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A general approach to incorporating spatial and temporal variation in individual-based models of fish populations with application to Atlantic mackerel

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Abstract

Fish population dynamics are affected by multiple ecosystem drivers, such as food-web interactions, exploitation, density-dependence and the wider environment. While tactical management is still dominated by single-species models that do not explicitly account for these drivers, more holistic ecosystem models are used in strategic management. One way forward in this regard is with individual-based models (IBMs), which provide a single framework in which these drivers can be represented explicitly. We present a generic marine fish IBM that incorporates spatial and temporal variation in food availability, temperature and exploitation. Key features of the model are that it (1) includes realistic energy budgets; (2) includes the full life cycle of fish; (3) is spatially-explicit and (4) incorporates satellite remote-sensing data to represent the environmental drivers. The rates at which individuals acquire and use energy depend on local food availability and temperature. Their state variables, including life stage, size and energy reserves, are updated daily, from which population structure and dynamics emerge. To demonstrate the use of the model we calibrate it for mackerel (*Scomber scombrus*) in the North East Atlantic. Most parameters are taken from the literature, except the background early mortality rate and the strength predator density dependence, which were estimated by fitting the model to data using Approximate Bayesian Computation. The calibrated model successfully matches the available data on mackerel population dynamics and structure. We demonstrate the use of the model for management purposes by simulating the population effects of opening and closing a sector of the North Sea to mackerel fishing. Our model uses basic principles of behavioural and physiological ecology to establish how spatial and temporal variations in ecosystem drivers affect the individuals in the population. Population dynamics and structure are calculated from the collective effects on individuals. Application to a test case shows the method can fit available data well. Individual-based approaches such as this study have potential for use in strategic management because they can account for spatial structuring, food-web interactions, density dependence, and environmental drivers within a single framework.

Keywords: Atlantic mackerel, bioenergetics, energy-budget, individual-based model, spatially-explicit

43 **1 Introduction**

44 The aim of fish stock assessment is to enable management to maximise the long-term yield from a
45 fishery, without doing irreversible damage to the stock or wider environment (Hilborn and Walters,
46 1992). This traditionally involved estimating one or more reference points, such as spawning stock
47 biomass or the rate of exploitation, by fitting mathematical models to the available data on the
48 fishery and its population dynamics (Cadrin and Dicky-Collas, 2013). Increasingly, regulatory bodies
49 worldwide are adopting an ecosystem-based approach to fisheries management (Garcia and
50 Cochrane, 2005). This stems from the realisation that a stock's biological reference points will
51 depend on other components of the ecosystem, including food-web interactions, the associated
52 density-dependent processes (e.g. growth), and the wider environment (Skern-Mauritzen et al.,
53 2015). Accordingly, a variety of more holistic models have been developed that can account for
54 these drivers. Examples include age/size structured models such as OSMOSE (Shin and Cury, 2004,
55 2001) and LeMANS (Hall et al., 2006); food-web models such as Ecopath with Ecosim (Polovina,
56 1984); and multispecies oceanographic models such as Atlantis (Fulton et al., 2004). These
57 "ecosystem" models have been applied to strategic management questions, such as testing the
58 response of fish populations or communities to different fishing scenarios (e.g. Kaplan et al., 2013;
59 Thorpe et al., 2016; Travers et al., 2010).

60 The population effects of ecosystem drivers, including the wider environment, food-web interactions
61 and associated density-dependent processes, often arise from their effects on the constituent
62 individuals (Ward et al., 2016). Modelling these individual-level effects requires inclusion of
63 processes such as adaptive traits (e.g. physiology), variation among individuals and local interactions,
64 which traditional population models cannot easily accommodate (DeAngelis and Grimm, 2014). One
65 way forward in this regard is with individual-based models (IBMs, also called agent-based models)
66 (Grimm et al., 2005). In IBMs the lives of individual animals are simulated as they interact with each
67 other and their environment (DeAngelis and Grimm, 2014). Individuals have a unique set of state
68 variables (e.g. size and location), while the landscapes are often dynamic and characterised by
69 environmental drivers (McLane et al., 2011; van der Vaart et al., 2016). Individual's state variables
70 are updated when they interact with each other and their environment, and it is from simulation of
71 all the individuals that population dynamics and structure emerge. In this way, IBMs can incorporate
72 food-web interactions, density dependence and environmental drivers, and predict the fate of
73 populations in defined spatially-explicit landscapes that vary over time.

74 IBMs have long been applied to fish populations. A major area of interest has been the merger of
75 IBMs with bioenergetics as a way to model the response of populations to their physical and
76 biological environment (Lett et al., 2009). Initial focus was on the food and temperature dependence
77 of growth and survival in young-of-the-year fish (e.g. Bartsch and Coombs, 2004; Rose et al., 1999;
78 Scheffer et al., 1995). Since then, increasing computer power has permitted the development of
79 multi-generational bioenergetics IBMs that include the full life cycle (e.g. Politikos et al., 2015). It is
80 these IBMs that can address strategic management questions, including the effects of environmental
81 drivers on migrations and reproductive output, and the effects of fishing scenarios (Lett et al., 2009).
82 Because of their complex nature, existing full life cycle bioenergetics IBMs are typically species-
83 specific (e.g. Pethybridge et al., 2013; Politikos et al., 2015). Yet, there are many similarities among
84 species in terms of their energy budgets and the way they scale with body size and temperature. The
85 same functional forms often well describe the rates of energy uptake and its expenditure on vital
86 processes such as maintenance, growth and reproduction (Clarke and Johnston, 1999; Peters, 1983;
87 Sibly et al., 2013), raising the hope that a minimum generic bioenergetics model can be developed.

