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# 1 Simulating the summer feeding distribution of Northeast Atlantic 2 mackerel with a mechanistic individual-based model

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## 15 Abstract

16 Over recent years the summer feeding distribution of Northeast Atlantic mackerel (NEAM,  
17 *Scomber scombrus*) has expanded from its traditional core in the Norwegian Sea, northwards  
18 towards Svalbard, and westward as far as Greenland. Food availability, temperature and an  
19 increase in spawning stock biomass (SSB) are reported to be possible drivers of the  
20 distribution, but quantifying the relative contributions of these factors is difficult. Previously  
21 we developed a bioenergetics individual-based model (IBM) that uses satellite-derived maps  
22 of food availability and temperature to predict NEAM population dynamics. Here, we extend  
23 the model to explore the ways in which individuals move in search of food in the summer.  
24 We construct models of four possible search mechanisms differing in 1) the extent of the area  
25 over which individuals can perceive the environment; and 2) whether or not individuals  
26 respond to the local density of conspecifics by avoiding areas in which competition is more  
27 intense. We report that the best matches to available data over 2007 to 2015 are obtained  
28 when the local density of competitors is taken into account, and individuals move in response  
29 to local gradients in feeding opportunities. To determine whether the IBM is able to  
30 reproduce the observed north and westward expansion, we record total distribution area, and  
31 predicted centre of gravity in terms of latitude and longitude, over 2005 to 2015. The IBM  
32 successfully predicts an increase in distribution area, and a northward shift in centre of  
33 gravity, over the time series. It also predicts a westward shift in centre of gravity, but to a  
34 much lesser extent than has been observed in surveys and the fishery. The inability of our  
35 IBM to capture the full extent of the westward expansion suggests that it does not account for  
36 all relevant drivers of the NEAM summer distribution. Going forward we hope that our  
37 model can be: 1) extended to explore additional drivers of the summer distribution (e.g.  
38 currents); and 2) used in a strategic capacity to predict how the NEAM stock may respond to  
39 future climate and management scenarios.

## 40 Key words

41 Individual-based model; Atlantic mackerel; geographical distribution; movement  
42 mechanisms; bioenergetics; satellite remote-sensing

# 1. Introduction

Changes in the spatial distribution of fish stocks in relation to jurisdictional boundaries can complicate the division of catch quotas among nations (Fernö et al. 1998, ICES 2016). One recent example is that of Northeast Atlantic mackerel (*Scomber scombrus*, NEAM), a stock with high economic and ecological importance (Trenkel et al. 2014). The majority of the NEAM stock spawns to the west of the British Isles in spring, before migrating northwards to feed in the Nordic seas over summer (Walsh et al. 1995, Uriarte and Lucibob 2001). Over recent years the spawning distribution has shifted gradually northwards, likely in response to increasing temperature (Hughes et al. 2014, Bruge et al. 2016). The most extreme change in the NEAM distribution, however, has occurred in the feeding period over summer.

Traditionally, the summer feeding distribution was largely restricted to the Norwegian Sea, but in recent years it has expanded northwards as far as Svalbard, and westwards as far as Greenland (Berge et al. 2015, Jansen et al. 2016). This geographical expansion has resulted in a mismatch between the stock distribution and the historical allocation of catching opportunities, causing 1) political disputes among coastal states in the region (e.g. <https://www.bbc.co.uk/news/uk-scotland-north-east-orkney-shetland-21385888>); and 2) a lack of agreement on overall catch limits such that exploitation has been significantly in excess of scientific advice. Better understanding of the mechanisms driving the NEAM summer expansion would be beneficial from both a scientific and management perspective.

Previous studies have shown that the availability of food is likely a driver of the NEAM summer distribution (Pacariz et al. 2016, Nikolioudakis et al. 2018, Olafsdottir et al. 2018). The geographical expansion coincided with roughly a 100% increase in NEAM spawning stock biomass (SSB) (ICES 2017a), which may have intensified intraspecific competition for the available food in the traditional feeding area. It has been suggested that the resulting food limitation may have provided an incentive for the stock to expand north and westwards in search of better feeding opportunities (Olafsdottir et al. 2018). This hypothesis is supported by a reduction in growth rate over recent years, as reflected in the metrics weight- and length-at-age (Olafsdottir et al. 2016), likely as a result of competition for food among NEAM (Jansen and Burns 2015). Another possibility is that there has been a shift in the locations of the most profitable feeding areas independent of mackerel SSB, i.e. from the bottom-up (Pacariz et al. 2016). In the latter case the shift in the NEAM distribution may simply reflect a similar shift in the distribution of the prey field. The relative contributions of these density dependent and bottom-up drivers to the NEAM geographical expansion are not fully clear.

Recent attempts to investigate the spatial distribution of NEAM have explored the use of correlative species distribution models (SDMs, sometimes called habitat suitability models) (Hughes et al. 2014, Bruge et al. 2016, Nikolioudakis et al. 2018, Olafsdottir et al. 2018). Correlative SDMs are widely-used for establishing relationships between the environment and fish distribution (Robinson et al. 2017), but typically provide limited insight into the underlying mechanisms. It is possible to obtain some mechanistic information using SDMs. For example, Bruge et al. (2016) fitted two separate SDMs to data on NEAM spawning distribution. The first model is based on geographical predictors, and the second is used to determine a thermal niche for spawning activity. By comparing changes in the distribution as predicted by the first model with changes in the location of the thermal niche, the authors were able to show that NEAM spawning activity has shifted northwards at least in part due to ocean warming. There have also been attempts to incorporate mechanisms that underpin species' distributions in SDMs, such as dispersal capacities, i.e. the rates at which animals can move (Holloway et al. 2016), and physiological constraints (Teal et al. 2012, Evans et al. 2015). Despite these advances, however, SDMs are fundamentally correlative and it would

91 therefore be useful to develop mechanistic models with which hypotheses can be tested about  
92 how various drivers affect the distribution of fish stocks.

93 One mechanistic approach that is becoming increasingly popular as a way to predict fish  
94 distribution is with individual-based models (IBMs, also called agent-based models) (e.g. Tu  
95 et al. 2012, Utne and Huse 2012, Utne et al. 2012, Watkins and Rose 2017, Heinänen et al.  
96 2018). In IBMs animal populations are represented by their constituent individuals in real-  
97 world mapped landscapes (Uchmanski and Grimm 1996, McLane et al. 2011). The  
98 individuals each have a unique set of characteristics (e.g. size, location), and the landscapes  
99 are characterised by environmental drivers. Detailed models are constructed that describe  
100 how the individuals respond to each other and their local environment, and it is from  
101 simulation of all the individuals that population measures emerge (van der Vaart et al. 2016).  
102 Previously we developed a bioenergetics IBM that predicts NEAM population dynamics  
103 based on the rates at which individuals can acquire and use energy from food in the  
104 environment (Boyd et al. 2018). This IBM is able to predict temporal variation in population  
105 measures (e.g. SSB), but the spatial distribution of the population was largely imposed. For  
106 spatial distribution to become an emergent feature of the IBM, algorithms must be  
107 incorporated that describe how individuals move in response to their environment (Politikos  
108 et al. 2015b, 2015a, Watkins and Rose 2017, Scutt Phillips et al. 2018).

109 To assess potential mechanisms for the NEAM geographical expansion, we extend our  
110 existing IBM (Boyd et al. 2018) to include four alternative models describing how  
111 individuals move in search of food during summer. Generally, the profitability of an area in  
112 terms of potential feeding opportunities is calculated from sea surface temperature (SST) and  
113 surface phytoplankton biomass, both of which are derived from satellite remote-sensing. The  
114 movement models represent four search mechanisms which differ in: 1) whether or not the  
115 local density of mackerel, and hence competition for food, affects the perceived profitability  
116 of an area; and 2) extent of the area over which individuals can detect the environment.  
117 Competition for food is central to these movement models, so we start by testing whether or  
118 not they can simultaneously fit data on spawning stock biomass (SSB) and weight-at-age. If a  
119 model matches these data, we suggest that, at a given stock size, competition for food is  
120 realistic as reflected in the individual body weights of the fish. We then use data on the  
121 presence/ absence of mackerel in the Nordic seas in July/ August to gauge the relative  
122 abilities of each of the four search mechanisms to reproduce the distribution. Finally, we test  
123 whether the IBM is able to reproduce the observed north and westward expansion. To do this,  
124 we assess how predicted distribution area and the stock's centre of gravity in terms of latitude  
125 and longitude change over 2005 to 2015.

## 126 **2. Methods**

### 127 **2.1. Model overview**

128 In this section we first give a brief overview of the previous IBM (Boyd et al. 2018) on which  
129 we build here, followed by the additions made for this paper. For the IBM's full technical  
130 specification see the "TRAnsparent and Comprehensive model Evaluation" (TRACE)  
131 document in the supplementary material. In section 2 of the TRACE we provide a full model  
132 description in the standard Overview Design concepts and Details (ODD) format (Grimm et  
133 al. 2006).

