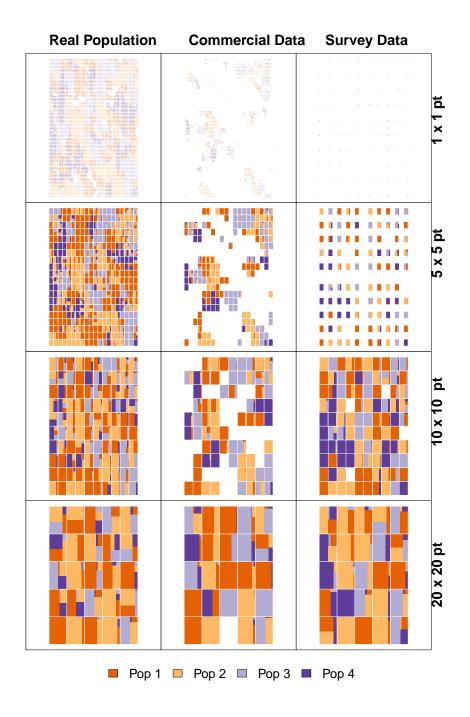


Figure 5: Data aggregation at different spatial resolutions over a ten year period

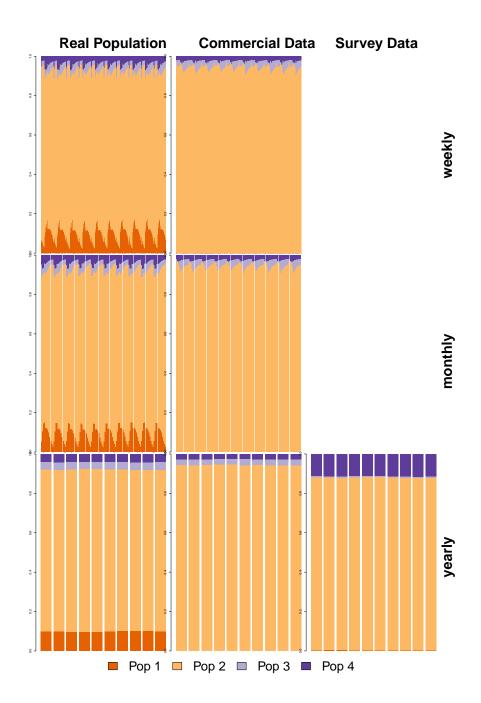


Figure 6: Data aggregation at different temporal resolutions over a ten-year period

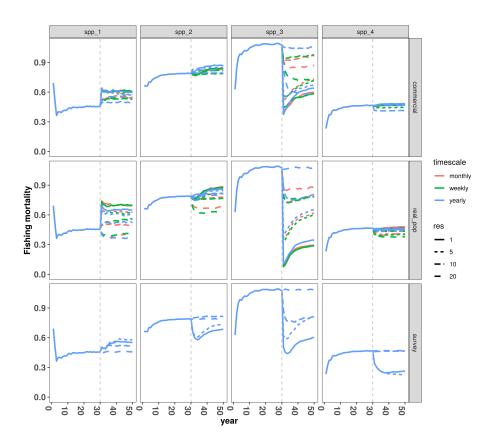


Figure 7: Comparison of closure scenarios effect on fishing mortality trends. Line colour denotes the timescale, while linestyle denotes the spatial resolution. The vertical dashed line indicates the onset of the spatial closures.

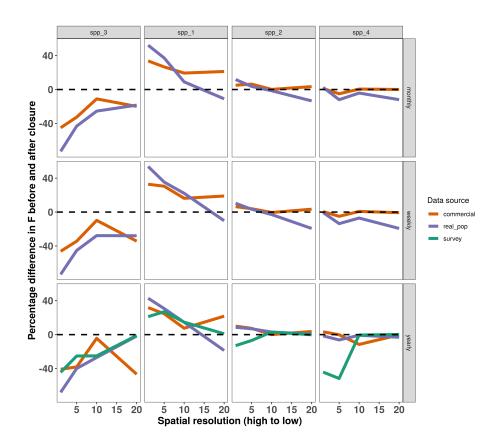


Figure 8: Comparison of closure scenario effectiveness based on different spatial and temporal resolutions.

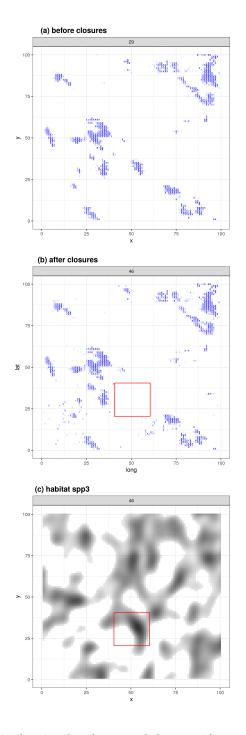


Figure 9: Closure fishing locations based on annual closures with a coarse spatial resolution. Closure location can be seen in red in relation to a) before the closure fishing locations, b) after the closure fishing locations, c) species 3 habitat distribution  $42\,$ 

## 62 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.
- 667 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
- 669 human-environmental systems: the POSEIDON model of ocean fisheries.
- 670 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.
- 673 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,
- 675 715-736.
- <sup>676</sup> 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.
- 679 Beverton, R.J., Holt, S.J., 1957. On the Dynamics of Exploited Fish Populations , 533.
- Boonstra, W.J., Hentati-Sundberg, J., 2015. Classifying fishers' behaviour. An invitation to
   fishing styles. Infancy .
- 682 Branch, T., Hilborn, R., Bogazzi, E., 2005. Escaping the tyranny of the grid: a more realistic
- way of defining fishing opportunities. Canadian Journal of Fisheries and Aquatic Sciences
- 684 642, 631–642.
- Catchpole, T.L., Revill, A.S., 2008. Gear technology in Nephrops trawl fisheries. Reviews in
- Fish Biology and Fisheries 18, 17–31.
- 687 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.
- 689 Cosgrove, R., Browne, D., Minto, C., Tyndall, P., Oliver, M., Montgomerie, M., McHugh,
- $_{690}$  M., 2019. A game of two halves: By catch reduction in Nephrops mixed fisheries. Fisheries
- 691 Research 210, 31-40.