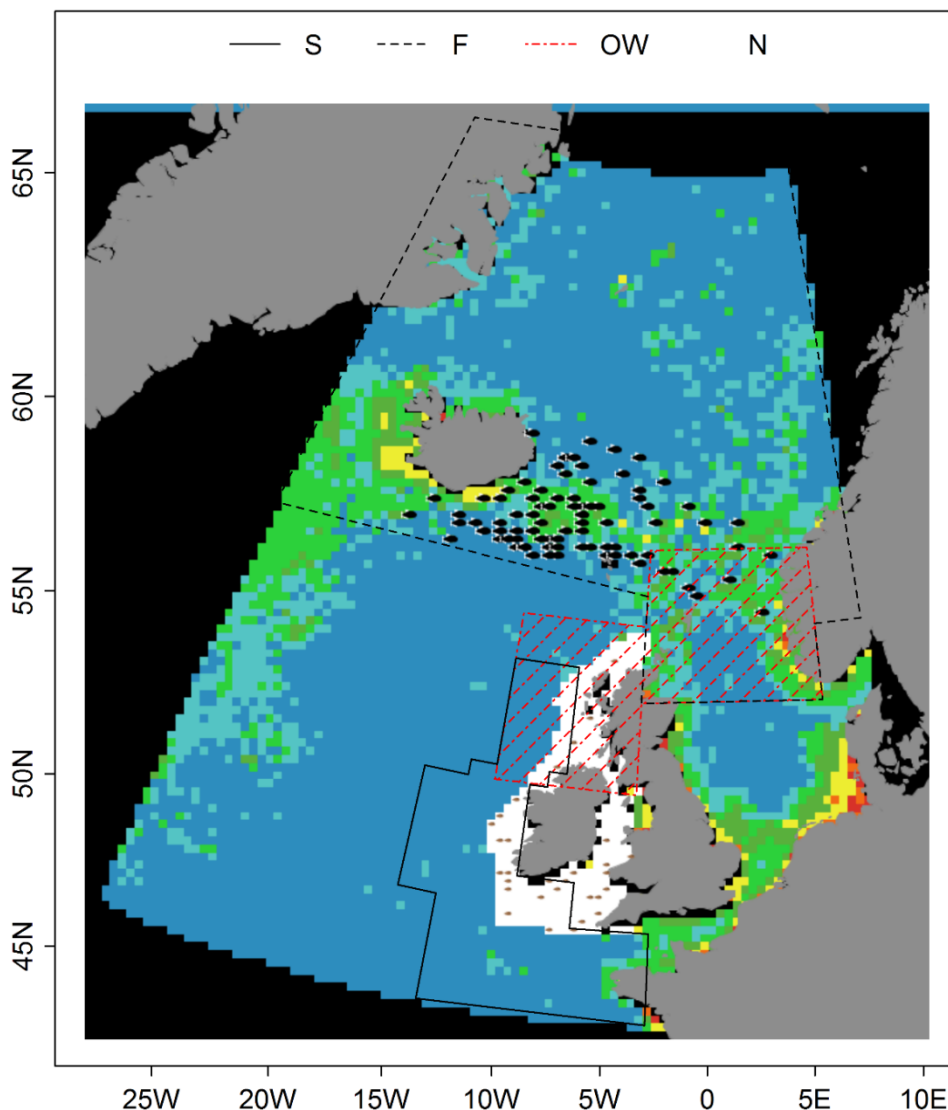
88 We present a generic marine fish IBM built on basic principles of behavioural and physiological
89 ecology (Sibly et al. 2013; van der Vaart et al. 2016). Our model is spatially-explicit, includes a
90 realistic energy budget and the full fish life cycle. The model landscape consists of dynamic maps of
91 two variables derived from satellite remote-sensing (RS): sea surface temperature (SST), and
92 chlorophyll concentration, a proxy for phytoplankton biomass, which we use to represent baseline

93 food availability. Individuals respond to their local food availability and SST according to their energy
94 budgets. To demonstrate the use of the model we calibrate it for the western component of the
95 North East Atlantic mackerel (*S. scombrus*) stock. We chose this particular stock to demonstrate the
96 potential of the IBM approach because (1) it is well-defined and subject to a specific management
97 regime; (2) density dependence within the stock is strong, both in terms of passive competition for
98 food (Jansen and Burns, 2015) and cannibalism (Fortier and Villeneuve, 1996); (3) its population
99 dynamics are sensitive to environmental drivers (e.g. recruitment) (Borja et al., 2002; Villamor et al.,
100 2011); (4) it is widely-distributed and has distinct spawning, feeding, overwintering and nursery
101 areas (Petitgas et al., 2010), meaning spatial variation in exploitation and environmental drivers are
102 important; (5) its wide distribution raises important management questions that cut across
103 international jurisdictions; and (6) there is much field data available on its population dynamics and
104 structure, and experimental data for parameterizing the energy budget. We report that the model
105 fits data on mackerel population dynamics and structure well, and demonstrate how it may be
106 applied by simulating the consequences of hypothetical spatial management scenarios.

107 **2 Methodology**

108 2.1 Model overview

109 In broad terms, the model landscape consists of dynamic maps of sea surface temperature SST and
110 food availability (Fig. 1). Fish are grouped into super-individuals (hereafter termed individuals), which
111 comprise a number of individuals with identical variables (Scheffer et al., 1995). Individuals move
112 around the landscape according to their life cycles (e.g. to spawn or feed) (Fig. 1). Each individual has
113 an energy budget which determines how its characteristics (e.g. body size, life stage, energy
114 reserves) change in response to local food availability (including smaller fish) and SST. Fishing
115 pressure at different locations determines the rate of mortality from exploitation. The abundance
116 represented by each super-individual when it enters the model at the egg stage is determined by the
117 amount of energy the spawning stock has put into egg production. Abundance reduces as mortality
118 is applied throughout life. Population measures are calculated as the sum of the characteristics of all
119 the individuals including their abundances. The model is implemented in Netlogo 5.3.1 (Wilensky
120 1999).



121

122 Figure 1. An example model interface showing potential spawning S (solid line), feeding F (dashed
 123 line), overwintering OW (dotted red line) and nursery (white filled) areas (referred to later). Black fish
 124 are adults, brown fish are juveniles and the colour of the landscape corresponds to phytoplankton
 125 biomass. Phytoplankton biomass and SST are obtained from satellite remote sensing, and the
 126 landscape is updated at regular intervals. This example is taken from the case study of Atlantic
 127 mackerel described later.

128 In the following we describe the generic model and its application to Atlantic mackerel. For a full
 129 technical specification see the “TRANSPARENT and Comprehensive model Evaluation” (TRACE)
 130 document (Augusiak et al., 2014; Grimm et al., 2014; Schmolke et al., 2010) in the supplementary
 131 material. In section 2 of the TRACE we provide a model description in the standard Overview, Design
 132 Concepts and Details (ODD) format (Grimm et al., 2010, 2006).

