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A Comparison of Fleet Dynamics Models for Predicting Fisher Location Choice

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ABSTRACT

Scientific advice for fisheries management rarely takes into account how fishers react to regulations, which can lead to unexpected results and unrealistic expectations of the effectiveness of the management measures. Short-term decisions about when and where to fish are one of the greatest sources of uncertainty in predicting management outcomes. Several models have been developed to predict how fishers allocate effort in space and time, including mechanistic methods such as gravity and dynamic state variable models, and statistical methods such as random utility and Markov models. These have been individually used to predict effort allocation for various fisheries, but there is no comparative synthesis of their structure and characteristics. We demonstrate strong theoretical links between utility and choice in gravity, random utility, Markov and dynamic state variable models. Using an advanced event-based simulation framework, we find that mechanistic models bias effort allocation to certain areas when applying commonly used strong assumptions about drivers of effort allocation; and conversely, statistical models accurately predict the distribution of fishing effort under business as usual. However, predictive performance degrades with previously unobserved dynamics, such as a spatial closure. Mechanistic models were less suited to general application under business as usual but provide a useful framework for testing hypotheses about a fishery system in response to policy change. Comparison of simple model formulations yielded significant insight into the characteristics of the models and how they could be used to evaluate alternative management approaches for mixed fisheries.

1 | Fleet Dynamics Modelling

It is widely accepted that successful fisheries management requires understanding the human elements that determine how fishers, individually and collectively, react to varying fishing opportunities and regulations (Hilborn 2007; Fulton et al. 2011; Van Putten et al. 2012). Fishers' behavioural reactions can be broadly divided into short-term, such as decisions about when and where to fish (Holland and Sutinen 2000; Rijnsdorp et al. 2011) or changes in fishing practices such as discarding certain sizes or species of fish (Gillis et al. 1995; Batsleer et al. 2016); or longer-term, such as investing or divesting in vessels, new fishing gear or technology (Hilborn and Walters 1992; Nøstbakken et al. 2011; Eigaard et al. 2014). Together, these 'fleet dynamics' have a major effect on the exploitation of fish stocks and the economic performance of fishers. Although fleet dynamics are acknowledged to be of importance and some elements are well studied (e.g., Salas and Gaertner 2004; Pelletier and Mahévas 2005; Branch et al. 2006; Van Putten et al. 2012), progress in incorporating them into operational management decision support tools such as Management Strategy Evaluation (MSE; Butterworth and Punt 1999) has been limited. This is due to the difficulty of predicting human behaviour and the lack of suitable models available on an appropriate scale (Andersen et al. 2010).

1.1 | Location Choice Models for Fisheries

Fishers' decisions regarding when and where to fish are usually modelled as an extension of the discrete choice problem in economics, with fishers being seen as actors who strive to maximise their utility through their choice of location (McFadden 1973). This utility includes both monetary and non-monetary objectives (Hess et al. 2018; Holland and Sutinen 2000; Marchal, Lallemand, et al. 2009; Girardin et al. 2017). Other models have been developed to explain why observed choices differ from the utility maximisation theory, including bounded rationality. These lead to suboptimal decisions playing a major role in the pursuit of what are known as 'satisficing' objectives for individuals, where the goal is not to achieve the best possible outcome but to meet some minimum requirement for profit or other motivation (Holland 2008; Robinson and Pascoe 1997).

Analogous to utility maximisation models in economics, models from ecological literature suggest that fishers behave like predators, using optimal prey foraging strategies to maximise their fitness (Gillis 2003; Marchal et al. 2007; Bertrand et al. 2007). Examples of such models include Ideal Free Distribution (IFD), where predator density is based on prey density (Fretwell and Lucas 1969), and Central Place Foraging (CPF), where predators search for prey from a central point and then return (e.g., to feed young or nest; Frid et al. 2016). In the context of fisheries, these models have been extended to take into account uncertain knowledge about resource distribution (Abernethy et al. 2007), competition (Gillis et al. 1993; Poos, Quirijns, et al. 2010; Rijnsdorp et al. 2022), information sharing (Gaertner and Dreyfus-Leon 2004) and risk sensitivity (Dowling et al. 2015). As utility and fitness are complex concepts, most modelling studies use proxies to define them. These proxies are often monetary, such as expected revenues and costs of visiting areas, but more complex proxies are possible, such as those that include whether locations have been visited previously.

Location choice models can be broadly divided into two categories: mechanistic and statistical. Mechanistic models attempt to explain the relationship between the components of a system so that the entire system is the result of these connections. Statistical models, on the other hand, assume a categorical distribution (Agresti 2006), with the parameters of the distribution being determined by covariates. These parameters are then estimated using either maximum likelihood or Bayesian inference.

1.1.1 | Mechanistic Models

Mechanistic models are derived from first principles and generally conditioned or tuned so that parameter values describe the observed dynamics (Cuddington et al. 2013). In the literature, we have identified ideal free distribution, central place foraging, gravity models and dynamic state variable models (DSVMs) as process-driven mechanistic approaches to predicting location choice. However, as gravity models can be formulated to resemble both IFD and CPF, we focus only on gravity models for comparison. Similarly, we exclude models that require detailed case-specific conditioning, such as the individual-based model of Bastardie et al. (2014) because they are less suited to general application in an MSE framework and share similar features to the gravity model approach.

1.1.1.1 | Ideal Free Distribution and Central Place Foraging. The concept of ideal free distribution and central place foraging is based on the idea that individuals strive to maximise their fitness by using food patches in the most effective way possible (Fretwell and Lucas 1969). For IFD, it is assumed that there is no travel cost when moving between feeding sites and that predators distribute proportionally to the density of prey, equalising density across the area through predation pressure. In contrast, CPF assumes that predators are based at a single point and repeatedly exploit the same patches that are optimal in terms of travel cost and reward. In fisheries literature, IFD has received more attention than CPF; CPF is considered a suitable framework mainly for recreational or artisanal small-scale fisheries that leave and return from the same place, lasting a single day (Frid et al. 2016). It may be less applicable to large-scale commercial fisheries that exploit numerous distant areas before returning to port (Frid et al. 2016).

1.1.1.2 | Gravity Model. The fundamental concept of gravity models is that the movement of goods and services (Isard 1954) or people (Duddy 1932) can be represented by a measure of attraction and an inverse relationship to distance. Commonly used in social sciences, a gravity model was first applied to fisheries by Caddy (1975). In that study, the attractiveness of a fishing ground was modelled as proportional to the observed catch rates in the area, measured in terms of weight or value of catch.

The basic assumptions of a fisheries gravity model are that catch rates are known precisely and there are no travel costs to get to each fishing area; thus, the density of vessels will equalise the catch rates across areas by allocating more effort to areas with higher catch rates. Predictions of effort allocation are based on the expected catch in each spatial area and season, similar to the idea of IFD (Fretwell and Lucas 1969). However, since fisheries often deviate from IFD (Gillis 2003), the gravity model is often adjusted to take into account other factors such as bias towards areas of high abundance (e.g., Walters et al. 1993), adjusting for travel costs (Caddy and Carocci 1999) and prices of different species (Hilborn and Walters 1987), taking into account information exchange between fishers (Allen and McGlade 1986) or tradition (Marchal et al. 2013). Gravity models have been used in MSE routines (e.g., Walters and Bonfil 1999; Mahévas and Pelletier 2004), although the accuracy of the predictions is rarely tested.

1.1.1.3 | Dynamic State Variable Model. Dynamic state variable models (Clark and Mangel 2000) specify that actors are maximisers of a defined utility. The options are evaluated in terms of their contribution to the overall utility, and the choice with the highest marginal utility is chosen. Individuals' decisions, influenced by long-term and short-term factors such as costs, quotas or any other restrictions such as fines (Poos, Bogaards, et al. 2010; Alzorriz et al. 2018) determine the amount of effort allocated to each area. It is dynamic in the sense that it keeps track of the 'state' of an individual and that the optimal choice depends on this state. In fisheries, this state can be, for example, the total cumulative catch, profit, bycatch or any other factors over time. The results of choices in DSVM such as the catch in a time step can be random variables, so that individuals will gradually differ in state, even when making the same choices. Therefore, the optimisation depends on the actions in the previous time steps. Optimisation is achieved recursively through backward iteration, which may be computationally challenging if there are a large number of variables, as the number of potential states increases exponentially, known as the curse of dimensionality (Bellman 1987). DSVMs also generally have a forward-step algorithm that simulates the trajectory of individuals using Monte Carlo simulation. In this forward simulation, the choices are modelled for a set of errors in decision-making which can be introduced so that a distribution of choices over options are modelled given an individual state, rather than only the optimal solution (Dowling et al. 2012).

The DSVM approach has the unique advantage of being able to take into account short-term decisions about location choice (including staying in port) given long-term constraints (Babcock and Pikitch 2000). For example, it has been used to predict location choice given quota limits and discarding practices in mixed fisheries (Gillis et al. 1995; Poos, Bogaards, et al. 2010; Batsleer et al. 2016), as well as the response of fishers to a marine protected area (Dowling et al. 2012), allowing the models to provide a detailed understanding of the potential response of fishers to developing or new policies.

1.1.2 | Statistical Models

Commonly applied statistical models for location choice include random utility and Markov models.