134 In broad terms, the model landscape consists of dynamic maps of sea surface temperature  
135 SST and surface phytoplankton density, which we use to represent baseline food availability  
136 (Fig. 1). Both variables are derived from satellite remote-sensing. The modelled fish  
137 population represents the western spawning component of the North East Atlantic mackerel

stock as defined by the International Council for the Exploration of the Seas (ICES). It should be noted that, while ICES treat NEAM as comprising isolated spawning units, there is evidence of straying between the western and North Sea spawning components (Jansen and Gislason 2013). Before its collapse in the 1970s the North Sea component was substantial (Jansen 2014). However, over the time period considered in this study, there has been limited spawning in the North Sea (typically < 5% of spawners) whereas the western component has remained stable at around 80% of the stock's total biomass (ICES 2014a, 2014b, 2017b). Fish are grouped into super-individuals (SI), which comprise a number of individuals with identical variables (Scheffer et al. 1995). SIs move around the landscape according to their life cycles (e.g. to spawn, feed and overwinter). Each SI has an energy budget which determines how its characteristics (e.g. body size, life stage, energy reserves) change in response to local food availability and SST. Time- and age-varying fishing pressure determines the rate of mortality from exploitation. Each year a constant number ( $n_{\text{cohort}}$ ) of SIs are introduced as eggs at spawning time, but the abundance that they represent is determined by the amount of energy the spawning stock has put into egg production. The amount of energy that can be allocated to egg production is an emergent feature of the energy budget and reflects the feeding opportunities available to adults prior to spawning. Abundance reduces as mortality is applied throughout life. Population measures such as SSB and recruitment are obtained by summarising the characteristics of all the SIs including their abundances.

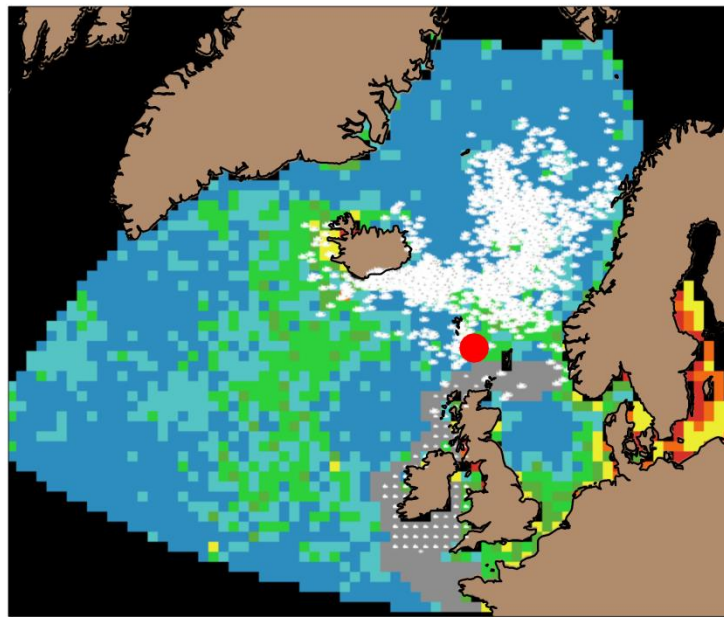
In this paper we focus on the adult feeding period, specifically July and August, so as to match the available data. After spawning, adults enter the feeding area and begin to actively seek out the most profitable locations. Profitability is defined as potential ingestion rate in that area, based on food availability and SST. We further divide this into two assumptions about what defines a profitable area: one including an effect of competition for food among the mackerel; and a second that is independent of mackerel density (see section 2.3.3). The ways in which SIs are directed towards the most profitable areas are modelled with one of a gradient area search (GAS) or ideal free distribution (IFD) feeding strategy (see section 2.3.4), which contain different assumptions about how much environmental information they have access to. We combine the assumptions about feeding strategy and density dependence to generate four possible search mechanisms: a density-dependent (includes competition for food) gradient area search ( $\text{GAS}_{\text{dd}}$ ); a density-independent (does not include competition for food) gradient area search ( $\text{GAS}_{\text{di}}$ ); a density-dependent ideal free distribution ( $\text{IFD}_{\text{dd}}$ ); and a density-independent ideal free distribution ( $\text{IFD}_{\text{di}}$ ). See Table 1 for a summary of the characteristics of each search mechanism and section 2.3 for full details. We then test which model best matches various mackerel population data.

Table 1. Summary of the characteristics of each search mechanism (movement model). Competition effect indicates whether or not individuals take conspecific density into account when assessing a patch's profitability. Temporal resolution is the frequency at which individuals' positions are updated. Environmental information accessible indicates the extent of the area over which individuals can detect the environment. Space indicates whether the model works in the continuous or discrete (patch by patch) space of the model grid.

| Search mechanism         | Competition effect? | Temporal resolution | Environmental information accessible | Space    |
|--------------------------|---------------------|---------------------|--------------------------------------|----------|
| $\text{IFD}_{\text{dd}}$ | Yes                 | Five-day            | Area reachable in five days          | Discrete |

|   |                         |     |          |                |            |
|---|-------------------------|-----|----------|----------------|------------|
| 1 | <b>IFD<sub>di</sub></b> | No  | Five-day | Area reachable | Discrete   |
| 2 |                         |     |          | in five days   |            |
| 3 |                         |     |          |                |            |
| 4 | <b>GAS<sub>dd</sub></b> | Yes | One-day  | Neighbouring   | Continuous |
| 5 |                         |     |          | cells          |            |
| 6 |                         |     |          |                |            |
| 7 | <b>GAS<sub>di</sub></b> | No  | One-day  | Neighbouring   | Continuous |
| 8 |                         |     |          | cells          |            |
| 9 |                         |     |          |                |            |

11 180



44 181

182 Figure 1. Snapshot of the IBM interface on August 1<sup>st</sup> 2011. Grey patches denote the shelf  
 183 edge (cells to the North and West of the British Isles on which  $50\text{m} < \text{depth} < 550\text{m}$  and  
 184 latitude  $< 60.5^\circ\text{N}$ ). The red point shows the entrance to the feeding area in the Norwegian Sea  
 185 ( $61.5^\circ\text{N}$ ,  $-4.8^\circ\text{W}$ ). Large white fish in the Nordic sea are adults, and the smaller fish to the  
 186 west of the British Isles are juveniles. The colour of the landscape corresponds to  
 187 phytoplankton density: blue represents low density, then green, yellow and red which  
 188 indicates high density. The colour bins are arbitrary.

## 189 2.2.State variables and scales

190 The model landscape comprises a two-dimensional grid of patches of sea surface (Fig. 1).  
 191 The spatial extent spans from  $47$  to  $77^\circ\text{N}$ , and from  $-45^\circ$  to  $20^\circ\text{E}$ . Each patch represents  $60 \times$   
 192  $60 \text{ km}$  (Lambert Azimuthal equal area projection) and is characterised by food density, sea  
 193 surface temperature (SST) and mackerel density ( $\text{g patch}^{-1}$ ), from which profitability indices

61  
62  
63  
64  
65

194 are calculated (section 2.3.3). The mackerel population is represented by a constant 4000 SIs;  
 195 as  $n_{\text{cohort}}$  new SIs enter the model at spawning time each year an equal number reach terminal  
 196 age ( $>15$  years) and are removed from the model. Each SI is characterised by age, gender, life  
 197 stage (egg, yolk-sac larvae, larvae, juvenile or adult), length, mass (structural, lipid and  
 198 gonad), abundance and location (see TRACE section 2 for details of initialisation). The  
 199 temporal extent spans from January 1<sup>st</sup> 2005 to December 31<sup>st</sup> 2015. The model proceeds in  
 200 discrete five-day time-steps.

### 2.3. Model description

201 For the purposes of this study, key aspects of the model are: 1) the bioenergetics; 2) the  
 202 migrations of adult mackerel into and out of the feeding area; 3) the cues used to determine  
 203 how profitable each patch is; 4) the feeding strategies used to direct adults to the most  
 204 profitable patches; and 5) the coupling of the movement and the bioenergetics. See TRACE  
 205 section 2 for a full description of the IBM including the bioenergetics and the pre-adult  
 206 phases of the life cycle.

#### 2.3.1. Bioenergetics

207 Individuals obtain energy from phytoplankton which is used as a proxy for prey availability.  
 208 Size-based cannibalism is possible in the IBM, but adults do not overlap with sufficiently  
 209 small individuals over summer so it is not relevant here. Ingestion rate is a function of food  
 210 density, body surface area, SST and local mackerel density. A proportion of the energy  
 211 ingested from food is assimilated and made available to the vital processes maintenance  
 212 (metabolic rate), growth, reproduction and energy storage. The rates at which energy is  
 213 allocated to these processes depend on temperature and body size. The effect of temperature  
 214 on energy acquisition and expenditure is generally given relative to a reference temperature  
 215  $T_{\text{ref}}$  using an exponential Arrhenius function  $A(SST)$ , as:

$$A(SST) = e^{\frac{-E_a}{K} \left( \frac{1}{SST} - \frac{1}{T_{ref}} \right)} \quad (1)$$

216 where  $E_a$  is the activation energy,  $K$  is Boltzmann's constant (see TRACE section 2 for a full  
 217 list of parameters and section 7 for a local sensitivity analysis). The partitioning of energy to  
 218 vital processes depends on an individual's life stage and time of year. See Sibly et al.  
 219 (2013) for an overview, and TRACE section 2 for full details.