133 2.2 Generic model description

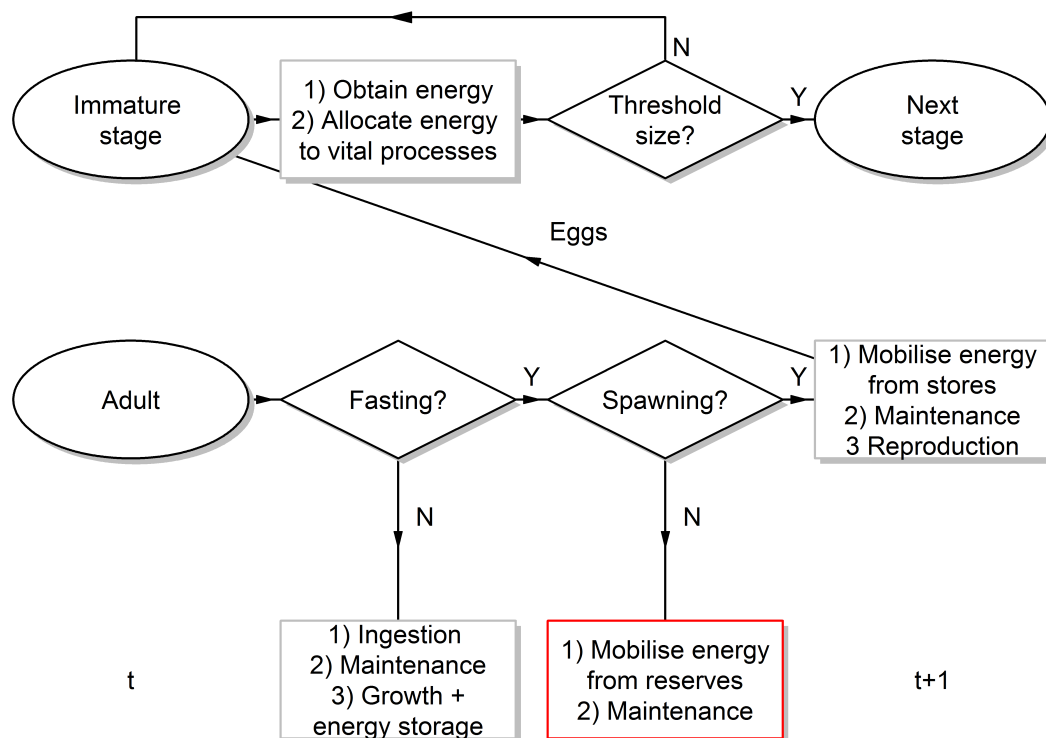
134 2.21 State variables and scales

135 The model landscape comprises a two-dimensional grid of patches of sea surface (Fig. 1). Each patch
136 is characterised by its baseline food density (phytoplankton biomass), sea surface temperature (SST),
137 latitude, longitude, area type (e.g. spawning, feeding, transitory), fishing division (see ICES.dk),
138 whether or not it is open to fishing, and depth. Fish populations are represented by a number of
139 individuals, characterised by age, gender, life stage (egg, yolk-sac larvae, larvae, juvenile or adult),
140 length, mass (structural, lipid and gonad) and abundance. The model proceeds in discrete daily time-
141 steps.

142 2.22 Model schedule

143 Full details of the model processes are given in section 2.23 (*Sub-models*). In each daily time-step,
144 phytoplankton, SST and fishing mortality F are updated first. Individuals begin their daily schedule by
145 calculating their mortality (see *Mortality*). Next, they calculate their swimming speed (*Swimming*
146 *speed*) and move (*Movement*). Individuals then calculate their energy budgets, except for
147 reproduction (*Energy budget*). Energy is allocated to different components of the energy budget,
148 depending on life stage and time of year (Fig. 2). Most state variables have been updated at this
149 point. If certain conditions are met, individuals proceed to the subsequent life stage
150 (*Transformation*). If in the spawning period, adults then calculate the costs of reproduction, allocate
151 energy to reproduction (*Energy budget*), and spawn. This involves the introduction of new individuals
152 (eggs) into the model in each year. Eggs then calculate their development (*Egg development*) and all
153 individuals age by one day. At the end of each time-step population measures are recorded. The
154 order in which individuals or patches carry out a given process is random.

155



156

157 Figure 2. Conceptual model showing the processes that individuals implement between time t and
 158 $t+1$. Individuals start as eggs, then become yolk-sac larvae at the end of their development period.
 159 They then grow to become larvae, juveniles and finally adults when reaching size thresholds.
 160 Juveniles can only become adults at a certain time of year. The first process in each day is obtaining
 161 energy, generally by ingestion, although yolk-sac larvae absorb energy from the yolk-sac. Obtained
 162 energy is allocated first to maintenance, with the remainder going equally to growth and energy
 163 reserves (except yolk-sac larvae which do not store energy, and larvae which prioritise growth). Red
 164 boxes indicate an effect of SST, and grey boxes an effect of SST and food availability.

165 2.23 Sub-models

166 In this section we provide details of the model processes. See TRACE section 2 for a full list of
 167 parameters; values of most parameters are taken from the literature.

168 *Swimming speed:* The speed at which individuals can sustainably swim S_a is given as a function of
 169 their body length L and their caudal fin aspect ratio A_r (Sambalay Jr, 1990). From this their daily search
 170 radius is calculated.

171 *Movement:* Movement patterns are species-specific so we do not provide a generic model.

172 *Energy budget:* The following sub-models describe the energy budgets of larvae, juveniles and adults
 173 (for overview see Fig. 2) in terms of individual physiology. We assume the yolk-sac provides sufficient
 174 energy for eggs and yolk-sac larvae to achieve maintenance and maximal growth/development rates.

175 *Temperature dependence:* We use the exponential Arrhenius function to describe the effects of
 176 temperature SST on rates of energy uptake and allocation. This has the form $e^{-E_a/K SST}$, where E_a is
 177 the activation energy and K is Boltzmann's constant.

178 *Food:* Other individuals within the focal individual's search radius and ≥ 3.5 times smaller (see Shin &
 179 Cury 2001) constitute potential prey. If multiple prey are available then one is chosen at random to
 180 be eaten. Food density (g m^{-2}) is calculated from the mass of the chosen prey and the predator's
 181 search area. The energy content of prey depends on how much lipid it has stored. When individuals
 182 do not overlap with potential fish prey they instead eat phytoplankton, which has an energy content
 183 E_p . Although most fish do not feed directly on phytoplankton, we use it as a proxy for baseline food
 184 availability because it provides a synoptic view of the base of the food chain.

185 *Ingestion and energy uptake:* Ingestion rate IR is given as a function of predator density D , food
 186 density X , SST and body surface area (body mass^{2/3}) (Kooijman and Metz, 1983), according to the
 187 Beddington-DeAngelis functional response (Beddington, 1975; DeAngelis et al., 1975). IR is converted
 188 from g day^{-1} to kJ day^{-1} using the energy content of food (kJ g^{-1}). A proportion of ingested energy, an
 189 assimilation efficiency A_e , becomes available for allocation to the processes in Fig. 2.

190 *Maintenance:* Standard metabolic rate SMR, the level below which an individual cannot survive (Fry,
 191 1971), is used as a baseline measure of maintenance. SMR scales with body mass M and with SST.
 192 For many species migrations represent a significant energy cost. We incorporate this by substituting
 193 SMR for an elevated active metabolic rate AMR (kJ day^{-1}) when migrating, given as a function of M ,
 194 SST and swimming speed.

195 *Growth:* Fish growth typically has a different form and rate in the first growing season than in later
 196 life. We use the sigmoid Gompertz function to describe growth rate in optimal conditions as a
 197 function of L and SST in the first growing season (Gluyas-Millan et al., 1998; Goldman, 2005; Sirnard
 198 et al., 1992). After reaching an age threshold G_{thresh} , growth switches to von Bertalanffy form (von
 199 Bertalanffy, 1938), again as a function of L and SST (Goldman, 2005). We assume that fish species
 200 which exhibit fasting periods grow only when feeding. Daily growth increment ΔL (cm) is converted
 201 to the difference in structural mass ΔM (g) using a standard allometric relationship (see FishBase
 202 weight-length table at www.fishbase.org and TRACE section 3). We define structural mass as body
 203 mass minus lipid stores and gonads. Growth costs are calculated using $\Delta M (E_c + E_s)$, where E_c is the
 204 energy content of flesh (kJ) and E_s is the energy costs of synthesising flesh (kJ g^{-1}). If insufficient
 205 energy is available to support maximum growth, the growth rate is reduced accordingly.