1.1.2.1 | Random Utility Model. Random utility models (RUMs) are a discrete choice modelling approach derived from micro-economic theory on individuals making decisions among competing options (McFadden 1973). A central tenet is that an individual seeks to choose the option that maximises their utility, with attractiveness defined by a combination of deterministic explanatory variables and a random component (McFadden 1973). RUMs can have case-specific components (variable constant between choices, e.g., time of year) and choice-specific components (variable differs between choices, e.g., expected catch rate). RUMs have been applied in various ways to consumer choice and marketing (Boxall and Adamowicz 2002), transport planning (De La Barra 1989) and labour market analysis (Maier and Fischer 1985), as well as to the allocation of fishing effort (Hutton et al. 2004; Tidd et al. 2012; Hynes et al. 2016). They can take a number of different forms, with the key property that choice is conditional on all the choices available to the actor (hence, also being known as conditional logit models).

RUMs are the primary method by which location choice has been evaluated and predicted in the past with numerous examples (see Girardin et al. 2017, for a review). A potential limitation is the need to comply with the assumption of Independence of Irrelevant Alternatives (IIA) where removing a choice or area should not affect the relative probabilities for the other choices. This is particularly relevant for spatial discrete choice models, as two areas may be substitutable due to their similar catch compositions or other characteristics, meaning that removing one option increases the probability of choosing the other relative to the other options available. However, it is possible to relax this assumption by using a nested logit (Wilen et al. 2002; Campbell and Hand 1999) that ensures independence between choices, or a mixed logit model, which treats variation between individuals as a probability distribution (Tidd et al. 2012).

1.1.2.2 | Markov Model. A Markov or semi-Markov model focuses on the transition probabilities between different states, with the probability of a transition between one state and another (including sojourns where actors stay in the same state) only dependent on the current state and not on any previous states (Howard 1971). The difference between a Markov and a semi-Markov is the presence of holding times in the latter, with time spent in a state separately estimable (Kingman and Howard 1972). Importantly, the dynamics can be described by the departing state transition, so there is an explicit link between current and future activity.

There are a few examples of the use of Markov models within the fisheries literature, but these have mainly been applied to understand the state of vessel activity to distinguish fishing from other activities (Vermard et al. 2010; Peel and Good 2011; Joo et al. 2013), with the notable exception of Venables et al. (2009) and Dichmont et al. (2008) where the location choice was modelled in the Australian northern prawn fishery.

1.2 | A Need for Synthesis

Management Strategy Evaluation (MSE), the evaluation of management strategies using simulation, has become the primary tool to support management decisions due to the explicit recognition of uncertainty in the outcomes when simulating complex fisheries-ecological systems (Butterworth and Punt 1999; Kell et al. 2006; De Oliveira et al. 2009; Punt et al. 2016). MSEs are now widely and routinely applied around the world to provide fisheries management advice (Goethel et al. 2019) but are generally applied on a stock-by-stock basis, with the interdependence between stocks resulting from biological and technical interactions ignored (e.g., Needle 2008). This results in suboptimal outcomes where, in the case of technical interactions, catches above the intended level can result from bycatch in fisheries targeting other stocks (Ulrich et al. 2017).

Because species differ in their spatial distribution, location choice by fishers has a direct impact on the composition of catch, which in turn affects management outcomes in a multi-stock fishery (Ono et al. 2018). The extension of MSEs to explicitly take account of how fishers respond to changing abundances and quotas of multiple species that are caught together is therefore necessary to improve management approaches for mixed fisheries. Although MSEs have started to incorporate fleet dynamics (see Table 1) including *inter alia* through effort allocation among métiers assuming economic optimisation (Hoff et al. 2010) or representation of fleet dynamics in simulation frameworks with simplified biological representation (e.g., Salz et al. 2011), there has been limited application in management advice.

Accounting for short-term fleet dynamics in a general way in MSEs remains a challenge (Andersen et al. 2010) but is vital to understand the impact of the changing spatial distribution of fishing effort on a population (Goethel et al. 2011; Cadrin 2020; Dolder et al. 2020). While several different approaches to location choice have been implemented, these have been specific applications for defined fisheries, and to date there have been no general comparisons to understand the strengths and weaknesses of each approach.

Understanding the structure, characteristics and predictive capability of the different location choice models will provide clarity on the assumptions they can introduce in a management simulation framework (Punt et al. 2016). This understanding provides confidence in interpreting the output of simulations to compare different management options when using one or more of the location choice models as an operating model in a full feedback MSE.

1.3 | Study Aims

The purpose of the study is to review the different methods and approaches that have been used to forecast how fishers allocate fishing effort in space and time, and how these relate to underlying heterogeneous distributions of multiple fish stocks. We compare the mechanisms of the models used, their underlying structure and their characteristics to predict future effort allocation in response to management change intended to protect a depleted stock using a simulated example. We also identify the strengths and weaknesses of the approaches under a plausible management intervention that disrupts the *status quo*, namely a spatial closure.

In doing so, we provide guidance on the most promising approaches for incorporation into MSEs, considering contemporary goals for the evaluation of different management tools.

The approach we take is to

1. Evaluate the formulation, structure, implementation and characteristics of the different models in predicting spatial effort allocation in mixed fisheries.
2. Illustrate theory demonstrating linkages and differences in how utility is related to choice among the location choice models.
3. Use a simple simulated example to assess the differences, including the strengths and weaknesses of each of the approaches and their potential for application within an MSE setting.

We compare the formulation and structure of the models via (i) a theoretical comparison of the mathematical structure of the models and (ii) an agent-based simulation framework where fleet dynamics are emergent properties of individual actors.

2 | Theoretical Comparison

We set out by defining a general model that seeks to predict the proportion of effort in each area as a basis for comparing predictions from each of the model classes (the 'choice model').

A general choice model gives that the effort $E_{a,t}$ in area a during time period t is a proportion of the total effort:

TABLE 1 | Examples of location choice models in management strategy evaluations.

Model	Geographical location	Fishery	References
RUM	Baltic and Kattegat	Demersal fish	Ulrich et al. (2007)
	North Sea	Flatfish	Andersen et al. (2010)
	Bay of Biscay	Anchovy	Vermard et al. (2012)
Markov	Australia	Prawn	Dichmont et al. (2008)
	Australia	Prawn	Venables et al. (2009)
Gravity	Torres Strait	Sea cucumber	Plagányi et al. (2013)
	Brunei	Demersal fish	Walters et al. (1999)
	New Zealand	Hoki	Marchal, Francis, et al. (2009)
	Bay of Biscay	Demersal	Briton et al. (2020)
	Australia	Demersal fish	Fulton et al. (2011)
	English Channel	Demersal fish	Lehuta et al. (2015)
	Australia	Prawn	Ives et al. (2013)
Rule-based	Baltic Sea	Cod	Bastardie et al. (2010)
	Bering Sea	Demersal fish	Ono et al. (2018)

$$E_{a,t} = p_{a,t} E_t \tag{1}$$

All of the methods predict $p_{a,t}$ and the goal is to compare them theoretically and practically.

First, we introduce each of the choice models and the notation used. Then we evaluate under which conditions each of the models can be formulated to produce identical predictions. The main results are demonstrations of equivalence.

2.1 | Gravity Model

For $a \in \{1, \ldots, A\}$, the proportion of effort in area a from the gravity model is given by

$$p_{a,t}^{(g)} = \frac{\Phi_{a,t-\tau}}{\sum_{j=1}^{A} \Phi_{j,t-\tau}} \tag{2}$$

where $\Phi_{a,t-\tau}$ is some function of utility (e.g., profit) τ time steps ago.

2.2 | Random Utility Model

A multinomial logit model typically models the log-odds of a given category relative to a baseline category. Setting area one j as the baseline category, log-odds based on utility per unit effort can be described as

$$\theta_{a,t} = \ln\left(\frac{\frac{\Phi_{a,t-\tau}}{\sum_{j=1}^{A} \Phi_{j,t-\tau}}}{\frac{\Phi_{1,t-\tau}}{\sum_{j=1}^{A} \Phi_{j,t-\tau}}}\right) = \ln\left(\frac{\Phi_{a,t-\tau}}{\Phi_{1,t-\tau}}\right) \tag{3}$$

This model is more formally a conditional logit model McFadden (1973) as the variables are choice-specific and can be generalised to

$$p_{a,t}^{(r)}\left(X_{a,t-\tau} \mid \beta\right) = \frac{e^{\beta X_{a,t-\tau}}}{\sum_{j=1}^{A} e^{\beta X_{j,t-\tau}}} \tag{4}$$

where $X_{a,t-\tau}$ is a set of area-specific covariates at time $t-\tau$ and can include any variables that contribute to the utility, such as cost and revenue (Girardin et al. 2017).

2.3 | Markov Model

The Markov property states

$$P\left(Y_t = y_t \mid Y_{t-1} = y_{t-1}, \ldots, Y_0 = y_0\right) = P\left(Y_t = y_t \mid Y_{t-1} = y_{t-1}\right), \tag{5}$$

where Y_t is the state (area) at time t. Therefore, the probability depends only on the previous state and not those preceding the previous step. A transition probability matrix governs the probability of transition among the available states of a Markov model. For A possible areas, the transition matrix can be written

$$\mathcal{P}(t) = \begin{bmatrix} \phi_{1,1}(t) & \phi_{1,2}(t) & \cdots & \phi_{1,A}(t) \\ \phi_{2,1}(t) & \phi_{2,2}(t) & \cdots & \phi_{2,A}(t) \\ \vdots & \vdots & \ddots & \vdots \\ \phi_{A,1}(t) & \phi_{A,2}(t) & \cdots & \phi_{A,A}(t) \end{bmatrix}, \tag{6}$$

where rows denote departing state and columns destination state (at time t) (probabilities sum to unity across rows). Note that the transition probabilities are here assumed time t specific. A state probability (as distinct from a transition probability) gives the probability that a given state is occupied at a given time and is denoted $p_{a,t}^{(m)}$, where

$$p_{a,t}^{(m)} = \sum_{j=1}^{A} p_{j,t-1}^{(m)} \phi_{j,a}(t), \tag{7}$$

that is the probability of being in state a at time t is the sum of the proportions moving into area a at time t from all areas j at time $t-1$.