#### 2.3.2. Migrations in to and out of the feeding area

220 The feeding migration of mackerel into the Norwegian Sea coincides with spawning, and  
 221 occurs primarily along the European shelf edge to the west of the British Isles (Brunel et al.  
 222 2017). We represent the shelf edge with a corridor around the British Isles in which  $-550\text{m} <$   
 223  $\text{depth} < -50\text{m}$  and  $\text{latitude} < 60.5^\circ \text{N}$  (Fig. 1). Each patch on the shelf edge is characterised by  
 224 its distance  $D$  (patches) from the target destination at the entrance to the Norwegian Sea  
 225 ( $61.5^\circ \text{N } 4.8^\circ \text{W}$ , red circle in Fig. 1). After spawning (see TRACE section 2 for details), SIs  
 226 move north and east along the shelf edge to the patch with the lowest  $D$  within their possible  
 227 swimming range. An individual's possible swimming range is calculated from its minimum  
 228 swimming velocity  $V_{\text{min}}$  ( $\text{km hr}^{-1}$ ), given as a function of standard body length  $L_s$  and the  
 229 caudal fin aspect ratio  $A_r$  (Sambilay Jr 1990):

$$V_{\text{min}} = V_0 L_s^{a_v} A_r^{b_v} \quad (2)$$

230 where  $V_0$  is a normalizing constant, and  $a_v$  and  $b_v$  are scaling exponents. Velocities are  
 231 converted to distance using the appropriate time period, here one time-step of five days. This  
 232 algorithm fulfils the needs to: 1) direct SIs from the spawning to feeding areas north and



eastward along the shelf edge; and 2) for migration rate to increase with body length (Jansen and Gislason 2011). To prevent all individuals congregating at the same destination patch as they enter the Norwegian Sea, each individual is forced to stop migrating at a randomly-selected distance from the destination in which  $D < 5$  patches (at this point one of the four search mechanisms in Table 1 start to direct movement). The return overwintering migration is simply the reverse of the feeding migration (back towards the entrance to the Norwegian Sea) and begins on October 1<sup>st</sup> (see TRACE section 2 for details).

### 2.3.3. Profitability cues

After reaching their destination in the feeding area, SIs begin to seek out the most profitable patches on which to feed. The profitability of a patch is defined using one of two cues, each representing possible ingestion rate with a different assumption about density dependence. The first cue  $c_{di}$  represents the bottom-up effect of phytoplankton density as a proxy for food availability, and the effect of SST (Kelvins), in the form of a Holling type 2 functional response:

$$c_{di} = A(SST) \frac{X}{X + h} \quad (3)$$

where  $X$  is phytoplankton density ( $\text{g m}^{-2}$ ) and  $h$  is a half saturation constant and  $A(SST)$  is an Arrhenius function (eq. 1). The second cue  $c_{dd}$  is similar to  $c_{di}$  but also includes a density-dependent effect of competition for food among the mackerel, according to a Beddington-DeAngelis functional response:

$$c_{dd} = A(SST) \frac{X}{X + h + cD} \quad (4)$$

where  $D$  is mackerel density and  $c$  determines the strength of the density dependence. It is important to note that although  $c_{di}$  does not include an effect of mackerel density, an individual's ingestion rate is always affected by the competition term,  $cD$ , in eq. 4.

Studies using sonar have shown that the prevailing swimming direction of NEAM in summer is northwards (Nottestad et al. 2016). One possible explanation for this is photoperiod; mackerel are visual feeders (Pepin et al. 1988) so moving to higher latitudes in summer would permit extended feeding periods, which is not captured by equations 3 and 4. To reflect this, we up-weight the values of  $c_{di}$  and  $c_{dd}$  on patches north of an individual's current position by a factor  $\text{photo}_{\text{effect}}$  (i.e. we include an implicit effect of photoperiod on patch profitability). For each search mechanism we test three values of  $\text{photo}_{\text{effect}}$ : 1 (i.e. no effect of photoperiod), 1.25 and 1.5. We adopt the value for each search mechanism that maximises its ability to match the occurrence data in Fig. 4. See TRACE section 7 for full details and for the sensitivities of predicted distribution to  $\text{photo}_{\text{effect}}$ .

### 2.3.4. Feeding strategies

The ways in which SIs seek out the most profitable feeding patches are modelled with one of an ideal free distribution (IFD) or gradient area search (GAS) feeding strategy, outlined below.

*Ideal free distribution:* in the IFD feeding strategy we assume that SIs can detect the environment in all patches within their five-day search area. This implies the use of predictive orientation, i.e. where individuals orientate towards areas that are predicted to be optimal, without necessarily using information in the near-field (Fernö et al. 1998). A five-

275 day search area was chosen to match the model time-step. The radius of an individual's  
 1 276 search area is calculated from its realised swimming velocity  $V_r$ , given as  $V_r = V_{\min} + (V_{\min}$   
 2 277  $\epsilon)$ , where  $\epsilon$  is drawn randomly from a uniform distribution over the range 0 to 1, and  $V_{\min}$  is  
 3 278 minimum swimming velocity (eq. 2). This algorithm produces realised swimming velocities  
 4 279 in the range 1.85 to 4.42 km hour<sup>-1</sup> (assuming body lengths in the range 30 to 40 cm). This is  
 5 280 similar to swimming speeds observed in the Norwegian Sea over summer using sonar. Godø  
 6 281 et al. (2004) observed the majority of NEAM schools to be swimming between 0 and 3.6 km  
 7 282 hour<sup>-1</sup>, but with many swimming considerably faster. In a laboratory setting a maximum  
 8 283 sustained speed of 4.41 km hour<sup>-1</sup> was observed for a 35 cm fish (He and Wardle 1988, cited  
 9 284 by Walsh et al. 1995). The IFD sub-model works in discrete space on a patch by patch basis:  
 10 285 SIs simply move each time-step to the most profitable patch within their search area and on  
 11 286 which SST  $\geq$  the lower boundary (7° C) below which mackerel avoid (Olafsdottir et al.  
 12 287 2018).

16 288 *Gradient area search:* the GAS feeding strategy is broadly similar to that presented by  
 17 289 Politikos et al. (2015) and Tu et al. (2012). It differs from the IFD in three keys ways: 1) SIs  
 18 290 can detect the profitability of the four neighbouring patches in x and y dimensions only,  
 19 291 meaning they have access to considerably less environmental information than in the IFD; 2)  
 20 292 the GAS model works in the continuous space of the model grid; and 3) SI's locations are  
 21 293 updated more frequently at five times per time-step (i.e. once per day), to ensure that they  
 22 294 cannot overshoot the neighbouring patch. Positions in x and y dimensions are updated by:

$$\begin{aligned} x_{t+1} &= x_t + (D_x + R_x) \\ y_{t+1} &= y_t + (D_y + R_y) \end{aligned} \quad (5)$$

25 295 where  $D_x$  and  $D_y$  are the directed search part of the equation, and  $R_x$  and  $R_y$  are the random  
 26 296 components.

27 297 In the orientated part of eq. (5)  $D_x$ ,  $D_y$ , SIs compare the profitability at their current location  
 28 298 with that of the day before. If it has become more profitable, they will continue to swim in the  
 29 299 same direction as the oriented part of their movement the day before. If a SI's current  
 30 300 environment is less profitable than the day before, they follow a gradient search towards what  
 31 301 is perceived to be the most profitable patch based on information in x and y dimensions, at  
 32 302 velocity  $V_r$  (see ideal free distribution in section 2.3.4), given by:

$$\begin{aligned} D_x &= V_r \frac{c_x}{\sqrt{c_x^2 + c_y^2}} \\ D_y &= V_r \frac{c_y}{\sqrt{c_x^2 + c_y^2}} \end{aligned} \quad (6)$$

33 303 where  $c_x$  and  $c_y$  are the gradients of the profitability cues (eq. 3, 4) in x and y dimensions.  
 34 304 This amounts to what is called a state-location orientation mechanism (basing new orientation  
 35 305 on a comparison of the current and previous environment), and there is some indication that  
 36 306 herring follow a similar strategy in the Norwegian sea (Fernö et al. 1998). Following  
 37 307 Politikos et al. (2015a) we assume that movement is directed ( $D_x$ ,  $D_y$ ) for 12 hours day<sup>-1</sup>, and  
 38 308 movement in the other 12 hours follows the random component of eq. 5  $R_x$ ,  $R_y$ , which we  
 39 309 give as swimming at velocity  $V_{\min}$  in a random direction. This assumption introduces

310 stochasticity into the GAS models and prevents unrealistic overcrowding on optimal patches  
311 (particularly in the GAS<sub>di</sub> model in which competition is not accounted for).

312 As with the IFD, we prevent SIs from moving into patches with intolerably low temperature.  
313 In the oriented part of eq. 5, we repel individuals from patches with SST < 7°C by setting  
314 profitability cues in those areas to 0. For the random component of eq. 5, if a SI's orientation  
315 would direct it on to a patch with SST < 7°C, its heading is reversed.