206 *Reproduction:* The energy cost of producing a maximum-sized batch of eggs B_{max} (kJ day^{-1}) is
 207 modelled as $B_{\text{max}} = F_p M_0 (E_c + E_s) / N_b$, where F_p is potential fecundity, M_0 is egg mass, E_c is the energy
 208 content of flesh, E_s is the cost of synthesising tissue and N_b is the number of batches produced. F_p is
 209 often related to body size (see FishBase fecundity table). For total spawners (i.e. $N_b = 1$) B_{max} equals
 210 the maximum total energy costs of spawning. For batch spawners energy is allocated to each batch
 211 over the inter-batch intervals. If less energy than B_{max} is available, batch size is reduced accordingly.
 212 We define gonad mass as equal to the mass of the eggs produced in a batch. This increases as energy
 213 is allocated to a batch, then is reset to zero when that batch is spawned. The egg production of all
 214 females is divided equally among n new individuals each year. We assume that male and female
 215 investment in reproduction is equal.

216 *Energy reserves:* Fish typically store energy as lipid (Martin et al., 2017). We propose that when
 217 feeding individuals can store lipid up to their maximum possible energy reserves E_{max} . The energy
 218 costs of synthesising lipid is accounted for when assimilated energy is converted to energy stores.
 219 The mass of stored lipid and, for adults, the gonads are added to structural mass to get total mass M .

220 *Egg development*: Egg development time D_e typically depends on temperature (Pepin, 1991) and can
 221 be modelled with an Arrhenius function.

222 *Transformation*: The transformations of eggs into yolk-sac larvae at length L_{hatch} , yolk-sac larvae into
 223 larvae, larvae into juveniles and juveniles into adults (sexual maturation) are defined using body
 224 length thresholds.

225 *Mortality*: The ways in which the number of individuals, or their sub-individuals, decrease are as
 226 follows. Starvation: If an individual's total mass reduces to its structural mass it dies. Explicit
 227 predation: Individuals die from the explicit portion of predation at rate M_{pred} , given as ingestion rate
 228 of the predator (g day^{-1}) / mass of prey (g). Background mortality: Eggs and larvae are susceptible to
 229 background mortality M_{back} at (typically very high) rate M_e . Juvenile susceptibility at length L is given
 230 by $M_{\text{back}} = M_a (L_{\text{mat}} / L)$, where M_a is a constant equal to adult mortality susceptibility (day^{-1}) and L_{mat}
 231 is the threshold length at which juveniles can sexually mature (Brodziak et al., 2011). Because M_{back}
 232 decreases with life stage or L , cumulative mortality depends on growth. Fishing mortality: Fishing
 233 mortality rates F (day^{-1}) at-age vary between years and are applied each day. F is set to 0 in areas that
 234 are closed to fishing (see *Hypothetical management scenarios* in section 2.3). Individuals with
 235 abundance < 1 are removed from the model.
 236

237 2.3 Application of the model to Atlantic mackerel

238 In the following we describe the model's application to *S. scombrus* in the North East Atlantic.

239 *Model landscape*: The model landscape spans from -30° W to 10° E and from 47° to 75° N.
 240 Landscape patches represent 30×30 km. Potential spawning, feeding, overwintering and nursery
 241 areas are shown in Fig. 1. The spawning area corresponds to the priority areas for sampling of *S.*
 242 *scombrus* eggs in the mackerel egg survey (MEGS, ICES, 2014b) in which $10^\circ\text{C} < \text{SST} < 12^\circ\text{C}$ (Sette,
 243 1943). The feeding area comprises all patches $\geq 62^\circ$ north and the northern North Sea (division 4a),
 244 above the lower temperature limit $\text{SST}_{\text{lim}} (> 7^\circ\text{C})$ (Nøttestad et al., 2016). The overwintering area is
 245 assumed to be ICES divisions 6a (west of Scotland) and 4a (northern North Sea). The nursery area
 246 includes all patches that are ≤ 200 m deep (Jansen et al., 2014) to the west of the British Isles ($< 4^\circ$
 247 west).

248 *Life cycle and spatial patterns*: In broad terms, eggs and larvae drift from the spawning towards
 249 nursery areas at a fixed rate; juveniles move locally in the nursery areas until maturing as adults; and
 250 adults cycle between spawning, feeding and overwintering areas. Migration triggers imposed, but
 251 arrival times in destination areas depend on an individual's swimming speed. Adults fast from
 252 November until after spawning the following year. See TRACE section 2 for full details.

253 *Data*: Input data includes fishing mortality F (day^{-1}), phytoplankton biomass (g m^{-2}), SST (kelvins) and
 254 bathymetry. F comes from the stock assessment as age-specific rates that vary annually.
 255 Phytoplankton biomass and SST were derived from data from the MODIS sensor on NASA's Aqua
 256 satellite (NASA OBPB, 2017a, 2017b). Eight-day composites are used at a spatial resolution of 30×30
 257 km. Bathymetric data was obtained from the British Oceanographic Data Centre. See TRACE section 3
 258 for details of data processing.

259 The model was calibrated with indices of spawning stock biomass (SSB) (Nøttestad et al., 2016,
 260 2015), total annual egg production (TEP) (ICES, 2017) and recruitment (Jansen et al., 2014).

261 Data on population structure used to validate the model included maturity ogives (from
 262 stockassessment.org), average weight-at-age (Nøttestad et al., 2016), monthly variation in the
 263 weight of 36 cm fish (Olafsdottir et al., 2016), and age (Nøttestad et al., 2016) and length
 264 distributions (ICES, 2017). Details of all data are given in section 2 of the TRACE.

265 *Initialization:* The population size and structure on January 1st 2007 was approximated using
 266 estimates of spawning (SSB) and total stock biomass (TSB), and length and age compositions from
 267 commercial catch samples (ICES, 2008) and bottom-trawl surveys (ICES, 2017). This population is
 268 then apportioned into 150 super-individuals. Each simulation begins with a 20-year spin up using
 269 2007 data in an annual loop. See TRACE section 2 for full details.

270 *Model simulations:* The model simulates the mackerel population from Jan 1st 2007 to December 31st
 271 2015. We represent the population with 150 individuals, representing a compromise between
 272 computational demands and realism. See TRACE section 8 for the sensitivity of model outputs and
 273 execution speed to changes in the number of individuals. Simulations are forced by F, phytoplankton
 274 biomass and SST. F at-age is updated each year and applied each day. SST and phytoplankton
 275 biomass are updated every eight days.