2.4 | Dynamic State Variable Model

Dynamic state variable models (DSVMs) introduce a discretised utility state that affects choice. For example, profit utility is discretised and movements between areas (patch) would result in increments or decrements of the profit state. A fundamental difference with the statistical models that focus on area transitions (e.g., Markov models) is that DSVMs focus on utility transitions, and the optimal choice emerges from the calculation procedure. A simple DSVM predicts that the optimal policy (set of choices) is to go to the sequence of areas that results in the highest utility.

After defining how utility is affected by a state $\mathbb{X}$ at the end of a period (e.g., by comparing the accumulated profit over that period), a value function links the maximum utility between time step t and final time step T where the expected utility is

$$U(\mathbb{X}, t) = \max_a\left(\Phi_{a,t} + U\left(V_a[\mathbb{X}], t+1\right)\right), \tag{8}$$

where $\Phi_{a,t}$ is the utility per unit effort of an individual going to area a in the time step t, and $X_a\left[V\left(\Phi_i, t+1\right)\right]$ the expected future utility over all possible states resulting from choice a.

In a simple DSVM, the option that maximises the highest future utility is chosen, which means that a DSVM has the explicit assumption that utility of a choice depends on the expected state change that results from that choice; hence, this model cannot generally be equated with the other models. Equivalence can only occur where choice at a given time step has no impact on future choices, with the utility contribution arising from state change being zero, and the decisions at each time step being effectively independent. This would negate the purpose of developing a DSVM approach. To ensure that predictions have the same proportions as statistical models, the distribution of vessels between utility states multiplied by the optimal transition matrix among utility states and summed by area must be equal to that of the statistical model, as suggested by (Reimer et al. 2019). Errors-in-decision-making can be introduced, in which choices are not assumed to be optimal, but proportional to the expected utility. To achieve this, Dowling et al. (2012) introduced a tuning parameter which determines how optimally decisions are made by actors. The tuning parameter was such that where U^* is the optimal choice, the actual choice was

$$\Delta_{a,t} = U_t^* - U_{a,t}, \tag{9}$$

and the distribution of choices determined by

$$p_{a,t}^{(d)} = \frac{e^{-\Delta_{a,t}/\sigma}}{\sum_{a=1}^{A} e^{-\Delta_{a,t}/\sigma}}, \tag{10}$$

where the utility is time independent (i.e., without any long-term constraints), the predictions can be equated to the gravity model, where the gravity is treated as a multinomial so that there is a σ per area in Equation (10), being

$$\sigma_{a,t} = \frac{U_{a,t} - \max\left(U_{a=1\ldots A,t}\right)}{\log\left(\frac{U_{a,t}}{U_{a=1,t}}\right)}, \tag{11}$$

where utility is treated narrowly as profit $U_{a,t} = \Phi_{a,t}$ the predicted proportions from the gravity model (Equation 2) and DSVM are equal.

2.5 | Equating Utility in Choice Models

Conditional on the utility, we demonstrate that the link between utility and choice can be equivalent across all models. The choice from DSVMs, following the formulation in Dowling et al. (2012), is

$$p_{a,t}^{(d)} = \frac{e^{-\left(U_t^* - U_{a,t}\right)/\sigma}}{\sum_{i=1}^{A} e^{-\left(U_t^* - U_{i,t}\right)/\sigma}}, \tag{12}$$

where $U_t^* = \max_{i \in A}\left(U_{i,t}\right)$. If we let $\sigma = 1$, then

$$p_{a,t}^{(d)} = \frac{e^{-\left(U_t^* - U_{a,t}\right)}}{\sum_{i=1}^{A} e^{-\left(U_t^* - U_{i,t}\right)}} \tag{13}$$

$$= \frac{e^{U_t^*} e^{-\left(U_t^* - U_{a,t}\right)}}{\sum_{i=1}^{A} e^{U_t^*} e^{-\left(U_t^* - U_{i,t}\right)}} \tag{14}$$

$$= \frac{e^{U_{a,t}}}{\sum_{i=1}^{A} e^{U_{i,t}}} \tag{15}$$

If we let the utility of location a be $U_{a,t} = X_{a,t-\tau}\beta$, then

$$= \frac{e^{X_{a,t-\tau}\beta}}{\sum_{i=1}^{A} e^{X_{i,t-\tau}\beta}} \tag{16}$$

$$= p_{a,t}^{(r)}. \tag{17}$$

Therefore, the link between utility and choice in a DSVM following Dowling et al. (2012) can be equated to the link between utility and choice in a RUM with $\Phi_{a,t-\tau} = e^{X_{a,t-\tau}\beta}$. Further, a choice utility in a RUM is

$$p_{a,t}^{(r)} = \frac{e^{X_{a,t-\tau}\beta}}{\sum_{i=1}^{A} e^{X_{i,t-\tau}\beta}} \tag{18}$$

$$= \frac{\Phi_{a,t-\tau}}{\sum_{i=1}^{A} \Phi_{i,t-\tau}} \tag{19}$$

$$= p_{a,t}^{(g)}, \tag{20}$$

can be equated to choice in a gravity model.

If in a Markov model the transition probabilities did not depend on $\phi_{i,a}(t) = \phi_a(t) \cdot \forall i$. The transition matrix would be written

$$\mathcal{P}(t) = \begin{bmatrix} \phi_1(t) & \phi_2(t) & \cdots & \phi_A(t) \\ \phi_1(t) & \phi_2(t) & \cdots & \phi_A(t) \\ \vdots & \vdots & \ddots & \vdots \\ \phi_1(t) & \phi_2(t) & \cdots & \phi_A(t) \end{bmatrix}, \tag{21}$$

If $\phi_a(t) \propto e^{X_{a,t-\tau}\beta}$, then the link between utility and choice in a Markov model can also be equated to the link between utility and choice in the other models

$$\phi_a(t) = \frac{e^{X_{a,t-\tau}\beta}}{\sum_{i=1}^{A} e^{X_{i,t-\tau}\beta}} \tag{22}$$

$$= \frac{\Phi_{a,t-\tau}}{\sum_{i=1}^{A} \Phi_{i,t-\tau}} \tag{23}$$

$$= p_{a,t}^{(g)} = p_{a,t}^{(r)} = p_{a,t}^{(d)}. \tag{24}$$

3 | Agent-Based Simulation Study

To evaluate the characteristics of the four location choice modelling frameworks, we performed an agent-based simulation study. Each location choice model was fitted to simulated data generated by an event-based mixed fishery simulation tool based on individual vessels, *MixFishSim* (Dolder et al. 2020). A summary of the simulation is provided here, and full simulation details are provided in the Data S1.

Briefly, four species with different spatiotemporal population demographics were simulated. Each population had a different time-homogeneous habitat preference and thermal tolerance but a common spatially varying temperature field, along with diffusive (random but according to habitat preference) and directive movement (towards spawning locations at certain times of year), which operated on a weekly time step. The populations were replenished by recruitment (new fish entering the population), which was a function of population size. Natural and fishing mortality were included using a spatially explicit two-stage Deriso-Schnute delay difference model (Deriso 1980; Schnute 1985).

Each fish population was calibrated to represent a species found in a typical mixed fishery. The first population mimicked a low value but widely distributed roundfish, such as whiting (*Merlangius merlangus*), whereas population 2 was a more densely and locally distributed roundfish of medium value but high abundance, such as cod (*Gadus morhua*). Population 3 was established as a patchily distributed medium-value species such as haddock (*Melanogrammus aeglefinus*), whereas population 4 was a densely populated high-value species having lower overall biomass (e.g., *Nephrops norvegicus*).

Fishing was simulated with individual vessels with an exploration-exploit strategy, where fishing was characterised by (i) a period of exploration through a correlated random walk to explore unknown fish distributions and (ii) a period of established fishery dynamics where fishing location choice is based on expected revenue and costs of moving between fishing grounds known to the individual. It is important to highlight that vessel decisions are made individually in a micro-economic manner, with location choice across all vessels being an emergent property. The outcome is individually generated patterns, with data typically available to researchers (i.e., vessel logbook data).

Five 20-vessel fleets were defined with different species catch preferences for each fleet. The simulation was run for 29 years to establish the fishery before spatial closures were introduced in year 30 and then ran for a further 20 years (50 years in total). No quotas or other restrictions are put in place, and effort is fixed each year at the same level for each vessel. Spatial closures were designed to minimise fishing mortality on a population by closing the areas with the highest catch rates for this species.

Simulated logbook data were clustered to define fishing grounds with consistent catch compositions to define a choice set (Dolder et al. 2020; Branch et al. 2005) before we fitted two variants of the gravity model, a dynamic state variable model, two variants of random utility models and a Markov model. As a null model, we included predictions where the effort share remained unchanged from previous years.

The formulation of each of these models (Table 2) is briefly summarised in the following, and the notation is collected in Table 3.

3.1 | Model Formulations

3.1.1 | Past Effort Share ('PastShare')

As a null model (superscript p), we include predictions where the proportion of effort $p^p_{a,t}$ in area a at time t is

$$p^p_{a,t} = \overline{p}_a \tag{25}$$

where $\overline{p}_a$ is the average proportion of effort in the area previously, calculated as the sum of the effort in an area over 3 years divided by the sum of the total effort in all areas over the same period.

TABLE 2 | Model name and description.