### 316 **2.3.5. Movement-bioenergetics coupling**

317 The energy cost of searching for food is subsumed into an individual's active metabolic rate  
318 AMR. AMR is given as a function of SST, body mass M and swimming velocity V as:

$$319 \quad AMR = a_{AMR} M^{b_{AMR}} V^{c_{AMR}} A(SST) \quad (7)$$

319 where  $a_{AMR}$  is a normalizing constant,  $b_{AMR}$  and  $c_{AMR}$  are scaling exponents, and V is given  
320 by  $V = (V_r + V_{min}) / 2$ , i.e. assuming that half of each day is spent at  $V_{min}$ , and half at  $V_r$ .

## 321 **2.4. Model simulations**

322 The model simulates the full life cycle of the mackerel population from January 1<sup>st</sup> 2005 to  
323 December 31<sup>st</sup> 2015. In this paper we focus on the summer feeding period in each year, and  
324 model the ways in which individual adults move in search of the best feeding opportunities.  
325 This is represented by one of four search mechanisms spanning each combination of  
326 profitability cue and feeding strategy (e.g. IFD<sub>dd</sub>, IFD<sub>di</sub>, GAS<sub>dd</sub>, GAS<sub>di</sub>). Simulations are  
327 forced by fishing mortality F at age, phytoplankton density X and SST. F is updated every  
328 year. Maps of X and SST represent ten-day composites and are updated accordingly.

329 For the purposes of this paper, outputs that are recorded annually include: SSB at spawning  
330 time (May 1<sup>st</sup>), mean weight-at-age in summer (August 1<sup>st</sup>), whether or not mackerel were  
331 present on each patch in July or August, and mean mackerel density on each patch over July/  
332 August. From these measures we calculate total summer distribution area as the sum of the  
333 areas of patches on which mackerel was present, and the centre of gravity of the stock in  
334 terms of latitude (COG<sub>y</sub>) and longitude (COG<sub>x</sub>). As we have changed our IBM structurally  
335 since Boyd et al. (2018), we provide updated model fits to separate data on various aspects of  
336 the population structure in TRACE section 9. The times at which outputs are recorded were  
337 chosen to match the available data as closely as possible.

## 338 **2.5. Data**

339 Input data includes F (day<sup>-1</sup>), and maps of phytoplankton density X (g m<sup>-2</sup>) and SST (kelvins).  
340 F comes from the stock assessment as age-specific rates that vary annually, and are applied  
341 each day to the appropriate age group. X and SST were derived from data from the MODIS  
342 sensor on NASA's Aqua satellite (NASA OBPG 2017a, 2017b). Ten-day composites are used  
343 at a spatial resolution of 60 x 60 km. The satellite remote-sensing data required processing for  
344 use as model input (e.g. re-gridding and interpolations), the details of which can be found in  
345 TRACE section 3.

346 The model was calibrated with estimates of SSB (spawning time) from the 2017 NEA  
347 mackerel stock assessment, and mean weight-at-ages 3 and 13 in the summers of 2007 and  
348 2010-2015 from the International ecosystem survey in the Nordic Seas (IESSNS) (see  
349 Nøttestad et al (2015) for full details of the data). We scale the SSB data by a factor of 0.8 to  
350 reflect the fact that we only represent the stock's western spawning component which

351 comprises ~ 80% of its total biomass. We calibrated the IBM with data on SSB and weight-  
1 352 at-age because its ability to fit them simultaneously would indicate that competition for food  
2 353 at a given stock size is realistic as reflected in the body weights of the fish. This is important  
3 354 because density dependence is a key feature of the movement sub-models. Full details of the  
4 355 data are provided in TRACE section 3.

6  
7 356 To validate the model we used data from the IESSNS on the presence/ absence of mackerel in  
8 357 the Nordic seas in July/ August of 2007 and 2010 to 2015 (see Nøttestad et al. (2015) for  
9 358 details). We approximated these data from Fig. 2 of Olafsdottir et al. (2018) using Java's  
10 359 PlotDigitizer (<http://plotdigitizer.sourceforge.net/>).

## 12 360 **2.6. Model calibration**

13 361 For each search mechanism (IFD<sub>dd</sub> etc.) we calibrated three parameters: background early  
14 362 mortality  $M_e$  (natural mortality rate for eggs and larvae excluding explicit cannibalism in the  
15 363 IBM), strength of the density dependence ( $c$ ) and the half saturation constant ( $h$ ). We  
16 364 estimated the parameters by fitting the model to the calibration data (see data) using rejection  
17 365 approximate Bayesian computation (ABC) (van der Vaart et al. 2015). In broad terms, we ran  
18 366 1000 simulations for each search mechanism, while randomly sampling values of the three  
19 367 parameters from uniform prior distributions. We then “accepted” the parameters that  
20 368 minimised the sum of the squared deviations of the model outputs from the data. See TRACE  
21 369 section 3 for full details.

## 25 370 **2.7. Search mechanism model selection**

26 371 To determine which search mechanism was best able to reproduce the mackerel summer  
27 372 distribution, we compared their predictions of presence/ absence to the data in Fig. 4. First,  
28 373 we assessed the fits of each model by testing for an association between their predictions and  
29 374 the data with a chi square test. We then further quantified the performance of each sub-model  
30 375 using standard statistics for binary data: sensitivity, i.e. the proportion of observed presences  
31 376 correctly classified; specificity, i.e. the proportion of observed absences correctly classified;  
32 377 and the distance to the top left corner on a plot of sensitivity as a function of  $1 - \text{specificity}$   
33 378 (Fig. 5),  $d(0, 1)$ , chosen because this point (0, 1) corresponds to a perfectly classified model  
34 379 (sensitivity and specificity of 1) (Cantor et al. 1999, Liu et al. 2005). We include the measure  
35 380  $d(0, 1)$  instead of, for example, an overall accuracy rate, because it is robust to disparity in the  
36 381 prevalence of presences and absences which is high in these data (~82% presences). When  
37 382 comparing predictions of a continuous distribution (here density) to data on presence/  
38 383 absence it is useful to determine a threshold representing the minimum density that should be  
39 384 considered a presence, with everything below this density being classified as an absence. We  
40 385 optimised a threshold density for each search mechanism using the measure  $d(0,1)$  as a cost  
41 386 function (Cantor et al. 1999, Liu et al. 2005). See TRACE section 7 for full details and  
42 387 presence thresholds. By pooling the data for all years in our analysis we give extra weight to  
43 388 years with greater sampling effort, which we consider appropriate.

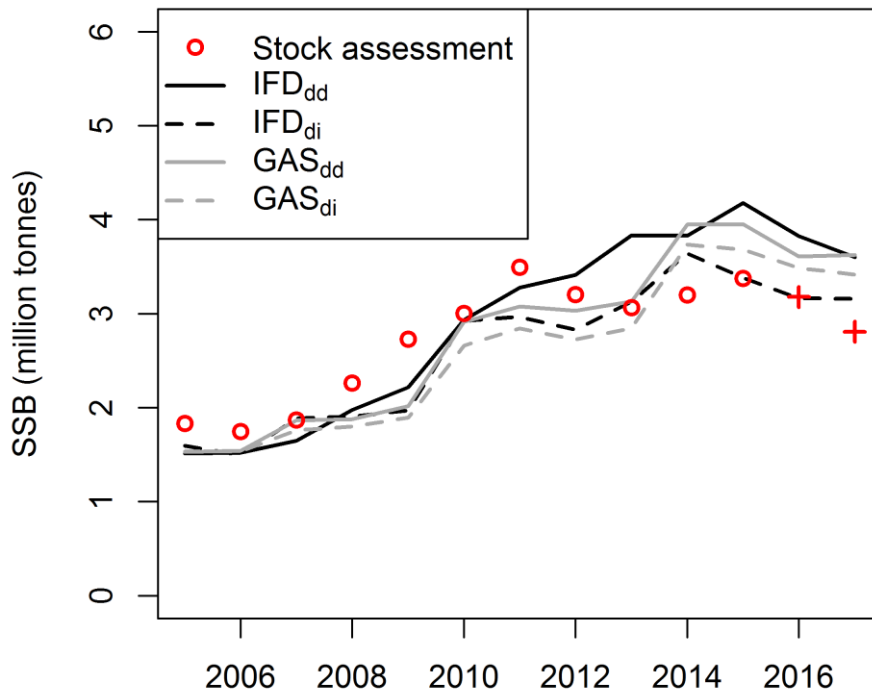
## 49 389 **2.8. Change in predicted distribution over 2005 to 2015**

50 390 To test whether our IBM can reproduce the observed north and westward expansion of  
51 391 NEAM over summer, we record total distribution area,  $\text{COG}_x$  ( $^\circ$  W) and  $\text{COG}_y$  ( $^\circ$  N) over  
52 392 July/ August of 2005 to 2015. We regress each summary statistic on simulation year and if  
53 393 the slopes are positive significant, then we consider the search mechanism able to reproduce  
54 394 the expansion.