- 692 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 .
- 695 Cotter, A.J., Pilling, G.M., 2007. Landings, logbooks and observer surveys: Improving the
- 696 protocols for sampling commercial fisheries. Fish and Fisheries 8, 123–152.
- 697 Crowder, B.L.B., Murawski, S.a., Crowder, L.B., Murawski, S.a., 1998. Fisheries Bycatch:
- Implications for Management. Fisheries 23, 8–17.
- 699 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.
- 701 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.
- 703 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.
- 707 Dinmore, T.A., Duplisea, D.E., Rackham, B.D., Maxwell, D.L., Jennings, S., 2003. Impact
- 708 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.
- 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-
- 722 phy 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 .
- 726 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.
- 729 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.
- Gillespie, D.T., 1977. Exact stochastic simulation of coupled chemical reactions, in: Journal
- of Physical Chemistry.
- 734 Gillis, D.M., Peterman, R.M., 1998. Implications of interference among fishing vessels and
- 735 the ideal free distribution to the interpretation of CPUE. Canadian Journal of Fisheries
- and Aquatic Sciences 55, 37–46.
- 737 Gillis, D.M., Rijnsdorp, A.D., Poos, J.J., 2008. Behavioral inferences from the statistical
- distribution of commercial catch: patterns of targeting in the landings of the Dutch beam
- trawler fleet. Canadian Journal of Fisheries and Aquatic Sciences 65, 27–37.
- 740 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.
- 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.
- 745 Hilborn, R., Walters, C., 1992. Quantitative fisheries stock assessment: Choice, dynamics and
- uncertainty. volume 2. arXiv:1011.1669v3.
- 747 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
- 750 Science 68, 1679–1688.
- 751 Kennelly, S.J., Broadhurst, M.K., 2002. By-catch begone: Changes in the philosophy of fishing
- technology. Fish and Fisheries 3, 340–355.
- 753 Kimura, D.K., Somerton, D.A., 2006. Review of statistical aspects of survey sampling for
- marine fisheries. Reviews in Fisheries Science 14, 245–283.

- Lande, R., Engen, S., Saether, B.E., 2010. Stochastic Population Dynamics in Ecology and
   Conservation.
- 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.
- 760 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.
- Liu, X., Heino, M., 2013. Overlooked biological and economic implications of within-season
- fishery dynamics. Canadian Journal of Fisheries and Aquatic Sciences .
- 765 Mahévas, S., Pelletier, D., 2004. ISIS-Fish, a generic and spatially explicit simulation tool for
- 766 evaluating the impact of management measures on fisheries dynamics. Ecological Modelling
- 767
- Mangel, M., Clark, C.W., 1983. Uncertainty, search, and information in fisheries. ICES
- Journal of Marine Science .
- 770 Martínez-Minaya, J., Cameletti, M., Conesa, D., Pennino, M.G., 2018. Species distribution
- modeling: a statistical review with focus in spatio-temporal issues.
- 772 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.
- 777 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.
- 789 R Core Team, 2017. R Core Team (2017). R: A language and environment for statistical
- 790 computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-
- project.org/., R Foundation for Statistical Computing.
- 792 Ricker, W.E., 1954. Stock and recruitment. Journal of the Fisheries Research Board of Canada
- 793 11, 559 623.
- 794 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.
- 796 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.
- 801 Rijnsdorp, A.D., Poos, J.J., Quirijns, F.J., Grant, J., 2011. Spatial dimension and exploitation
- dynamics of local fishing grounds by fishers targeting several flatfish species. Canadian
- Journal of Fisheries and Aquatic Sciences 68, 1064–1076.
- 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,
- 807 789-802.
- 808 Schlater, M., Malinowski, A., Menck, P.J., 2015. Analysis, Simulation and Prediction of
- Multivariate Random Fields with Package RandomFields. Journal of Statistical Software
- 810 63, 1-25, arXiv:1501.0228.
- 811 Schnute, J., 1985. A genera theory for analysis of catch and effort data. Canadian Journal of
- Fisheries and Aquatic Sciences 42, 414–429.
- 813 Sela, R., Simonoff, J., 2012. Package 'REEMtree'.
- 814 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.

- 817 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
- $_{\rm 819}$  distribution model frameworks. Canadian Journal of Fisheries and Aquatic Sciences .
- Tobler, W.R., 1970. A Computer Movie Simulating Urban Growth in the Detroit Region.
- 821 Economic Geography 46, 234. arXiv:1011.1669v3.
- 822 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,
- 826 S., 2012. Theories and behavioural drivers underlying fleet dynamics models. Fish and
- 827 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 spa-
- tiotemporal 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
- 836