Code	Description
Mechanistic models	
PastShare	Null model, effort share is the same as in the past
Gravity	Gravity model
GravityCombo	80% of PastShare and 20% gravity model
DSVM	Dynamic state variable model
Statistical models	
Markov	Markov transition model
RUM	Random utility model
RUMRparam	Reparameterised random utility model

3.1.2 | Gravity Model ('Gravity')

We defined a gravity model (g) such that the proportion of effort $p^g_{a,t}$ in area a at time t is given by

$$p^g_{a,t} = \frac{e^{\beta\overline{\Phi}_a}}{\sum_{a=1}^{A} e^{\beta\Phi_a}}, \tag{26}$$

where $\overline{\Phi}_a$ is the average profit for the preceding 3 years in area a, where \ for a given year is defined as

$$\Phi_{a,t} = \sum_{s=1}^{S} L_{a,t,s}\pi_s - E_{a,t}f \tag{27}$$

comprised of the sum of the landings L in tonnes for the area a at time t and species s multiplied by the price π_s per tonne minus fuel cost f per unit of effort, multiplied by effort $E_{a,t}$. This effort, in turn, is influenced by the distance travelled $D_{a,t}$. β is a tuning parameter which relates the influence of profit to the allocation of effort, where $\beta = 0$ results in effort being allocated equally across all areas, and $\beta = 1$ results in effort being allocated almost entirely to the area with the highest profit. In our case, β was estimated as the best-fitted model, with a Dirichlet error distribution.

3.1.3 | Gravity and Past Effort Share Combination (GravityCombo)

An alternative formulation of a gravity model was included, where 80% of the effort allocation was determined by the previous effort (tradition or inertia) and 20% by the gravity model (economic opportunism) after Marchal et al. (2013). The 80/20 split has been chosen for illustrative purposes, though the value could be tuned to best fit the data. This gravity–tradition combination model (superscripted c) is given by

$$p^c_{a,t} = \alpha \cdot p^p_{a,t} + (1-\alpha) \cdot p^g_{a,t}, \tag{28}$$

TABLE 3 | Model notation, including the interpretation of the symbols and units where relevant.

Notation	Meaning	Index	Units
a	Area	$a=1...A=9$	
y	Year	$y=1...Y=50$	
t	Time	$t=1...T=12$	
s	Species	$s=1...S=4$	
L	Landings		tonnes
π	Price	...	tonnes^{-1}
Φ	Utility		
D	Distance	...	km
f	Fuel cost per unit of effort	...	h^{-1}
E	Effort	hour	
$\lambda_a(l_s, t)$	Probability of landings l tonnes of species s	[0,1]	
β_a	Coefficients for area a	$1 \dots \infty$	
X_t	Covariates at time t for β coefficients	$1 \dots \infty$	
γ	Coefficients for individual	$1 \dots \infty$	
Za,t	Covariates for γ coefficients	$1 \dots \infty$	
n	Number of observations	$1...N$	Tow
p	Proportion of effort	[0,1]	
z	Past state	$z=1...Z=9$	
$\beta_{z,a}$	Coefficients for state z and area a	$1 \dots \infty$	
X_t	Covariates at time t	$1 \dots \infty$	

with $\alpha=0.8$ controlling the proportional weighting of each model.

3.1.4 | Dynamic State Variable Model ('DSVM')

Here, we define our utility function so that there is no effect of the individual state on the annual utility. We thus set the effect of a state on utility at the end of a year to zero for all possible states. This is a case where, for example, there are no individual quotas that affect choices over multiple time steps:

$$U(\mathbb{X}, T) = 0 \text{ for all } \mathbb{X}. \tag{29}$$

The value function is calculated recursively, back in time, linking the maximum revenue between year t and end T where the expected net revenue is

$$U(\mathbb{X}, t) = \max_a \left(\Phi_{a,t} + U\left(V_a[\mathbb{X}], t+1\right) \right), \tag{30}$$

where the $\Phi_{a,t}$ is the exponent of the expected profit in a time step, calculated using a probability distribution function for the landings, so that

$$\Phi_{a,t} = \left(\sum_{s=1}^{S} \lambda_a\left(l_s, t\right) \bullet \pi_s \right) - E_{a,t} \bullet f \tag{31}$$

where λ_a (l_s, t) is the probability of landing l tonnes of species s defined as a discretized normal distribution with mean $\mu_{s,a,t}$ and standard deviation $\sigma_{s,a,t}$ and π the price for species s. Φ_i (a, t), the Φ contribution from choice a at time t.

The tuning parameter σ that links the choice probability to the expected utility was set by optimising the root-mean-squared-error fit to the simulated observational data during the fitting period for each set of predictions. Because any state-dependent effect on utility was removed from the model, the choice probability became a pure function of the expected short-term profit with a time step. For estimation, we used the R implementation of a DSVM developed by Alzorriz et al. (2018).

3.1.5 | Random Utility Model ('RUM')

Here, we defined a case- and choice-specific multinomial logit RUM (superscript r) where

$$p^r_{a,t} = \frac{e^{\beta_a \bullet X_t + \gamma \bullet Z_{a,t}}}{1 + e^{\beta_a \bullet X_t + \gamma \bullet Z_{a,t}}} \tag{32}$$

and the multinomial distribution at time t given by

$$\frac{n_t!}{n_{1,t}! \cdots n_{A,t}!} p_{1,t}^{n_{1,t}} \cdots p_{A,t}^{n_{A,t}}, \tag{33}$$

where $n_{a,t}$ is the number of vessels choosing area a at time t, and n_t is the total number of vessels at time t. The r superscript has been dropped for simplicity.

The choice-specific covariates $Z_{a,t}$ comprised the profit from fishing at that location during the corresponding period in the data years, whereas the case-specific covariates included a month effect to capture season in the choice probabilities.

The fitting of the model was performed in the R software library *mlogit* (Liao 2011).

3.1.6 | Reparameterised Random Utility Model ('RUMReparam')

An alternative RUM was also included, where we reformulated the choice-specific covariate data as the log-ratio of revenue and costs relative to area A. This reparameterisation reflected theoretical results from the analytical analysis (see Results). Except for covariates, the model formulation was the same as in Equation (32).

3.1.7 | Markov Model ('Markov')

In the Markov model the proportion of effort in area a at time t is the sum of the transitioned proportions of effort from areas z (departing area) at time $t-1$:

$$p^m_{a,t} = \sum_{z=1}^{A} p^m_{z,t-1} p^m_{z,a,t} \tag{34}$$

where the transition probabilities are given by the logit function:

$$p^m_{z,a,t} = \frac{e^{\beta_{z,a} X_t}}{1 + e^{\beta_{z,a} X_t}}, \tag{35}$$

where we allowed seasonal changes in the model by including a month effect in addition to profit in the state being transitioned to in the vector X_t. We estimate transition matrices between each of the states of a Markov model (m), which were time inhomogeneous to capture seasonal dynamics. Additional covariates can be incorporated when estimating the Markov transition matrices (Davie 2013), but we focussed on a simple formulation for comparison.

The fitting of the Markov model was carried out in the R software library *nnet* (Venables and Ripley 2002).

3.2 | Model Fitting and Predictions

The formulation of each of the models was deliberately kept simple to facilitate cross-model comparison with the same data and variables. Each model was provided with the same data and covariates for model fitting and predictions. The covariates chosen included a seasonal effect (monthly) and past profit in a location. Inference on location choice was based on previous observations, profit when fishing during the observations, and how the model fits only the data. However, while the statistical models (RUM, Markov) are fit to the individual fishing event data, it is necessary for the mechanistic models (Gravity, DSVM) to be calibrated with the monthly mean of the data; in the case of the DSVM, this also includes the standard deviation of the profits.

Each of the models was fitted on a rolling basis to 3-year data on observed fishing locations for a single fleet, with predictions made for the following 2 years. This approach was deliberately taken to mimic a short-term forecast procedure carried out as part of an operating model in a management strategy evaluation. The predictions were made over 10 years spanning prior to the closure implementation through several years after the closure implementation, with the first predicted year being year 23 (training on years 20–22) and the last predicted year being year 39 (training on years 36–38). We chose to compare the proportion of effort in each area because the total effort required is subject to other factors such as quota availability and the management regime.

The characteristics of each of the models are summarised in Table 4. Full code for fitting, predictions and model output is provided at https://github.com/pdolder/FleetDynamics_code.

3.3 | Simulation Results and Model Performance Evaluation

The locations identified for the choice models, their profit-per-unit effort and the number of realised tows are summarised in Figure 1. It can be seen that the effort allocations to each métier broadly follows the profit per tow, though this can vary by métier and by month.

Model performance characteristics were assessed in three ways:

1. Forecast residual diagnostics: Comparison of the pairwise difference between the observed and predicted proportions in each area and month.
2. Root-mean-squared error deviation of the predictions: $\mathrm{RMSE} = \sqrt{\frac{1}{n}\sum_{i=1}^{n}\left(O_i - P_i\right)^2}$, where O_i is the observed proportion for an area in a given month and P_i is the predicted proportion.
3. Spearman's rank correlation coefficient of the proportions: $\rho = \frac{\mathrm{cov}(rg_O, rg_P)}{\sigma_{rg_O}\sigma_{rg_P}}$ where $\mathrm{cov}(rg_O, rg_P)$ and $\sigma_{rg_O}, \sigma_{rg_P}$ the covariance and standard deviation of the ranked observed and predicted proportions, respectively.

Statistical models generally showed less systematic bias in the forecast residuals than mechanistic models (Figure 2). Forecast residuals showed no inter-monthly correlations before or after the closure for the Markov, RUM or the reparameterised RUM, with the exception of the 'OTH' area (Figure 2). The Gravity and DSVM both consistently overpredict effort in some areas and underpredict in others (Figure 2).