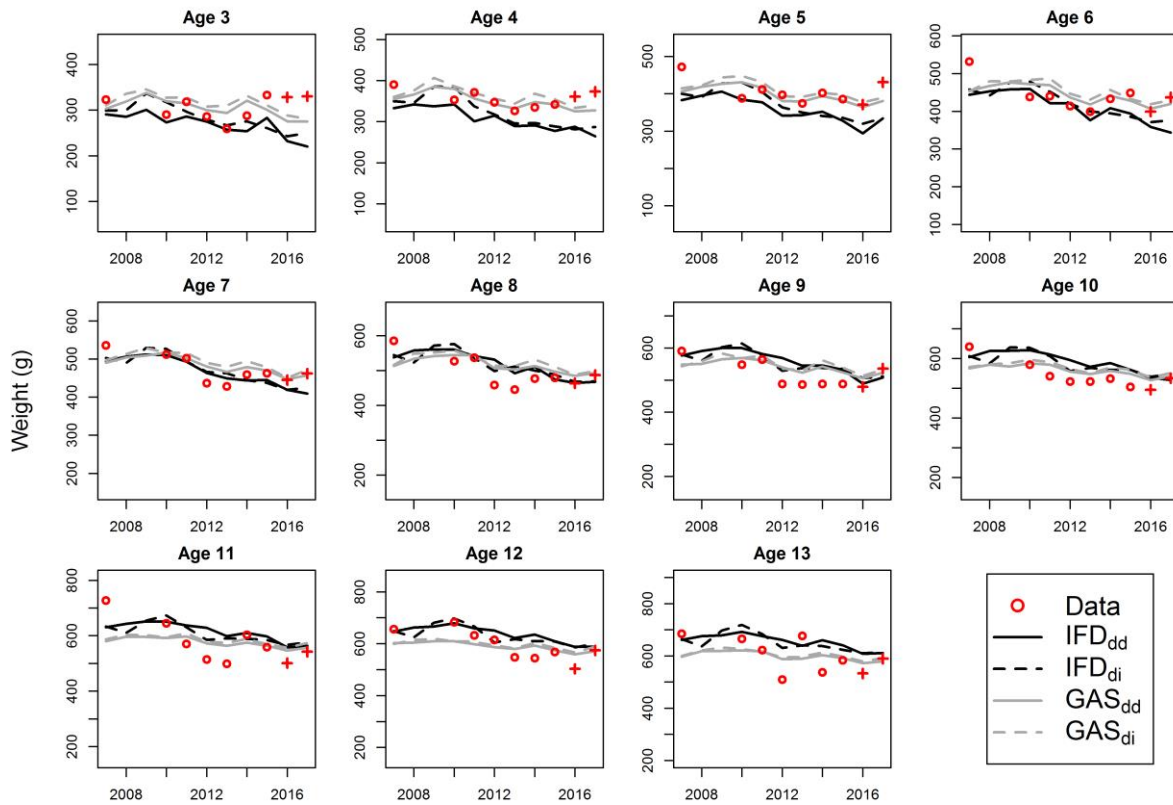
### 3. Results

#### 3.1. Model calibration

In order to test each model's ability to represent the effects of competition for food, we fitted them to available data on SSB and weight-at-ages 3-13 over 2005 to 2015 (Figs. 2, 3; see TRACE section 3 for estimated parameter values). We suggest that if a sub-model can simultaneously match these data, then competition for food at a given SSB is sufficiently realistic. SSB generally shows an increasing trend over the calibration period (Fig. 2), so we also present model predictions in 2016 and 2017 to show that the IBM predictions do not simply continue to rise. To quantify the goodness of fits to the data (including 2016 and 2017), we used three commonly-used diagnostics for each variable: the correlation coefficient  $r$ ; the root mean square error (RMSE); and the bias (Edwards et al. 2012, Formenti et al. 2015). Overall we suggest that each model can fit data on both SSB and weight-at-age reasonably well. The search mechanisms produce similar trajectories for SSB. From 2011 the IFD<sub>dd</sub> model diverges slightly from the other models because individuals have better feeding opportunities which is reflected in higher SSB. SSB is generally matched well, with  $r$  being  $\geq 0.84$  ( $p < 0.0003$ ) and RMSE  $< 0.51$  million tonnes in all cases (Table 1). For weight-at-age the correlations are lower than for SSB (0.36 to 0.50), but the overall biases are small at  $\leq 10.81$  g (Table 1). With all search mechanisms the IBM is able to capture the general downward trend in weight-at-age (Fig. 3). However, for ages seven and below, the IFD models are unable to predict the increase in weight-at-age observed near the end of the time series.



418 Figure 2. Predicted SSB from each feeding sub-model compared with estimates from the  
 419 stock assessment. Values represent means over ten simulations. Note that the IBM was fitted  
 420 to the data over the period 2005 to 2015 (red circles) and not to the data in 2016 or 2017 (red  
 421 crosses).



423  
 424 Figure 3. Predicted mean weight-at-ages 3-13 in summer from each feeding sub-model  
 425 compared with data from the International Ecosystem Survey in the Nordic Seas (IESSNS).  
 426 Values represent means over five simulations. Note that the model was fitted the data over  
 427 2007 to 2015, and not to the data in 2016 or 2017 (red crosses).

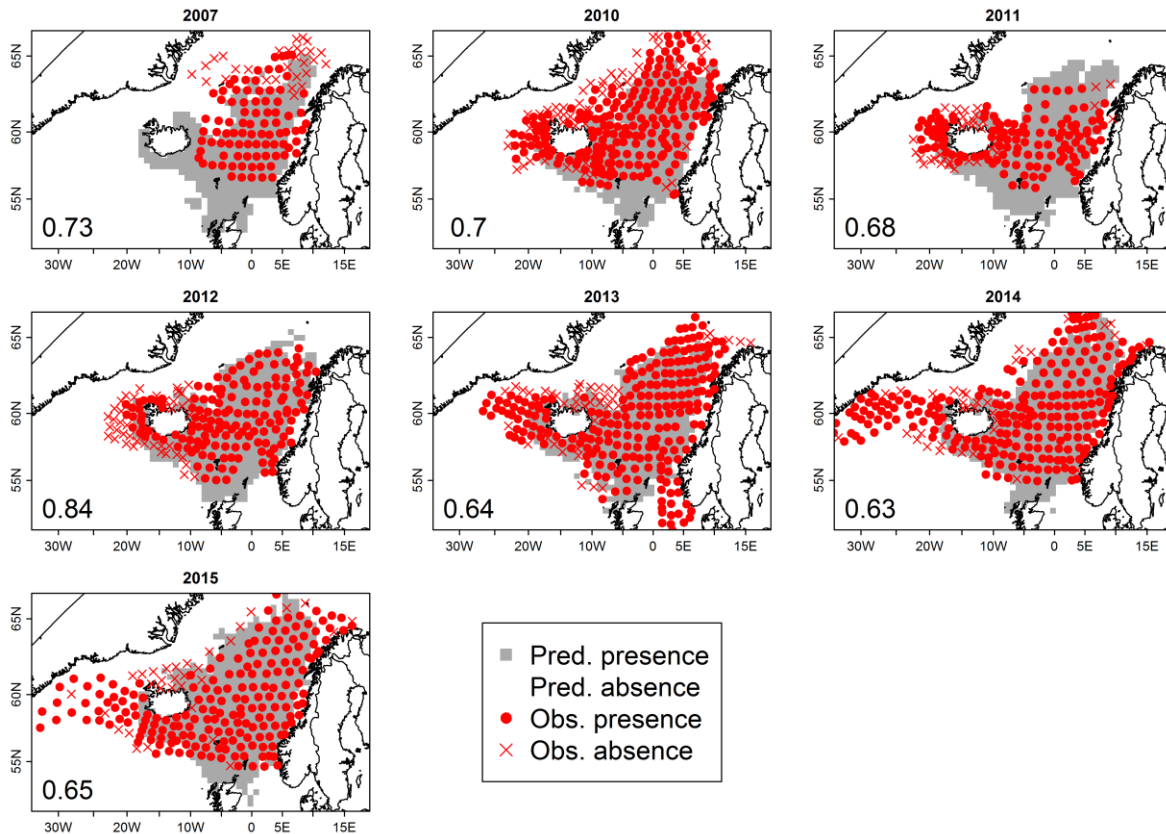
428 Table 1. The goodness of fit between predicted and observed SSB and weight-at-age for each  
 429 sub-model. For weight at age we present the mean r over all age groups, and RMSE and bias  
 430 are aggregated over all age groups. All diagnostics are based on means over ten simulations.  
 431 Units are in millions of tonnes for SSB, and grams for weight-at-age.

| Model             | SSB  |      |       | Weight-at-age |       |        |
|-------------------|------|------|-------|---------------|-------|--------|
|                   | r    | RMSE | Bias  | Mean r        | RMSE  | Bias   |
| GAS <sub>dd</sub> | 0.87 | 0.46 | -0.03 | 0.46          | 40.32 | -1.75  |
| GAS <sub>di</sub> | 0.84 | 0.46 | 0.14  | 0.36          | 43.48 | -10.81 |
| IFD <sub>dd</sub> | 0.91 | 0.51 | -0.15 | 0.50          | 55.30 | -0.67  |
| IFD <sub>di</sub> | 0.89 | 0.35 | 0.13  | 0.54          | 48.57 | -4.70  |