276 Outputs that are recorded annually include: SSB, the average weight at age, adult age distribution on
 277 the feeding grounds, TEP, recruitment (age 0), maturity ogives and length distributions at two times
 278 of the year. The average weight of 36cm individuals is also recorded monthly. All outputs are
 279 recorded to match the times at which corresponding data was collected (full details in TRACE section
 280 2).

281 *Local sensitivity analysis:* The sensitivities of predicted SSB, recruitment and egg production are
 282 presented as the change in output relative to 10% change in the energy budget parameters in Table
 283 1. Changes in outputs were averaged over an increase and decrease in the parameter, and over five
 284 simulations. While one parameter was tested all others were kept at their baseline values (TRACE
 285 section 2). See TRACE section 7 for a full list of parameters.

286 *Model calibration:* We calibrated the parameters background early mortality M_e and the strength of
 287 predator density dependence c using rejection approximate Bayesian computation (ABC), generally
 288 following the methodology of van der Vaart *et al.* (2015). This involved running the model 4500
 289 times, drawing M_e and c from uniform prior distributions and “accepting” the values that minimised
 290 the sum of the squared differences between the model outputs and the data. See TRACE section 3
 291 for full details.

292 *Hypothetical management scenarios:* To demonstrate the model’s potential to test spatial
 293 management strategies, we implemented two hypothetical scenarios: (1) closing the northern North
 294 Sea (ICES division 4a, see Fig. 5) to mackerel fishing all year; and (2) opening division 4a all year. In
 295 reality (and all other simulations) division 4a is closed from 15th February to 1st September (ICES,
 296 2014b). The closure of division 4a is designed to protect the smaller North Sea component of Atlantic
 297 mackerel which are found in the area (ICES, 2014b).

298 **3 Results**

299 3.1 Local sensitivity analysis

300 The sensitivities of SSB, recruitment and egg production to key model parameters are shown in
 301 Table 1. SSB is the most robust variable (relative sensitivities < 1 generally), and recruitment the
 302 least. In particular, recruitment is highly sensitive to the background early mortality rate M_e and the
 303 Gompertz growth constant k_1 . This is expected because M_e is very high and individuals are only
 304 susceptible to it until reaching a size threshold (3 cm), the duration of which is affected by k_1 . Hence
 305 these parameters jointly determine cumulative early mortality and recruitment.

306 Table 1. Sensitivities of SSB, recruitment and TEP to 10% changes in parameter values, presented as
 307 the change in output relative to change in parameter, averaged over ten simulations, and over an
 308 increase and decrease in the parameter value. Only the energy budget parameters are shown, along
 309 with their standard deviations

Parameter	Relative sensitivity of output		
	SSB	Recruitment	TEP
Normalizing constant for AMR (A_0)	0.14 ± 0.07	1.67 ± 1.25	1.31 ± 0.64
Assimilation efficiency (A_e)	0.38 ± 0.06	1.38 ± 0.48	0.95 ± 0.41
Strength of predator density dependence (c)	0.14 ± 0.05	1.58 ± 0.90	1.46 ± 1.07
Maximum consumption rate (C_{max})	0.35 ± 0.08	1.19 ± 0.50	1.31 ± 0.71
Activation energy (E_a)	0.24 ± 0.10	3.01 ± 0.82	1.38 ± 0.72
Half saturation constant (h)	0.22 ± 0.07	1.68 ± 1.87	1.53 ± 0.81
Bertalanffy growth constant (k)	0.17 ± 0.09	1.72 ± 1.30	1.06 ± 0.51
Gompertz growth constant (k_1)	0.18 ± 0.10	7.12 ± 1.66	1.68 ± 0.68
Maximum length after the first growing season (L_1)	0.10 ± 0.06	2.37 ± 1.28	1.38 ± 0.76
Asymptotic length (L_∞)	0.74 ± 0.05	1.44 ± 1.04	2.0 ± 0.84
Background adult mortality (M_a)	0.17 ± 0.05	1.65 ± 0.98	1.45 ± 1.10
Background early mortality (M_e)	0.11 ± 0.07	9.0 ± 1.90	1.77 ± 0.98
Normalizing constant for SMR (S_0)	0.15 ± 0.11	1.46 ± 0.94	1.58 ± 0.86

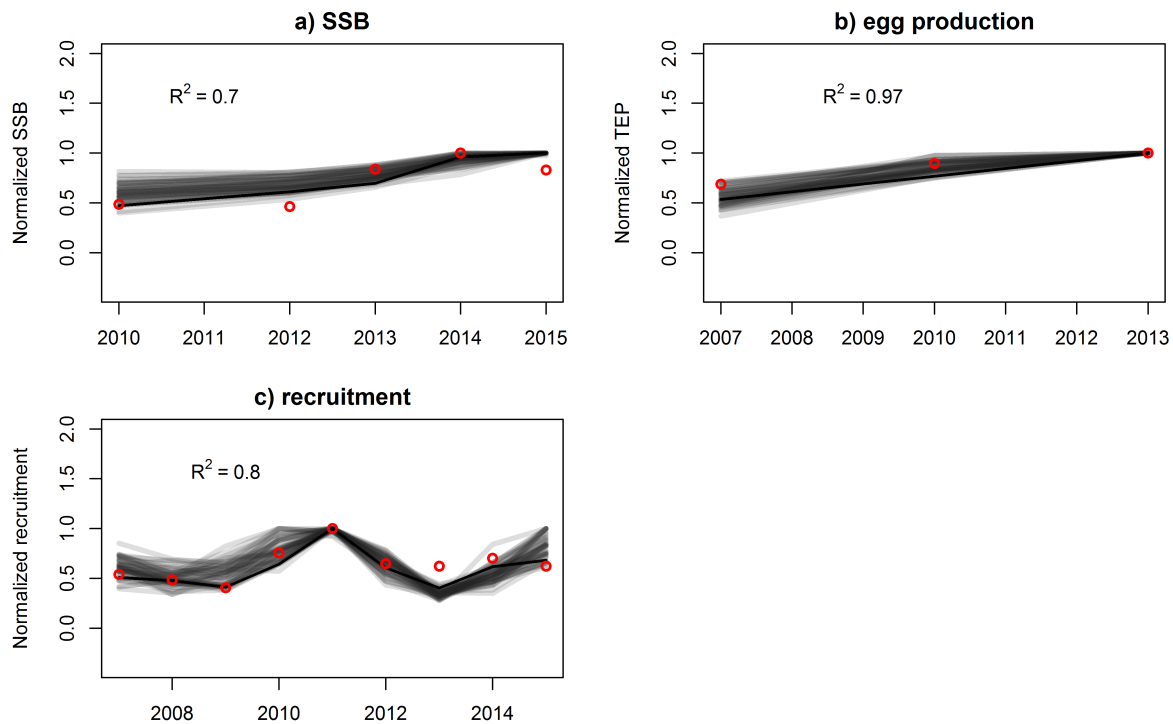
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311

3.2 Model calibration

312 M_e and c were calibrated from indices of SSB, TEP and recruitment using ABC. The values that
313 resulted in the best fits were $M_e = 0.325 \text{ day}^{-1}$ with credible interval 0.292 – 0.327, and $c = 0.98 \times 10^{-12}$
314 with credible interval $1.18 \times 10^{-13} - 4.86 \times 10^{-12}$. These were obtained from the best-fitting 1% of the
315 4500 simulations. The posterior credible intervals were significantly narrower than those of the
316 priors (Levene's test, $p < 0.01$), meaning the data had leverage over their values. See TRACE section 3
317 for cross validation and a comparison of the prior and posterior distributions.