Before the implementation of the spatial closure (<year 30), PastShare was the best prediction of the future effort allocation ($\mathrm{RMSE}=0.282\%$), but this was not the case immediately following the closure (year = 30), where the re-parametrised RUM outperformed the other models ($\mathrm{RMSE}=3.03\%$, Figure 3, Table 5) including PastShare ($\mathrm{RMSE}=3.66\%$). Of the other models PastShare, Gravity-Tradition and Markov performed broadly similarly to each other, with the RUM, Gravity and DSVM performing the worst (Figure 3). After a couple of years of closure, the prediction accuracy increased for most models except gravity and DSVM models, with the DSVM having a steadily decreasing accuracy after a few years (Figure 3). Over time, the PastShare model gradually re-establishes itself as having the best predictive accuracy (Figure 3).

Spearman correlation coefficients (ρ) show the strength of the relationship of individual predictions with the simulated observations of the models for the same area and month (Figure 4). Before the closure, PastShare ($\rho = 0.998$) was the best predictor of the future share of fishing effort, with GravityCombo ($\rho = 0.993$) and reparameterised RUM ($\rho = 0.984$) being the models that performed best. The Markov ($\rho = 0.951$) and the RUM ($\rho = 0.895$) also performed well. This generally remains true during and after the closure, with the reparameterised RUM performing best, both during ($\rho = 0.963$) and after closure ($\rho = 0.985$).

It is notable that during the closure the mechanistic models performed no worse (and in some cases better) than before the closure. The gravity model increased the accuracy before ($\rho = 0.508$)

TABLE 4 | Summary of the model characteristics and assumptions.

	Gravity model	Dynamic state variable model	Random utility model	Markov model
Key references	Caddy (1975)	Clark and Mangel (2000)	McFadden (1973)	Howard (1971)
Properties	Mechanistic. Effort allocated proportionately to cpue (or vpue in multispecies context)	Mechanistic. Optimises long-term objective function based on a defined utility and constraints	Statistical. Can incorporate choice-specific covariates and individual-specific covariates	Statistical. Choices are dynamic series of events with transition probabilities dependent on covariates
Key assumptions and limitations	Catch rates are known perfectly, negligible costs of travel, effort allocation matches cpue/vpue perfectly. Does not take account of within-trip decisions	Catch rates (and standard deviations) are known perfectly, actors seek to optimise utility to some degree (though degree of optimality optional), vessels maximise long-term profits	Independence of irrelevant alternatives (IIA), alternative choice set assumed to be the average of all other locations at that time period, does not take account of within trip decisions (though possible to include current state/area as a covariate)	Markov property assumes that the current state observed contains all the required information to predict the next state transitioned to, Complex to fit with a large number of areas and/or covariates
Basis of predictions (with/without closures)	With closures: estimated densities. Without closures: estimated densities excluding closure areas	With closures: estimated densities. Without closures: estimated densities excluding closure areas	With closures: predictions from RUM fit. Without closures: re-estimated parameters from RUM fit excluding the closed areas	With closures: transition probabilities as a time-series Without closures: transition probabilities as a time-series excluding closure areas and standardised to 1
Variations	Including distance from port (e.g., Caddy and Carocci (1999))	Including quota limits, discarding rules and other management restrictions	Including any covariates that affect area choice. Model that relaxes IIA assumption	Including any covariates that affect the log-odds of transitioning between pairs of areas
Advantages and disadvantages	Process driven so responds to changing conditions, biased if process not correctly captured, requires process to be understood	Accounts for short- and long-term constraints, biased if process not correctly captured, complex parametrisation and computationally intensive	Accounts for unexplained contributions to utility, poorly captures dynamics behind observation, requires defined choice set	Accounts for temporal dependencies, poorly captures dynamics behind observation, requires defined choice set

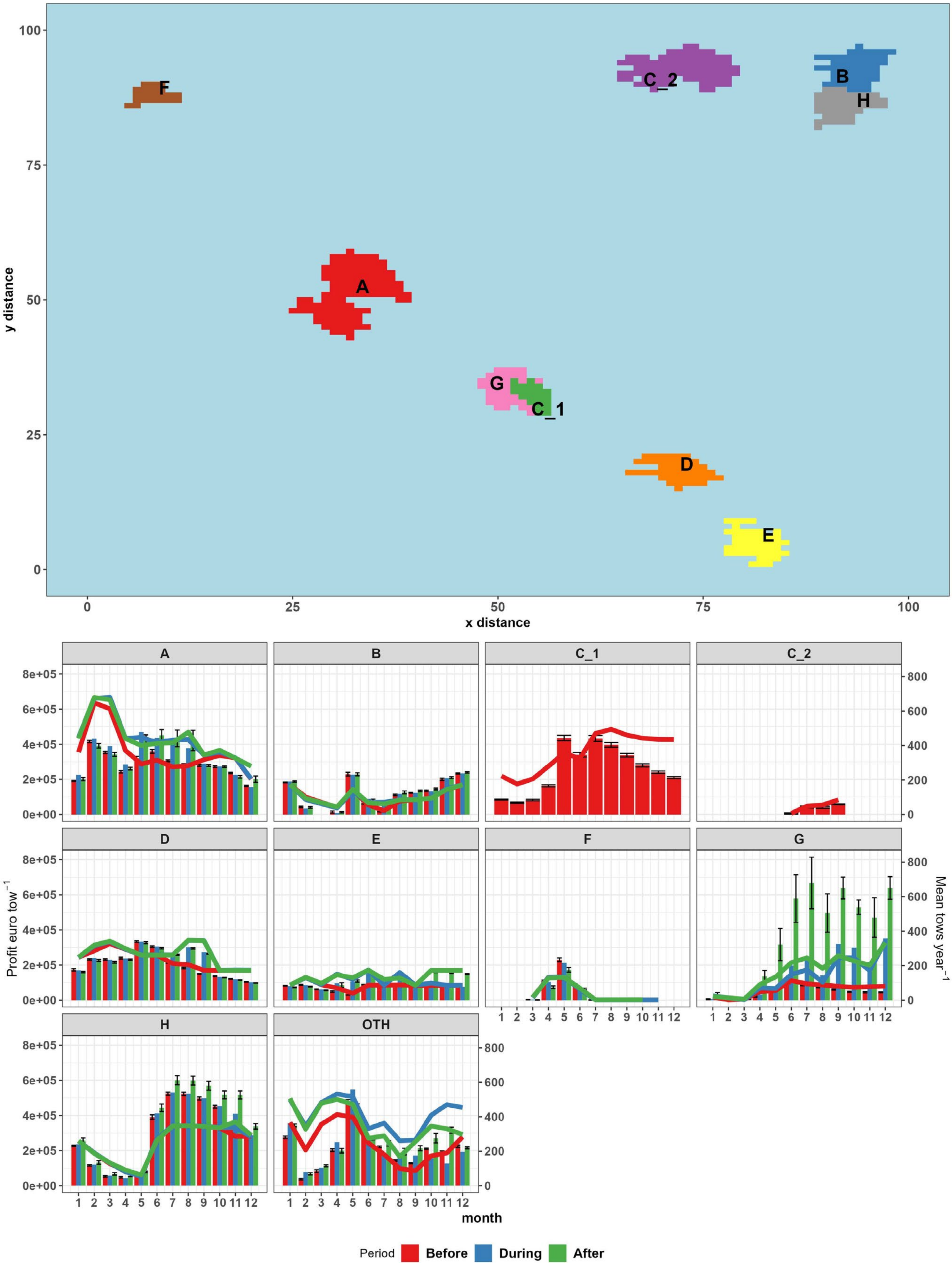

FIGURE 1 | Spatial location of métier (top panel) and profit per métier ($\pm 2\times\sigma$) per year in bars, and average tows per year in lines: before, during and after the spatial closures implemented in C_1 and C_2 (bottom panels).