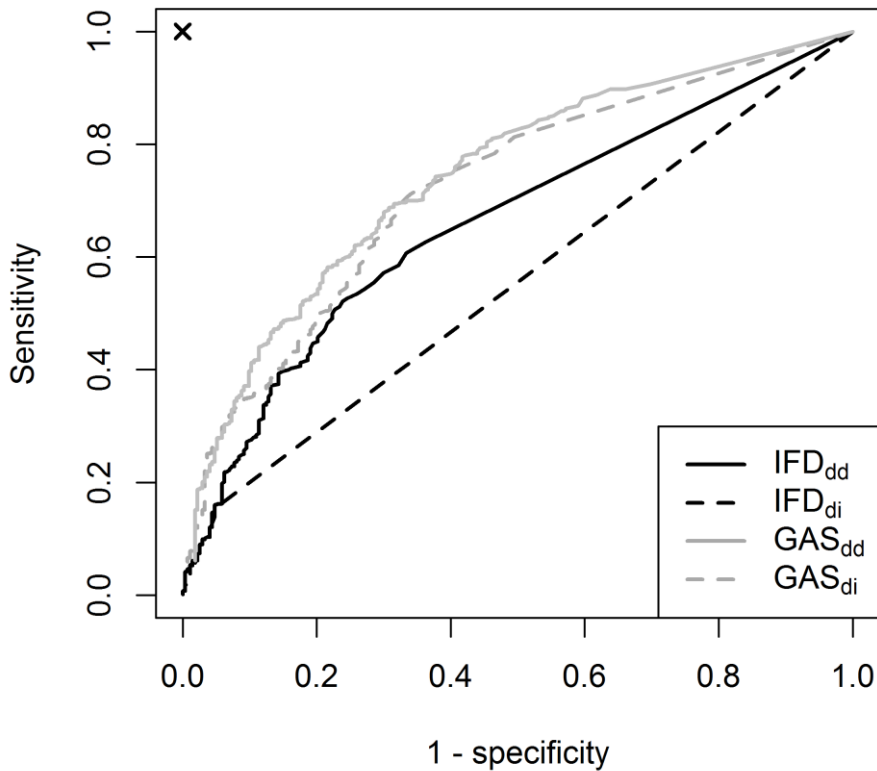
### 3.2. Search mechanism model selection

434 To determine which search mechanism is best able to reproduce the NEAM summer  
 435 distribution we compared their predictions to data on presence/ absence in the Nordic Seas. A  
 436

437 threshold was optimised for each search mechanism representing the minimum density that  
 438 should be classed as a presence (see TRACE section 7). Predictions obtained from all search  
 439 mechanisms are all significantly related to the data (Chi square,  $p < 0.01$ ). The GAS models  
 440 produce similar results in terms of sensitivity, specificity and hence  $d(0,1)$  (Table 2, Fig. 5).  
 441 The IFD models, on the hand, produce very different results. The IFD<sub>dd</sub> shows reasonably  
 442 good sensitivity and specificity (0.61 and 0.67, respectively). The IFD<sub>di</sub> search mechanism  
 443 has a high specificity, but a very low sensitivity (discussed in section 4). The measure  $d(0,1)$   
 444 suggests that the GAS models, in particular the GAS<sub>dd</sub>, are best able to reproduce the NEAM  
 445 summer distribution and should be used in future work.



447  
 448 Figure 4. Data from the IESSNS survey (approximated from Olafsdottir et al. (2018)) on  
 449 presence (obs. presence) and absence (obs. absence) of mackerel in the Nordic seas over July/  
 450 August. We also show simulated presence (pred. presence) and absence (pred. absence) as  
 451 predicted by the GAS<sub>dd</sub> search mechanism. It should be noted that predicted presence is  
 452 obtained after optimising a threshold density below which an area is classed as an absence.  
 453 This means that the areas of low density on the fringes of the distribution (e.g. in the western  
 454 area) are not shown as presences here. The numbers on each panel indicate the proportion of  
 455 data points in each year for which the model correctly predicted whether or not mackerel was  
 456 present.



458

459 Figure 5. Sensitivity plotted against 1- specificity (loss of specificity) for each search  
 460 mechanism's predictions of mackerel presence/ absence in July/ August. Curves represent  
 461 varying density thresholds (above which an area is classed as a presence) over the range 0 to  
 462 30% of maximum predicted density in each search mechanism. A model at point 0, 1 (black  
 463 cross) would have perfect sensitivity and specificity. Values are derived from means over 10  
 464 simulations.

465 Table 2. Statistics indicating the ability of each sub-model to reproduce the data on presence/  
 466 absence of mackerel in Fig. 4.  $d(0,1)$  is the distance of each model to point 0,1  
 467 (corresponding to a perfectly sensitive and specific model) on Fig. 5. Better models achieve  
 468 lower values of  $d(0,1)$ . Values are derived from means over ten simulations after optimising  
 469 the threshold density for what defines a presence.

| Model                   | Sensitivity | Specificity | $d(0,1)$ |
|-------------------------|-------------|-------------|----------|
| <b>GAS<sub>dd</sub></b> | 0.69        | 0.70        | 0.44     |
| <b>GAS<sub>di</sub></b> | 0.67        | 0.70        | 0.45     |
| <b>IFD<sub>dd</sub></b> | 0.61        | 0.67        | 0.52     |
| <b>IFD<sub>di</sub></b> | 0.15        | 0.95        | 0.85     |

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### 471 3.3. Predicted expansion

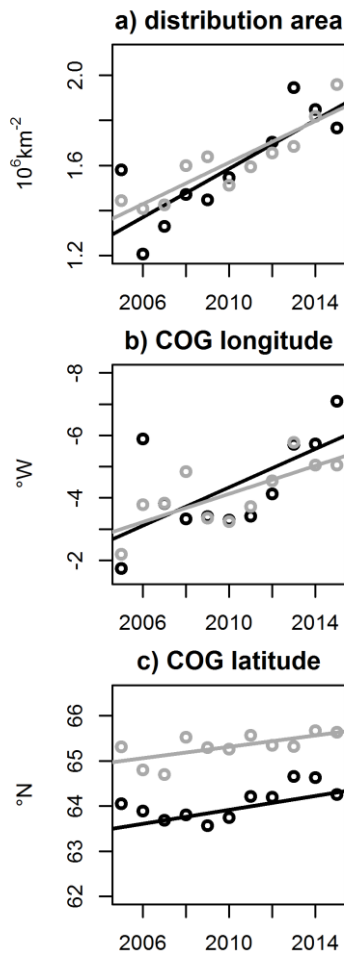
472 To test how predicted mackerel summer distribution changes through time, we recorded three  
 473 summary statistics in each year: total distribution area,  $COG_x$ , and  $COG_y$ . For these  
 474 simulations we used the best-performing GAS<sub>dd</sub> search mechanism (Fig. 5), but also the

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475 IFD<sub>dd</sub> as inspection of the outputs suggested that the latter was better able to capture the  
 476 western extent of the distribution (the IFD<sub>di</sub> and GAS<sub>di</sub> models were not). For both search  
 477 mechanisms we regressed distribution area, COG<sub>x</sub> and COG<sub>y</sub> on simulation year, and all of  
 478 the slopes were positive and significant ( $p < 0.05$ ). This shows that the models are in  
 479 agreement with the general consensus that the stock's distribution area increases through  
 480 time, and that its centre of gravity shifts north and westwards (Fig. 6).