318 To determine the goodness of fit between the model predictions and the survey indices of
319 population dynamics used for calibration, we used the coefficient of determination (R^2), i.e. the
320 proportion of the variance explained. The model predictions and survey indices for SSB, TEP and
321 recruitment are shown in Figs. 3a, b and c, respectively. Overall the fits are good, as indicated by R^2
322 values of 0.70, 0.97 and 0.80, respectively. The data used for calibration are relative indices, but see
323 TRACE section 8 for a comparison with the stock assessment's estimates of SSB and recruitment on
324 an absolute scale.

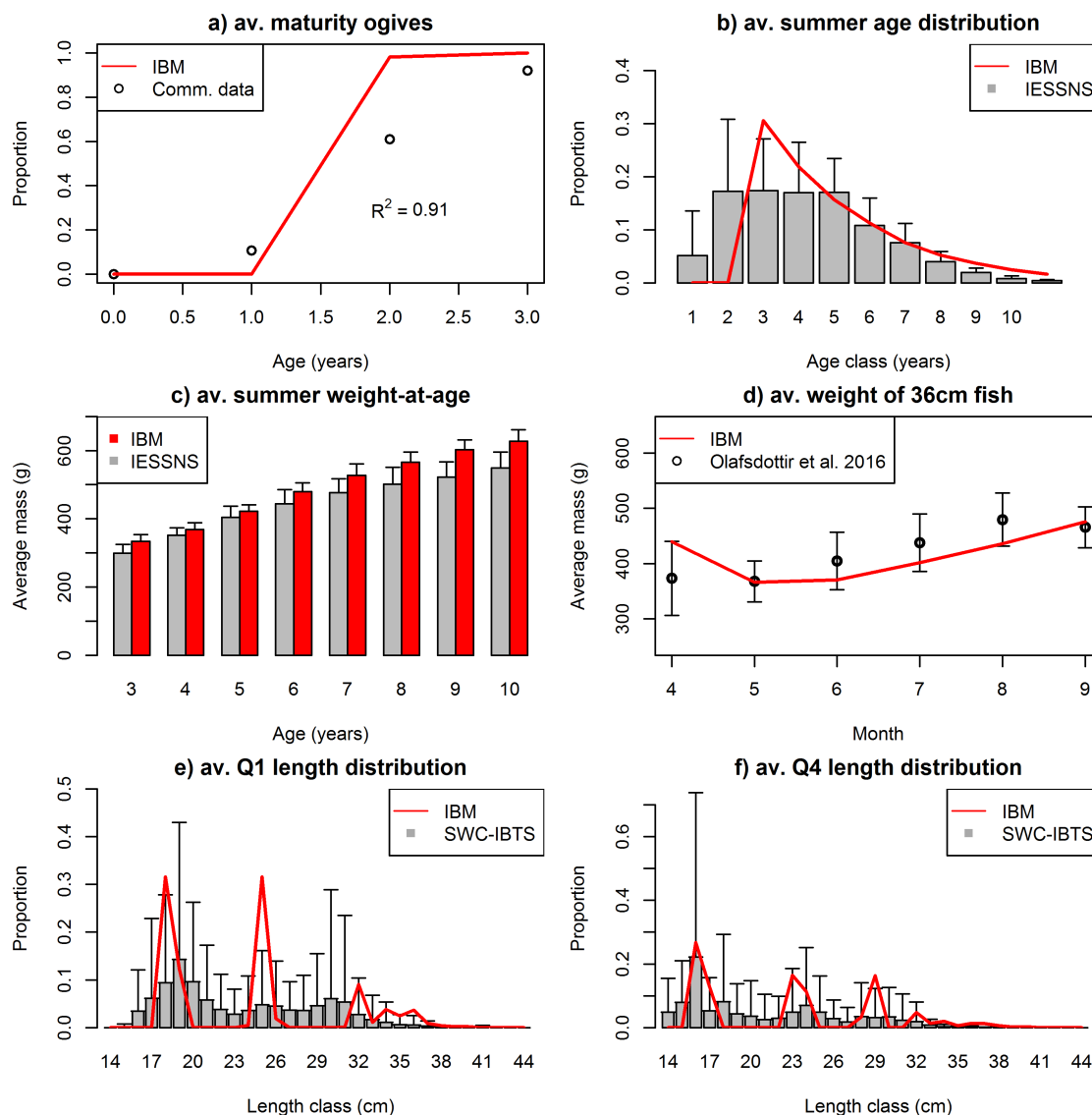


325

326 Figure 3. Fits of the best-fitting 1% of simulations from ABC (transparent lines with the single best-
 327 fitting simulation in black) to the survey indices (red circles) of: a) SSB from the International
 328 Ecosystem Survey in the Nordic Seas (IESSNS) on the feeding grounds in July-August of 2010 and
 329 2012 to 2015; b) TEP from MEGS in 2007, 2010 and 2013; and c) recruitment (see Jansen *et al.*,
 330 2014). Only outputs from the years with data are presented. Outputs and data were each
 331 normalized by dividing by their maximum value. R^2 values from the best-fitting simulations are
 332 presented on the plots

333 3.3 Model validation

334 To validate the model, we compared the predicted population structure to data. Fig. 4 shows the
 335 model predictions and data averaged over 2007 to 2015, except Fig. 4d where the data is averaged
 336 over 1984 to 2013. The proportion of each age class that is sexually mature in February is shown in
 337 Fig. 4a. The model and data agree that most individuals reach sexual maturity when aged two,
 338 although there is more variability in the age at maturity in the data. Fig 4b shows the age distribution
 339 on the feeding grounds in summer. The model predicts an absence of one or two-year-olds. The data
 340 suggests that there are few one year olds, but that two year olds are among the most abundant age
 341 groups. From the age of three both the model and data show a characteristic type 3 survivorship
 342 curve, i.e. declining abundance at age. Fig. 4c shows the mean weight at age three to ten in summer.
 343 The model matches the data well, albeit with a slight overprediction in older individuals. Fig. 4d
 344 shows the average weight of 36 cm mackerel (approximately 5 years old) from April to September.
 345 The model and data show a similar increase in weight-at-length each month. Figs. 4e and f show
 346 length distribution in ICES division 6a (West of Scotland) in quarters 1 (Q1) and 4 (Q4). The
 347 distributions have multiple modes, each representing a cohort. Predicted modal length of ages zero
 348 to two are all matched to within one cm, other than age two in Q1. However, within each cohort
 349 predicted length has considerably less variability than the data. Overall the model matches the
 350 observed population structure well, which supports our representation of the energy budget.