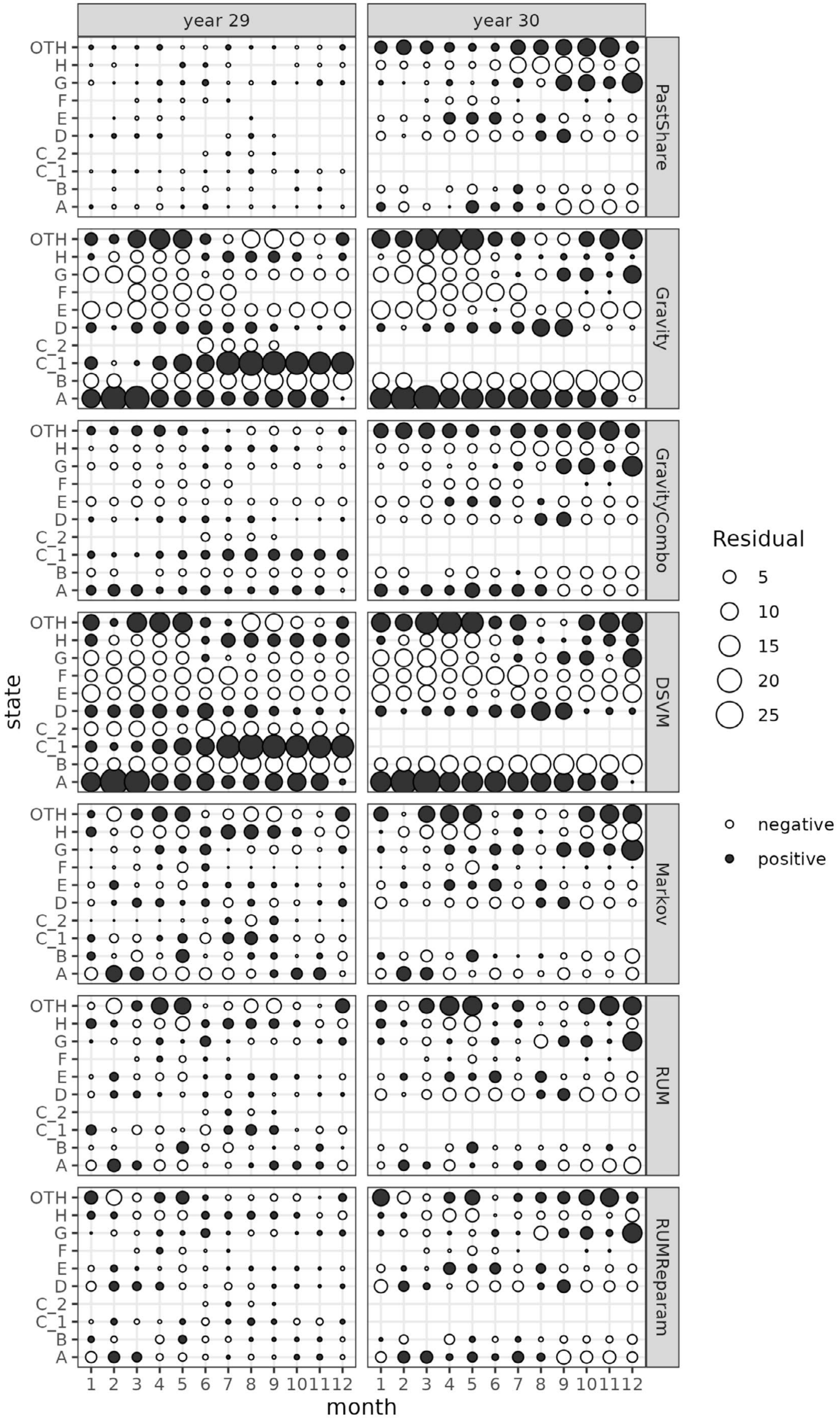

FIGURE 2 | Legend on next page.

FIGURE 2 | Forecast residuals ($O_i - P_i$) for each of the models by month for year 29 (before the closure) and year 30 (immediately after the closure) when fitting to data on years 26–28, where O_i is the ith observation (mean proportion across data years) and P_i the ith prediction. Blank spaces are where residual = 0.

to during ($\rho = 0.669$) and then decreased slightly after the closure ($\rho = 0.581$). The DSVM showed a similar pattern ($\rho = 0.391$ before, 0.615 during and 0.545 after), although for these models there were a number of predictions that were very different from the observations, with over or underestimated values (Figure 4). All statistical models performed worse during the closure than before and after, though still better than the mechanistic models in absolute terms for the model predictions. The performance of the Markov model degraded the least during closure ($\rho = 0.951$ compared to 0.937).

4 | Discussion

We compared four different types of location choice models, trying to develop a basis for understanding the similarities and differences among the commonly applied models.

4.1 | Theoretical comparison

We found that equivalent links between utility and choice could be derived for a gravity model and a random utility model under the condition that the covariate used in the multinomial model used to fit the RUM was the log of the ratio of utility between two areas. Where utility was defined as profit per unit effort only this resulted in predictions generated in line with the Ideal Free Distribution theory and is consistent with previous analyses that showed the structural similarities between the two classes of models and that model specification determines the difference between the two (Anas 1983; Sheppard 1978). It is rarely the case that relative profit between areas fished is the only driver of effort allocation; tradition is one predictor that is often found to be significant when fitting RUMs to data (Girardin et al. 2017). Tradition, along with a number of variables, can be incorporated into gravity models through the utility component, appropriately weighted. If the weighting is estimated from past data through calibration or estimation, it provides a conceptually similar model to a RUM that can achieve similar predictions. The advantage of specifying a gravity model in this way is that the model will better fit past observations of dynamics in the fishery. However, it limits flexibility with the model to respond to changing system dynamics, as tradition or 'inertia' is a concept that likely reflects many other past endogenous drivers rather than an explicitly stated dynamic. Therefore, it would be better that these drivers were explicitly included to provide the mechanistic representation required to improve future predictions.

Extending the theoretical comparison, we found that the link between utility and choice in the gravity and Markov models showed equivalence when the Markov transitions were the same irrespective of the starting area, and the probabilities of transition were determined by the relative utility of the different areas. This provides the ability to use similarly configured models to test for the presence of a Markovian property or if the decisions are independent of the departing area by demonstrating if the Markov model outperforms a similarly configured gravity model.

We found the link between utility and choice in a dynamic state variable model could be equated to the link between utility and state in a Gravity, RUM or Markov model within a single time step. However, DSVMs are distinct from the other classes of models in that a DSVM seeks to find the optimal long-term solution; in doing so, the model requires that the utility function is state-dependent, well defined and that relevant constraints are incorporated and then finds the single best set of decisions to maximise this utility. Some vessels may pursue suboptimal policies, and Dowling et al. (2012) and Alzorriz et al. (2018) offer an interesting solution with error-in-decision-making, which may be substitutable for a single time step to match a gravity model, but not with long-term constraints. Furthermore, Reimer et al. (2019) provide a method for exploring sub-optimality in dynamic state programming approaches. Another approach may be that defining constraints for individual vessels with heterogeneous conditions could lead to a spectrum of optimal solutions that more closely match those found with models that deal with heterogeneity among individuals. In this way, no single solution will exist for the fleet, but a set of solutions could be used as a probability set for the overall fleet.

4.2 | Simulation Study

The individual-based simulation framework used (Dolder et al. 2020) results in emergent fishing dynamics that are the aggregate effect of individuals seeking to maximise their profits based on an explore-exploit strategy with uncertain knowledge. An emergent feature of the simulation to which the models were fit was the ability to replicate the phenomenon of 'fishing the line' around a spatial closure, observed following implementation of spatial closures (Rijnsdorp et al. 2001; Armstrong et al. 2007; van der Lee et al. 2013). It can be seen that there is an increase in activity on the boundary of the closure C_1 in area G and that results in catch rates in the adjacent area (area G) increasing (Figure 5). Therefore, while the simulation was a simplified representation of reality, it captures some well-known features observed in real-world case studies following the implementation of a spatial closure. It also highlights the limits of modelling spatial behaviour limited to pre-selected choice sets where fishing locations are often precisely defined along gradients (Rijnsdorp et al. 1998; Branch et al. 2005).

We fitted several different location choice models to the simulated data to evaluate their performance characteristics under different fisheries management scenarios. All models were implemented in a general way to allow cross-comparison, and no attempt was made to define the best model. All models could have been improved in their overall predictive capacity, but the simple formulation allowed us to elicit some important insights

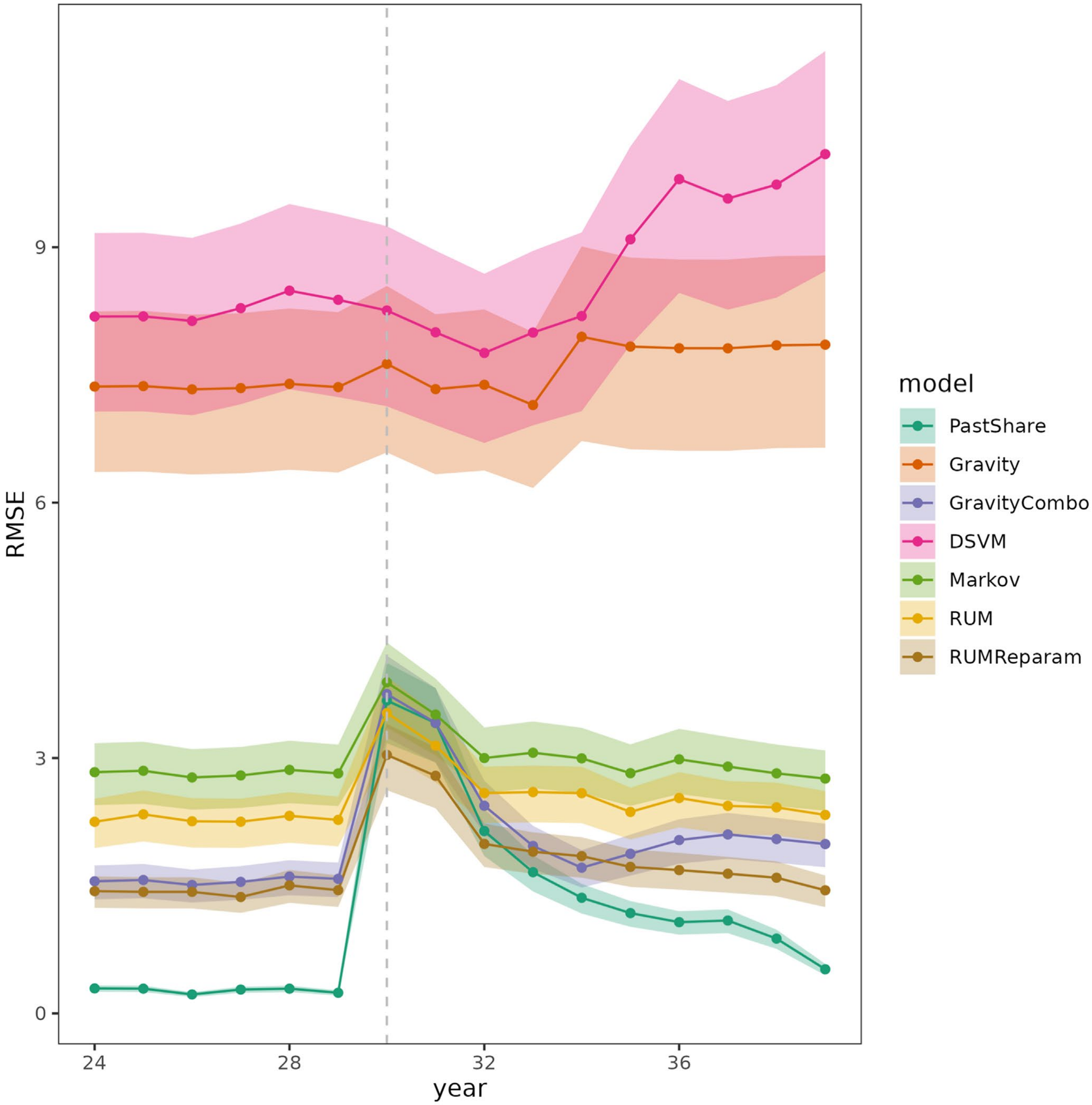

FIGURE 3 | The root-mean-squared error (RMSE) for each of the models predictions, 95% confidence intervals are shown in the shaded areas.

into the nature of the models and how they could be applied within a management strategy evaluation framework.