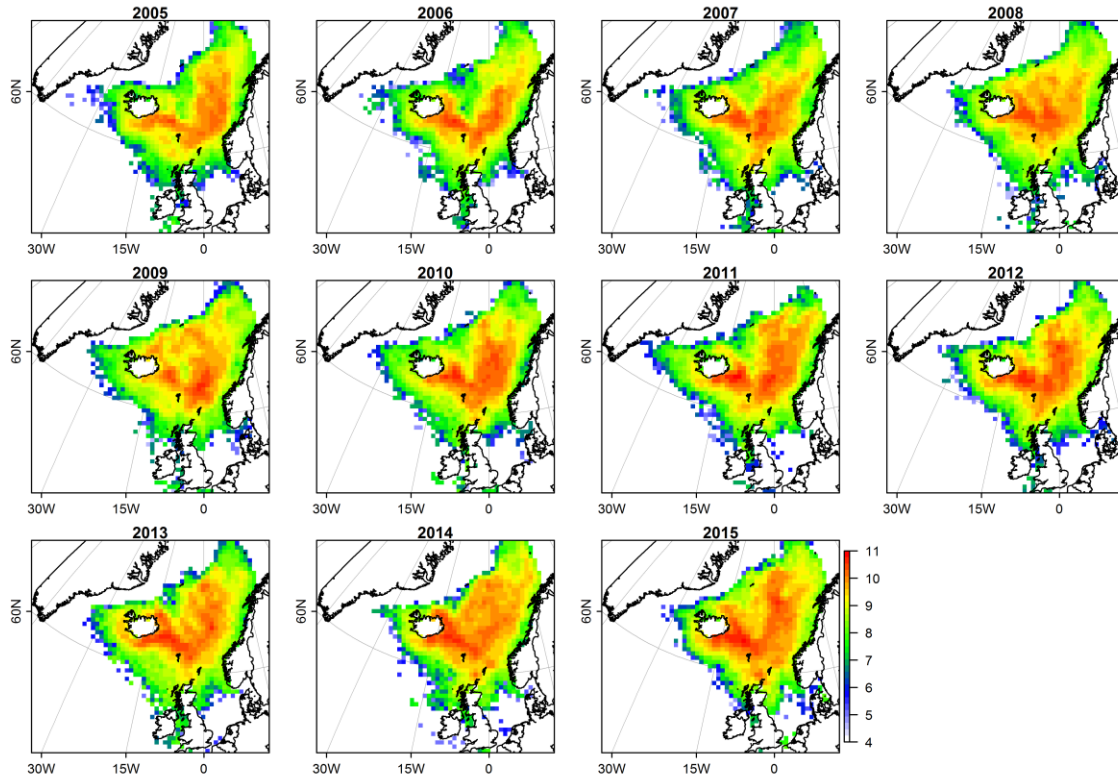
481 To explore possible differences in the distribution changes predicted by the GAS<sub>dd</sub> and IFD<sub>dd</sub>  
 482 search mechanisms, we compared their predictions of distribution area, COG<sub>x</sub> and COG<sub>y</sub>. For  
 483 each summary statistic, the rates of change are similar between search mechanisms (Fig. 6).  
 484 This is indicated by a lack of interaction effects between search mechanism and simulation  
 485 year (i.e. the slopes are not significantly different; ANCOVA,  $p > 0.05$ ). There is an effect of  
 486 search mechanism on COG<sub>y</sub> ( $p < 0.05$ ) which indicates that, although the slopes are similar,  
 487 there is a significant difference in y intercepts between models (Fig. 6c). This can be  
 488 explained by the fact that, while the cores of the distributions predicted by the two models are  
 489 similar (Norwegian Sea and around Iceland; Figs 7 and 8), the GAS<sub>dd</sub> model generally  
 490 predicts a more northerly distribution than the IFD<sub>dd</sub>. It should be noted that an increase in  
 491 distribution area with stock size is expected due the competition term,  $cD$ , in equation 4.



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 493 Figure 6. Comparisons of a) distribution area, b) centre of gravity in terms of longitude COG<sub>x</sub>  
 494 and c) centre of gravity in terms of latitude COG<sub>y</sub> as predicted by the GAS<sub>dd</sub> (grey circles)  
 495 and IFD<sub>dd</sub> (black circles) search mechanisms.

496 NEAM density in in July/ August of each year is presented for the GAS<sub>dd</sub> and IFD<sub>dd</sub> search  
 497 mechanisms in figs 7 and 8, respectively. Generally the models agree on the areas of highest

498 density such as the Norwegian Sea and around Iceland. The models also both produce a  
 1 499 similar boundary at the northern limit of the distribution around the position of the 7° C  
 2 500 isotherm (north of which mackerel avoid). This boundary is particularly evident to the  
 3 501 northwest of Iceland where the cool East Greenland Current flows south. The key differences  
 4 502 between the models are that the IFD<sub>dd</sub> produces a patchier distribution, but is better able to  
 5 503 capture the western extent of the distribution as observed in the IESSNS (e.g. high densities  
 6 504 west of Iceland; fig. 4; discussed in section 4).



505  
 506 Figure 7. Mackerel density ( $\text{g patch}^{-1}$ ) in the summer of each year on a log<sub>10</sub> scale as  
 507 predicted by the GAS<sub>dd</sub> search mechanism. Values represent means over July/ August, and  
 508 over ten simulations. Note that predictions here do not correspond exactly to those in fig. 4  
 509 where areas of low density (e.g. the fringes of the distribution here) are classed as absences.

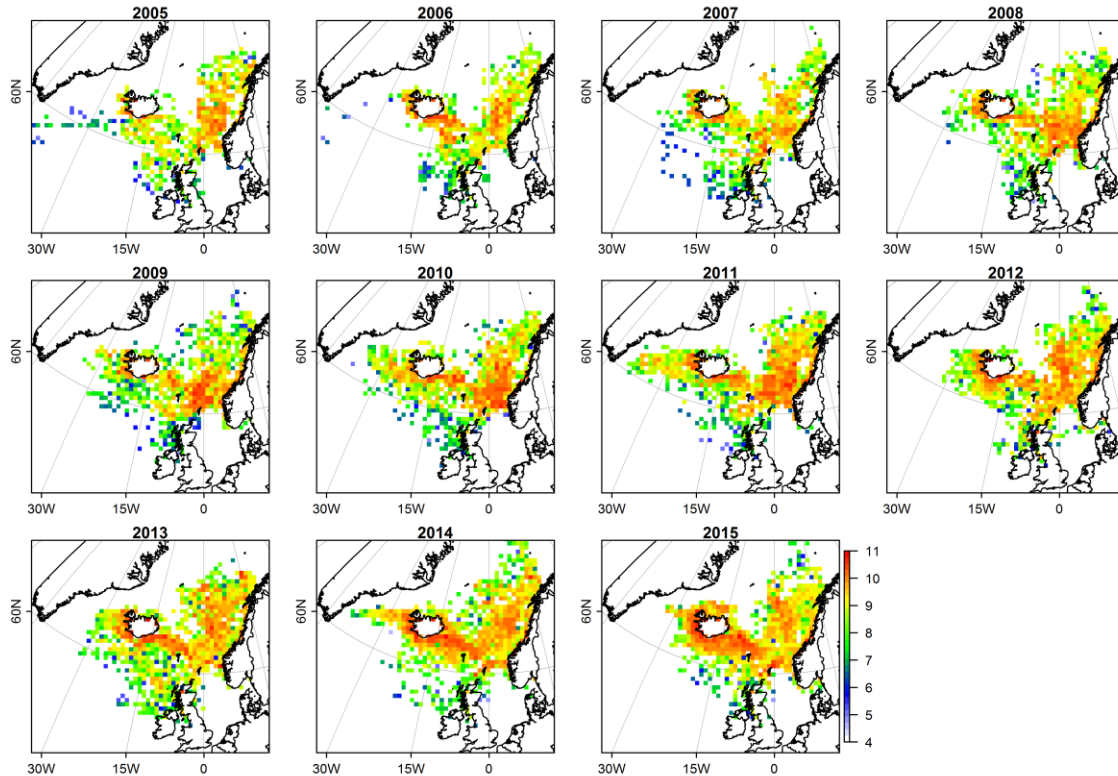


Figure 8. Mackerel density ( $\text{g patch}^{-1}$ ) in the summer of each year on a  $\log_{10}$  scale as predicted by the  $\text{IFD}_{\text{dd}}$  search mechanism. Values represent means over July/ August, and over ten simulations.

#### 4. Discussion

We have coupled an existing bioenergetics IBM to models describing how mackerel move in search of food during summer. The models contain alternative assumptions about: 1) whether or not mackerel density, and hence competition for food, affect the perceived profitability of an area; and 2) the extent of the area over which individuals can detect the environment. After comparing the outputs of each sub-model to data on SSB, weight-at-age and mackerel occurrence, we suggest that a gradient area search feeding strategy, in which competition for food affects the perceived profitability of an area, and SIs can detect the environment in the near field only, performs best. We then tested whether or not the IBM is able to reproduce the observed north and westward expansion. With the best-performing search mechanism the IBM is able to reproduce the change in distribution, as indicated by an increase in distribution area and a north and westward shift in centre of gravity. However, the IBM is not able to capture the full extent of the expansion in the western direction.

Selecting the best search mechanism based on the occurrence data was not straightforward. Initially we looked at the sensitivities and specificities of each search mechanism while assuming that patches with mean density  $> 0$  represent a presence. The GAS models performed poorly under this assumption because, due to inclusion of stochastic movements, they predict that a small number of individuals end up on sub-optimal patches. This was reflected by high “false positive” rates and specificities of  $< 40\%$ . However, when the threshold defining the minimum density that constitutes a presence is optimised, the GAS feeding strategy performs best. This is because patches with very low density (but  $> 0$ ) no longer count as presences hence the false positive rates of the GAS models are reduced.