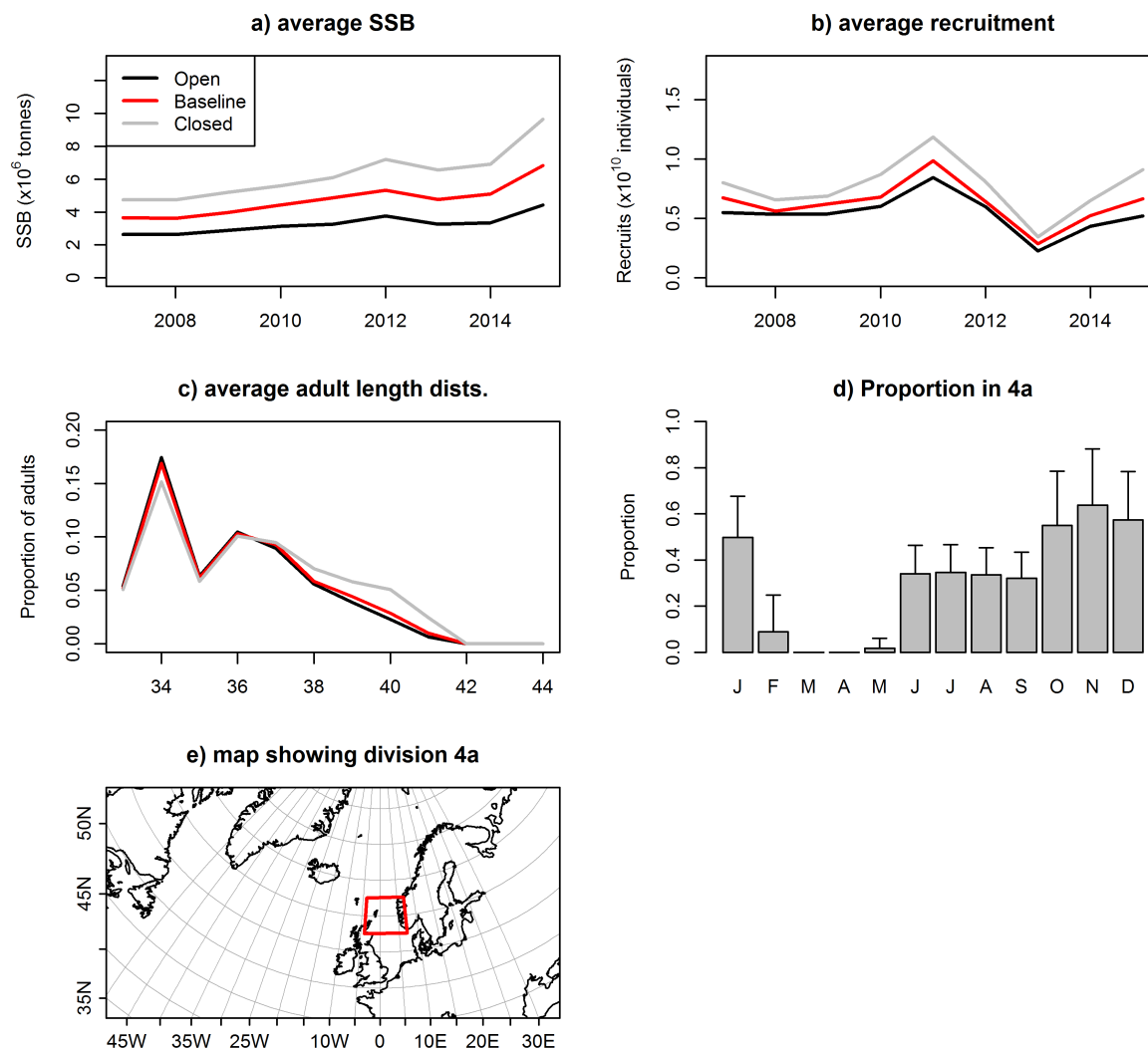


351

352 Figure 4. Comparisons of the IBM predictions with various data averaged over 2007 to 2015 on: a)
 353 proportion mature at age from sampling of commercial catches in quarter 1; b) the age distribution
 354 on the feeding grounds in July from the International Ecosystem Survey in the Nordic Seas (IESSNS);
 355 c) the average weight-at-age from the IESSNS in July; d) monthly variation in the average weight of
 356 36 cm fish (Olafsdottir et al., 2016); and e) and f) length distributions from the Scottish West Coast
 357 International Bottom-Trawl Survey (SWC-IBTS) in quarters 1 and 4 respectively. Dots show mean
 358 values and whiskers the standard deviation

359 3.4 Hypothetical management scenarios

360 To demonstrate how the model may be used in a management context, we simulated two
 361 hypothetical scenarios, in which ICES division 4a was (1) closed year-round and (2) open year-round,
 362 in addition to the baseline (closed 15th February to 1st September). Figs. 5a – c show how SSB,
 363 recruitment and the length distribution of large individuals (≥ 33 cm) on February 1st differ under
 364 each scenario. Fig. 5d shows the proportion of adults in division 4a averaged over each month of the
 365 year for reference. SSB and recruitment are highest, and length distribution is more skewed towards
 366 large individuals, when division 4a is closed, followed by the baseline then open. These results are
 367 expected but highlight the model's ability to test the consequences of spatial management
 368 scenarios.



369

370 Figure 5. Simulated a) SSB, b) recruitment and c) length distributions of large ($\geq 33\text{cm}$) fish, all on
 371 February 1st, when ICES division 4a was open to fishing year round (open), open to fishing only from
 372 Feb 15th to Sep 1st (baseline) and closed year round (closed). Predictions are averaged over five
 373 simulations in each scenario. Panel d) shows the mean proportion of the population in division 4a
 374 in each month of the year, averaged over 15 simulations, with error bars showing standard deviations.
 375 Panel e) shows the location of division 4a.

376 4 Discussion

377 We have developed, calibrated and evaluated a generic IBM which relates fish population dynamics
 378 and structure to spatial and temporal variation in food availability, temperature and exploitation.
 379 Key features of the model are that it (1) includes a realistic energy budget; (2) includes the full life
 380 cycle; (3) is spatially-explicit and (4) incorporates satellite remote-sensing (RS) data to represent the
 381 environmental drivers. To demonstrate the use of the model we calibrated it for mackerel in the
 382 North East Atlantic and showed it successfully matches the available data on population dynamics
 383 (Fig. 3) and population structure (Fig. 4). We then showed the model's ability to test the population
 384 consequences of simple hypothetical management scenarios (Fig. 5).