Although both the mechanistic and statistical models captured the temporal dynamics in the choice of fishing location, the mechanistic models were generally biased, whereas the statistical models were largely unbiased in their predictions. This is because statistical models infer utility directly from the data, including unobserved drivers.

The mechanistic models specified here assume that the profit per unit effort is the only driver of effort allocation among the areas and that the distribution of this value is known a priori. It would be expected that statistical models performed better since their estimated parameters explicitly encompass utility in their parameterisation (McFadden 1973) and an error component that captures the variance in the historical data, allowing unexplained factors to contribute to the fit of the model. The prediction bias in the mechanistic models demonstrates that more than profit is determining effort allocation by fleets, which may be captured by the parameters in the statistical models. The importance of past and personal knowledge of fishing locations can be inferred from the fact that the model where the effort allocation is a weighted average of predictions from the gravity

TABLE 5 | Summary of model comparison metrics. All Spearman's ρ values were significant at $p < 0.001$.

Closure period	Model type	Model	RMSE	MAE	Spearman's ρ
Before	Mechanistic	DSVM	8.299	6.775	0.371
		Gravity	7.723	5.842	0.506
		GravityCombo	1.566	1.181	0.993
		PastShare	0.282	0.179	0.998
	Statistical	Markov	2.827	1.960	0.951
		RUM	2.289	1.374	0.963
		RUMReparam	1.449	0.861	0.984
During	Mechanistic	DSVM	8.263	6.075	0.608
		Gravity	7.883	5.493	0.662
		GravityCombo	3.741	2.696	0.941
		PastShare	3.664	2.356	0.951
	Statistical	Markov	3.875	2.465	0.938
		RUM	3.524	2.105	0.948
		RUMReparam	3.032	1.936	0.963
After	Mechanistic	DSVM	9.057	6.550	0.552
		Gravity	7.225	5.088	0.621
		GravityCombo	2.122	1.439	0.983
		PastShare	1.471	0.688	0.988
	Statistical	Markov	2.931	1.953	0.955
		RUM	2.501	1.541	0.969
		RUMReparam	1.775	1.039	0.985

model and the PastShare in the fisheries much better reflects the observed allocations.

The accuracy of the mechanistic models was affected less than that of the statistical models following spatial closure, suggesting that they adapted better in relative terms. This may reflect that the mechanistic model predictions are better at dealing with previously unobserved situations, where the statistical models struggle to predict changes to the system. Cuddington et al. (2013) demonstrate how a good understanding of the mechanistic process may be able to outperform a statistical model in previously unobserved situations. However, due to the potential for bias to be introduced from misspecification, particular care should be taken in model calibration and consideration of bias adjustment (Kennedy and O'Hagan 2001). The re-parameterised RUM provides a useful contrast in this example, as it included both statistical and mechanistic properties derived from theoretical linkages between the models (Equation 3).

The performance of the DSVM and gravity models degraded in the years after closure. This is due to an overallocation of effort to particular areas where biomass increases for the species protected by the closure, thus as that stock increases, more effort is allocated to these areas. The overallocation is likely due to the models predicting effort based on catch rates and relative values of each fish species, where increasingly the simulated vessels allocate based on their own experience and traditional areas they exploit, leading to the differences in predictions and observations. The simulated fishery distributed the fishing effort more evenly across the remaining locations and to previously unexploited locations. These new locations were in areas where other populations were more abundant, suggesting a move to target these species (Figure 5).

The RUM and Markov model quantitatively describe the main drivers in location choice through a formal statistical framework, which provides inference on the importance of competing drivers for effort allocation. However, prediction from statistical models beyond observed conditions must be done with care. For example, when a spatial closure is implemented or a quota for a species is significantly reduced, the relationships between the predictor variables may change. This is because alternatives to the closure area may not be independent where, for example, the closed area can be substituted by another area that has similar characteristics (e.g., similar species caught) but was less favourable than the closed area. This changes the utility of the new area once the other opportunity is closed to an individual, violating the independence of irrelevant alternatives (IIA) principle. While there have been developments in RUM applications to address

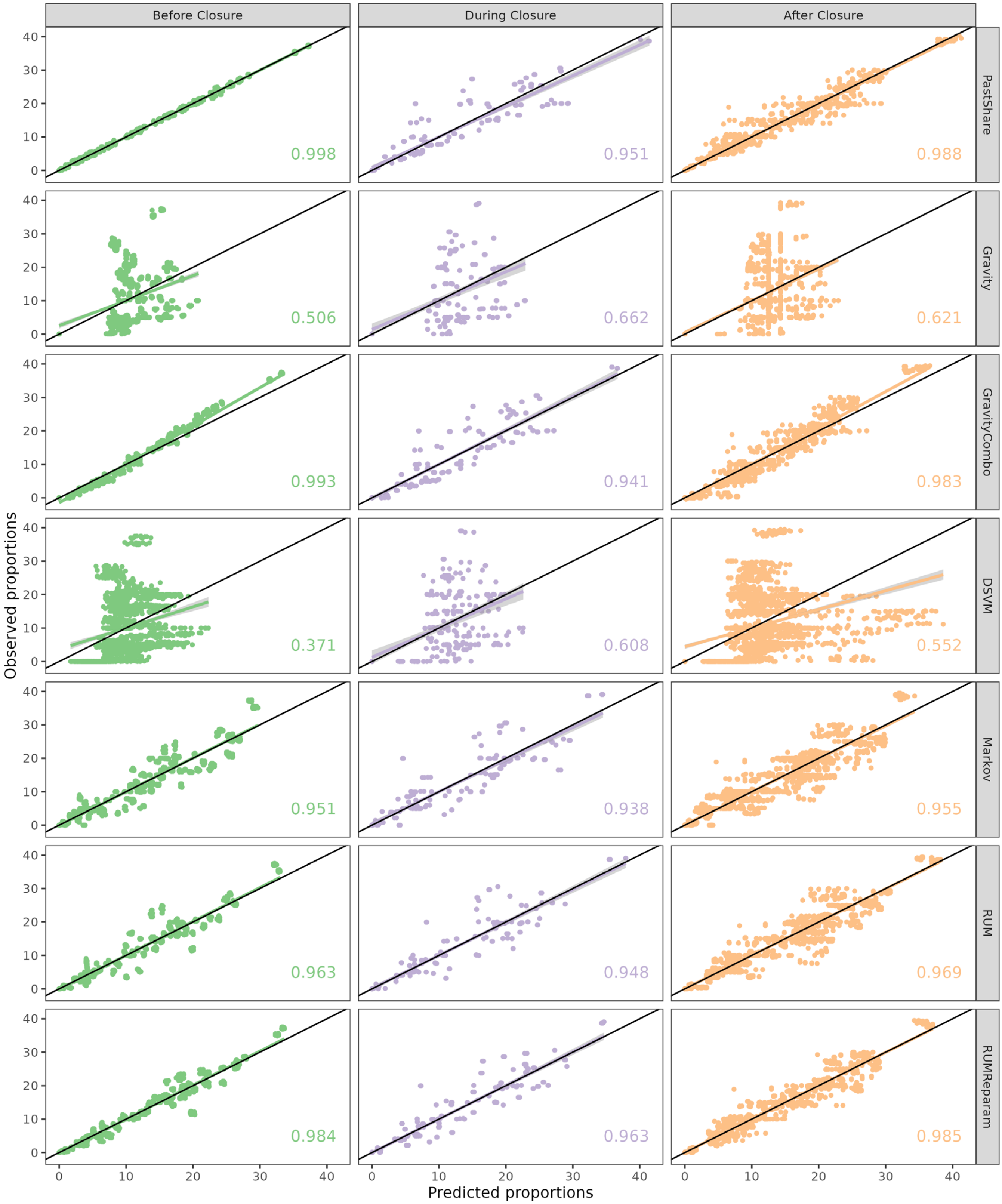

FIGURE 4 | Spearman correlation coefficients for predicted against observed proportions for each of the models and periods. Before is year < 30, during is year 30, and after is year > 30.

the IIA problem (e.g., nested or mixed logits), the alternative choices must be understood prior to implementation. The strong influence of the past choice as an explanatory variable (Girardin et al. 2017) may mask the understanding of these relationships.