536 Once the density thresholds are optimised we suggest that the GAS models are best and  
1 537 should be used in future work.  
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3 538 In Table 2 it can be seen that the GAS models perform similarly in terms of sensitivity and  
4 539 specificity, but the IFD models are very different. This reflects the different assumptions  
5 540 made in the feeding strategies. In the GAS models individuals can only detect the  
6 541 environment in neighbouring patches, and there is a stochastic component to their movement.  
7 542 As such under this feeding strategy individuals are less likely to locate optimal patches, and if  
8 543 they do it is possible that the random movement will displace them. On the other hand, in the  
9 544 IFD feeding strategy individuals can detect the environment over a much larger area, and  
10 545 there is less stochasticity in their movements. As a result, individuals are more likely to locate  
11 546 and move to optimal patches and are less likely to leave. This means that density dependence  
12 547 becomes very important in the IFD search mechanism. In the IFD<sub>dd</sub> patches become  
13 548 increasingly unattractive as mackerel density increases, causing individuals to spread out. In  
14 549 the IFD<sub>di</sub>, however, individuals do not account for local mackerel density; they congregate on  
15 550 patches with high phytoplankton density and of suitable temperature regardless of  
16 551 competition for the food. This is reflected in a very patch distribution, high “miss rates” and  
17 552 hence low specificity.  
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22 553 The relative abilities of the GAS and IFD search mechanisms to match data on NEAM  
23 554 presence/ absence give insight into the possible ways in which mackerel seek out the best  
24 555 feeding opportunities. In the GAS search mechanism, the directed search component of  
25 556 movement is based solely on a reactive mechanism, i.e. a near-field response to gradients in  
26 557 the profitability cues. In this feeding strategy, individuals are directed to locally-optimal  
27 558 areas, but often do not reach the most profitable areas which can be further afield (e.g. in the  
28 559 western expansion area). On the other hand, in our IFD sub-model individuals can access  
29 560 information about the environment over a much larger area, and, at least in the IFD<sub>dd</sub>  
30 561 formulation, tend to reach more profitable areas. The IFD implies at least some use of a  
31 562 predictive orientation mechanisms, i.e. where individuals orientate towards areas in which the  
32 563 environment is predicted to be optimal, without following gradients in the near-field (Fernö et  
33 564 al. 1998). Our results suggest that a simple gradient search based on reactive as opposed to  
34 565 predictive orientation is best able to reproduce the mackerel distribution (Table 2, Fig. 5).  
35 566 This is supported by observations using sonar which indicate that NEAM swimming direction  
36 567 over summer is variable, suggesting reactions to food in the near field (Nottestad et al. 2016).  
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41 568 Our use of two feeding strategies with distinct assumptions about knowledge of the  
42 569 environment does not account for the possibility that NEAM may use a combination of both  
43 570 predictive and reactive orientation mechanisms. Nottestad et al. (2016) suggest that mackerel  
44 571 may use some directional cue to reach areas where feeding is predicted to be best, but react to  
45 572 local feeding opportunities along the way. An interesting possibility is that currents provide a  
46 573 directional cue (Nottestad et al. 2016). The North Atlantic Current enters the Nordic seas  
47 574 from the south. It branches into the Norwegian current, which flows Northwards into the  
48 575 Norwegian Sea, and the Irminger Current, which generally flows North and Westwards from  
49 576 the south of Iceland towards Greenland (Wanamaker et al.2012;  
50 577 <https://oceancurrents.rsmas.miami.edu/atlantic/north-atlantic.html>). These currents are  
51 578 generally in line with the prevailing direction of the mackerel feeding migration, and could be  
52 579 used as a cue on which to base predictive orientation until they arrive at suitable feeding  
53 580 locations (i.e. areas of high prey density). In addition to the feeding migration, it has been  
54 581 suggested that *S.scombrus* use currents for navigation at other times of year. For example, in  
55 582 the Northwest Atlantic mackerel may use tidal streams to reach their spawning grounds  
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583 (Castonguay and Gilbert 1995). In future it may be possible to extend our IBM and include  
1 584 currents explicitly (see e.g. Scutt Phillips et al. (2018)).

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3 585 Our GAS<sub>dd</sub> model is in general agreement with the consensus that the summer distribution of  
4 586 Northeast Atlantic mackerel has shown a recent north and westward expansion (Berge et al.  
5 587 2015, Nøttestad et al. 2015, Pacariz et al. 2016, Olafsdottir et al. 2018) (Fig. 6). It does,  
6 588 however, considerably under-predict the extent of the expansion in the western direction (Fig.  
7 589 4). This could be explained by several factors. First, there is the possibility that NEAM use  
8 590 both reactive and predictive orientation (possibly based on currents) in order to navigate  
9 591 towards the most productive feeding grounds. In the IFD<sub>dd</sub> search mechanism, which is based  
10 592 on predictive orientation, individuals inhabit areas west of Iceland in large densities (Fig. 8).  
11 593 Second, our IBM does not include any competing species. It would be difficult to extend our  
12 594 highly detailed approach from a single to multiple species (e.g. specifying bioenergetics and  
13 595 movement models for the full ontogeny of multiple species). Omission of competing species  
14 596 may be problematic, however, as it is not possible to account for the food limitation arising  
15 597 from interspecific competition which could force the mackerel into fringe areas. Indeed, there  
16 598 is high diet overlap between herring and mackerel in the Nordic seas (Bachiller et al. 2016),  
17 599 although species distribution modelling suggests that the two species can successfully cohabit  
18 600 (Nikolioudakis et al. 2018). Third, we use chlorophyll as a proxy for food availability. We  
19 601 use this data because it is available with greater coverage, spatial and temporal resolutions  
20 602 than that available for zooplankton. This does, however, leave our model vulnerable to the  
21 603 usual assumptions associated with extrapolating from primary to secondary production such  
22 604 as possible lag times between peaks of phyto- and zooplankton. In all, due to data and  
23 605 technical constraints, our results are limited to the effect of mackerel SSB, temperature and a  
24 606 proxy for food availability, and should be viewed as such.

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31 607 Much of the variation in the summer distribution of mackerel appears to be explained by  
32 608 three main factors: a bottom-up effect of prey distribution; a density-dependent effect of  
33 609 mackerel stock size; and the effects of temperature (Pacariz et al. 2016, Nikolioudakis et al.  
34 610 2018, Olafsdottir et al. 2018). We have incorporated these drivers into a mechanistic IBM  
35 611 which also explicitly accounts for movement behaviour. The IBM is able to match data on  
36 612 NEAM occurrence in the Nordic Seas over 2007 to 2015 reasonably well (Fig. 4). It is also  
37 613 able to produce a north and westward expansion (Fig. 6), although, interestingly, it fails to  
38 614 capture the extent of the observed expansion in the western direction. Despite performing  
39 615 reasonably well, it should be kept in mind that our IBM has only been validated using  
40 616 presence/ absence data. Moreover, the IESSNS survey in which this data was collected has  
41 617 variable spatial coverage between years, with greater coverage in more recent years  
42 618 (Nøttestad et al. 2015). The time-series is also relatively short at present as data are not  
43 619 available for the years 2008 and 2009 (Olafsdottir et al. 2018). As more data become  
44 620 available (in particular catch per unit effort) we plan to further validate our IBM.

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48 621 The inclusion of environmentally-driven movement represents a significant improvement to  
49 622 the initial version of our IBM (Boyd et al. 2018). The model is now able to make predictions  
50 623 about both the spatial distribution of the mackerel stock and its population dynamics (though  
51 624 further validation, testing, and possibly development, is needed to ensure its predictive  
52 625 power). Other bioenergetics IBMs have been applied to the summer feeding distribution of  
53 626 Atlantic mackerel (Utne and Huse 2012, Heinänen et al. 2018). However, our model differs  
54 627 in that it is multi-generational and includes the full life cycle, i.e. what happens outside of the  
55 628 feeding period. This is important because distribution at one point in time is affected by both  
56 629 what has gone before and the need to close the life cycle (Payne et al. 2017). For example, in  
57 630 our model the production of a very strong year class could lead to an increase in SSB, which  
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631 would then have knock-on effects for the stock's distribution. It should be noted, however,  
1 632 that in our model movement outside of the feeding period is still to some extent hard-wired.  
2 633 In future the model could be extended to predict NEAM distribution at other times of year.  
3 634 For example, it may be possible to use the GAS model presented here to predict NEAM  
4 635 spawning distribution. The only difference would be that profitability would be some  
5 636 measure of habitat suitability for egg development as opposed to adult feeding opportunities.  
6 637 Data on egg distribution from the mackerel and horse mackerel egg survey (ICES 2013)  
7 638 could be used to validate the model. By modifying the movement models presented here and  
8 639 validating them with data on NEAM distribution outside of the feeding period, spatial  
9 640 distribution at other times of year could become a fully-emergent feature of the IBM.

11 641 Going forward we plan to use our IBM in a strategic capacity. For example, it could be used  
12 642 to project possible consequences of different environmental and management scenarios for  
13 643 NEAM. Forecasts of SST and chlorophyll, the environmental inputs needed for our model,  
14 644 are available under different anthropogenic emissions scenarios from several earth system  
15 645 models (ESMs). The outputs of ESMs are already being used as forcing for ecosystem and  
16 646 fisheries models as part of the fisheries and marine ecosystem model inter-comparison project  
17 647 (Lotze et al. 2018, Tittensor et al. 2018). As for management scenarios, our model is able to  
18 648 look at the effects of both spatial and temporal measures. Projections of how temporal  
19 649 management measures (e.g. catch limits) will affect fish stocks are already commonplace in  
20 650 tactical management (see ICES 2018 for NEAM catch scenarios). Predicting the likely effects  
21 651 of spatial management measures is, however, more difficult. Because our model is spatially-  
22 652 explicit, and predicts the geographical distribution of the mackerel population, it should be  
23 653 able to capture the local effects of spatial measures on the appropriate subset of the  
24 654 population. For these reasons we think that our model could be used to make predictions  
25 655 about how changes in environmental and spatial harvesting scenarios may affect the stock.

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## 37 662 **Author contributions**

38 663 RB led the writing of the manuscript and model development. All authors contributed to  
39 664 model development and gave critical comments on each draft of the manuscript. All authors  
40 665 gave permission for submission having seen the final draft.

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