385 Model fits to the data on mackerel population structure (Fig. 4) give insight into how well different
 386 aspects of the energy budget are represented. For example, we consider growth in length to be
 387 reasonable because individuals reach sexual maturity at about the right age (Fig. 4a), which is
 388 determined by length, and because the modes of the length distribution of different cohorts match

389 well at two different times of year (Figs. 4e and f). However, there is less variability in the predicted
390 length of individuals in a cohort than in the data. One reason could be that each cohort in the model
391 is represented by a small number (ten) of super-individuals, chosen for computational reasons. We
392 consider growth in mass to be reasonable because predicted weight-at-age in summer matches the
393 data well (Fig. 4c). Storage of lipid when feeding in summer is reflected in increased weight-at-length
394 and is supported by the good model fit to data on the monthly variation in the weight of 36cm
395 individuals (Fig. 4d). Lastly, total mortality is reasonable because the adult age distribution in
396 summer is matched well (Fig. 4b). The model also fits data on the mackerel population dynamics that
397 were used for calibration well (Fig. 3). However, it is because they were not used for calibration that
398 we consider the data on population structure to support our energy budget structure.

399 The main advantage of the IBM approach is that it provides a single framework that can explicitly
400 incorporate food web interactions, environmental drivers, density dependence and spatial
401 structuring. This allows the model to capture two key processes that affect recruitment in many
402 species. Firstly, the model captures the generally-accepted “growth-mortality hypothesis”
403 (Anderson, 1988; McGurk, 1986; Ware, 1975). Larval and juvenile background mortality decreases
404 with body size. As a result, cumulative survival in a cohort depends on its growth rate, and hence
405 food availability, temperature and the density of competitors. The predator-prey size ratio also
406 dictates that individuals become less vulnerable to explicit predation with increasing size. Secondly,
407 the model captures the effects of parental condition on spawning success, which has been shown for
408 many taxa (Mcbride et al., 2015). The initial abundance of a cohort (i.e. the number of eggs initially)
409 depends on the amount of energy the spawning stock is able to accumulate before spawning. This
410 depends on the history of food availability, temperature and density of competitors when adults
411 were last feeding (see TRACE section 8 for more details). In sum, recruitment in the model emerges
412 from parental condition and early survival. Predictions are process-based and should be less
413 vulnerable to the problems of extrapolation than those obtained from standard stock-recruitment
414 curves.

415 We hope the model will be used to explore the effects of multiple ecosystem drivers in future. We
416 have demonstrated its ability to test the population consequences of management scenarios by
417 simulating hypothetical fishery closures in one sector of the North Sea. These simple scenarios
418 produced expected population responses (Fig. 5), but highlight how it may be applied going forward.
419 This feature is in demand because spatial management in fisheries is increasingly prevalent (Halpern
420 et al., 2012), whether as no-take zones like marine protected areas, or more nuanced measures such
421 as spatially-explicit quotas (Rassweiler et al., 2012). Alongside the effects of fishing, the model could
422 also be used to explore the effects of climate change. This may involve coupling the model to lower
423 trophic level biogeochemical and hydrodynamics models, which can provide various forcing variables
424 under climate change scenarios. One particular application could be to investigate change in fish
425 distribution in response to increasing in SST, and its implications to management.

426 Although we parameterised the model for mackerel in the North East Atlantic, it should be
427 applicable to other species and locations. This is because: (1) the energy budget is based on
428 fundamental principles of behavioural and physiological ecology and incorporates generic laws for
429 the scaling of energy uptake and expenditure with body mass and temperature (Sibly et al., 2013);
430 (2) it captures key processes that relate the environmental drivers to the population structure and
431 dynamics of many species, such as the effects of parental condition and early survival on
432 recruitment; and (3) the RS data is freely-available and has global coverage. Although RS-based
433 estimates of SST and chlorophyll come with a certain level of uncertainty associated with the
434 satellite retrievals, the level of these random errors are generally bounded (often <30%,GCOS
435 2011)). Moreover, with the continuous improvement of the quality of satellite data, the error
436 propagation through the model arising from the model inputs will be greatly reduced. As such we
437 hope that the model location and extent can be changed to utilize the satellite data matching the
438 distribution of the chosen species, and that it will be mainly the values of the parameters that will

439 need to be changed for different species, many of which can be found at FishBase. The model should
 440 also be able to accommodate multiple species, because interactions can occur via density dependent
 441 effects on ingestion, or by explicit size-based predation. Unlike previous generic marine fish IBMs,
 442 e.g., OSMOSE (Shin and Cury, 2004, 2001), our model includes bioenergetics, and we hope it will
 443 provide a step towards broadly applicable bioenergetics IBMs.

444 The main caveat of our generic approach is that fish populations exhibit a wide range of spatial
 445 patterns that vary over their ontogeny and thus it is not possible to provide a generic movement
 446 sub-model. Users will need to devise algorithms appropriate to the species being modelled. In this
 447 study we approximated spawning, feeding, overwintering and nursery areas geographically from
 448 various sources. We were able to further delineate these areas by environmental features, such as
 449 SST and depth, using information on *S. scombrus* from the literature. However, in the current model
 450 formulation, movement within each habitat type follows a random walk, and migration triggers are
 451 hard-wired. One goal of future work should be to develop a more realistic movement model. For
 452 example, the approach of Politikos et al. (2015) could be followed, using survey data on the spatial
 453 distribution of a species to construct environmentally-driven movement algorithms. Moreover, the
 454 delineation of different habitat types could be informed by habitat suitability modelling (e.g. Brunel
 455 et al., 2017; Morris and Ball, 2006). In this way a population's spatial distribution can become an
 456 emergent feature of the model just as its population dynamics are now.

457 IBMs can play an important role in conservation planning and wildlife management (McLane et al.,
 458 2011), and we hope that this work will benefit the fisheries management community. IBMs
 459 represent a single framework in which food-web interactions, density dependence, spatial
 460 structuring and the wider environment can be incorporated, thus being consistent with the
 461 ecosystems approach to fisheries management. The effects of these drivers on fish populations
 462 typically arise from their effects on the constituent individuals (Ward et al., 2016). Explicit
 463 incorporation of these drivers makes IBMs an improvement on age/size structured models. The basis
 464 for our model is a realistic energy budget, which represents a mechanistic framework by which the
 465 ecosystem drivers affect the characteristics of the individuals. Population measures are then
 466 calculated as the sum of these characteristics. This means that predictions of population-level
 467 processes such as recruitment emerge rather than being parameterised. Going forward our model
 468 can be used to address several strategic management questions, including the population
 469 consequences of different management and environmental scenarios.

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478 **Author's contributions**

479 SR, RS, RT and KH acquired funding for the project. All authors contributed the conception of the
 480 paper and design of the methodology. RB, RS and SR led the writing of the manuscript. All authors
 481 contributed critically to the drafts and gave final approval for publication.

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