Mechanistic process-based models require strong a priori assumptions about the drivers of dynamics in the fisheries, and if developed to characterise such satisficing and rule-based decisions, the emergent dynamics may be better able to provide

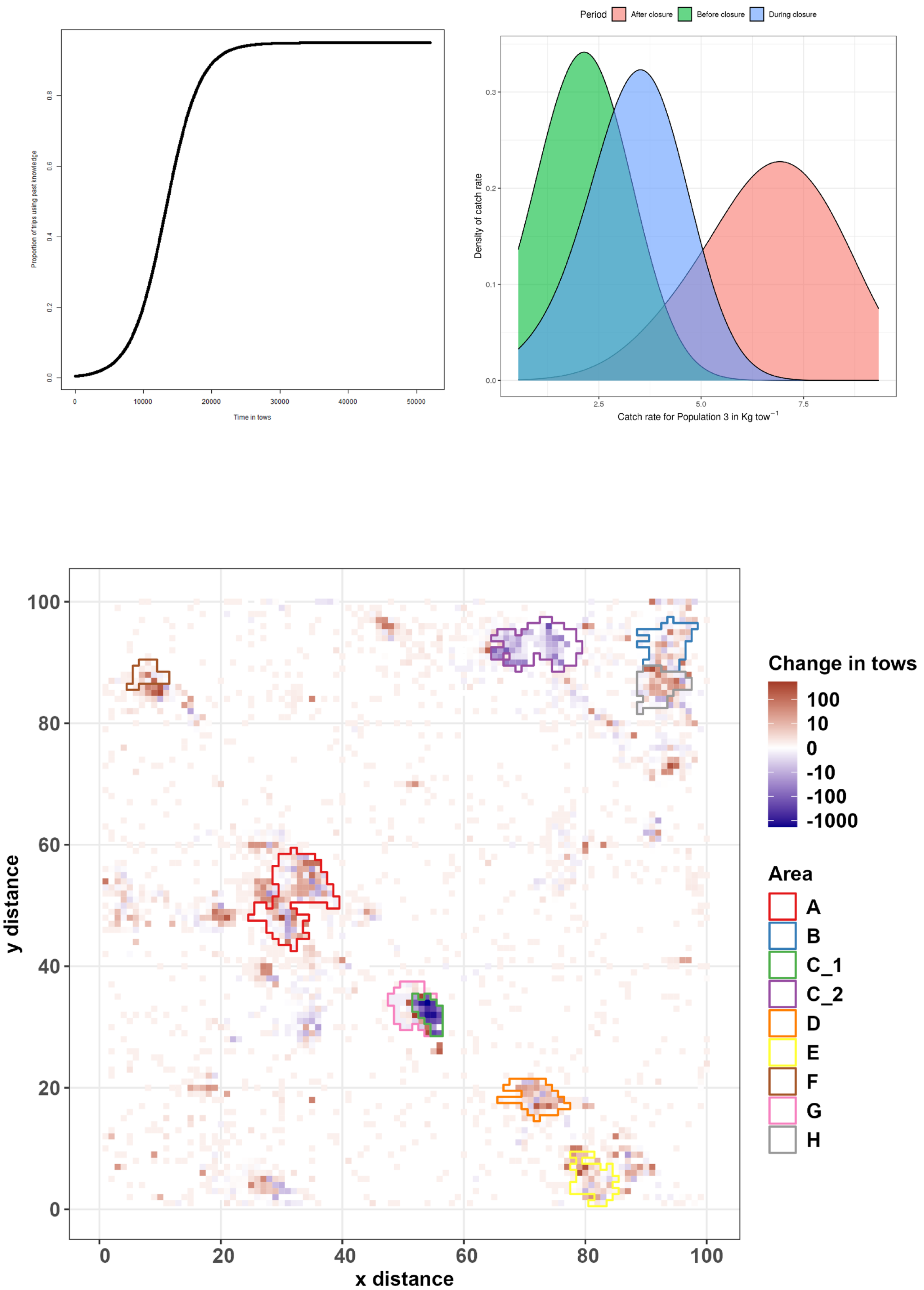

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FIGURE 5 | Effect of explore–exploit strategy following spatial closure. Top left figure shows the probability of a tow being based on past knowledge ($1 - p$ is the probability of exploratory tows), top right figure shows the effect of the closure on the catch rates of the adjacent area to one of the closure areas, bottom figure shows the change in fishing effort (number of tows per year) before and after the closures—with a red shaded area showing increased effort alongside the boundary of closure C_1.

insight into previously unobserved system dynamics. This explicit statement of assumptions allows for an unambiguous understanding of the mechanisms behind effort allocation but provides a challenge in describing all of the mechanisms that contribute to the dynamics and being able to distinguish among them in calibrating such models. Further, misspecified models run the risk of leading to biased predictions due to the over-influence of one or more variables.

The reparameterised RUM performed better than any of the other statistical- or mechanistic-based models. The model combines features of both in that it estimates the influence of profit from the fisheries relative to each other, similar to the Ideal Free Distribution principle in a gravity model that states effort allocates according to the relative distribution of the resource. By estimating the influence of the relative value, the reparameterised RUM does not assume a direct relationship but estimates the strength of this relationship in making predictions. Linking theoretical and statistical models provides a basis for combining strengths from each of the modelling approaches and highlights bases for inference among models.

The DSVM was applied here as a general location choice model, but our application did not include more detailed policy exploration that models have been developed for in the past. These applications include exploring the response of fisheries to different management measures in mixed fisheries, including catch limits (Babcock and Pikitch 2000) and catch limits in combination with discard bans (Poos, Bogaards, et al. 2010; Batsleer et al. 2016; Alzorriz et al. 2018). DSVMs are arguably the only class of model that can evaluate such detailed policies due to their ability to incorporate both short-term and long-term constraints in decisions about when and where to fish. Though the effect of quota availability could be incorporated in RUMs and Markov models, to our knowledge, this has not been considered to date (Girardin et al. 2017).

The predictions in our comparison are constrained by the limited definition of the fisheries in the study; activity in the 'elsewhere' category also shows some spatial patterns likely to be differentiated fisheries, and as such, all the models do a much poorer job of predicting effort allocation (including seasonal distribution) in the fisheries not specifically predefined. The exception to this is the predictions from the PastShare model that capture the dynamics and scale of the effort allocated to the 'elsewhere' areas well (Figure 5). It may be that the other models could similarly improve their prediction accuracy if the fisheries in the rest of the spatial domain were better characterised and could therefore be described in part by their past profit or other covariates. As the accuracy of predictions is not the goal of this paper, we did not refine the location choices further but highlighted the importance of accurate area definitions.

5 | Conclusions

We set out to establish the theoretical and applied basis for comparing location choice models commonly used in fisheries science. We derived the mathematical equivalence of the link between utility and choice in the models under specific circumstances, opening avenues for inference. We then used a simulation framework to compare and contrast predictions of the allocation of fishing effort following a spatial closure to identify characteristics of the different models. To our knowledge, this is the first cross-comparison of location choice models and provides a basis for the continual development of these methods and the inclusion of location choice models in an MSE setting.

We found that while several different models for location choice have been proposed from different foundations, including microeconomic and ecological theory, the models were more similar structurally than anticipated. We could equate the link between utility and state in gravity, random utility, Markov and dynamic state variable models under certain conditions and found that the data, formulation and covariate parameterisation are some of the main determinants of different predictions from the models. This was similar to the conclusions reached by Anas (1983) when comparing gravity and multinominal logit models.

Our simulation study demonstrated the different characteristics of location choice models. While based on a simplified framework that does not account for all the case-specific complexities that contribute to decisions about when and where to fish in mixed fisheries (Branch and Hilborn 2008; Forrest et al. 2020), it does allow us to draw some general conclusions about the characteristics of the different models compared here.

Before the introduction of spatial closure, no model outperformed the null model (*status quo* effort allocation among areas) to predict the future share of fishing effort between fisheries. However, the statistical models all performed significantly better than the mechanistic process-based models. This was because the mechanistic models biased effort allocation disproportionately towards particular fisheries. Following the implementation of the closure, the performance of the null model and the statistical model degraded, but the RUM and reparameterised RUM briefly outperformed the null model, the only period over which this happened. The performance of the mechanistic models, while remaining biased, did not degrade, suggesting they were able to make predictions that were accurate (but biased). The reparameterised version of a RUM performed best. This included predictions based on the relative profit from each fishery, equivalent to a gravity model, but where the influence of profit in each area was estimated rather than assumed to follow an Ideal Free Distribution. This model combined aspects of a statistical and mechanistic model in that it defined a mechanism but estimated the fit of the data to that mechanism.

There are advantages and disadvantages to both class of models explored here; statistical models are able to 'let the data speak for itself' and deal with both explained variance, for example, due to catch rates of different stocks and unexplained variance through an error term. However, when a major change is implemented, such as a spatial closure, some of the assumptions in the model may be violated, leading to extrapolation and degradation in performance. In this case, the inclusion of a mechanistic model either in combination or supplementing the statistical model should be considered.

Mechanistic and statistical models have different properties: statistical models capture dynamics well when there are no significant management interventions, while mechanistic models are able to reflect emergent properties of a system that allow them to better adapt predictions for unobserved states. We argue that these differences are complementary and recommend that a multi-model approach should be considered and, where possible, features of each approach formally combined. This could be achieved either by formulating the model to include elements of statistical and mechanistic process-based dynamics (Cuddington et al. 2013) as with the reparameterised RUM, or through an ensemble framework as a statistical meta-model (Spence et al. 2018). Doing so, in a fully formulated case-specific modelling framework, provides a robust mechanism to consider location choice when implementing MSEs for evaluations of mixed fisheries management plans.

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Data Availability Statement

The authors have nothing to report.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.