

*A spatially explicit individual-based model  
to support management of commercial  
and recreational fisheries for European  
sea bass *Dicentrarchus labrax**

Article

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1 **A spatially explicit individual-based model to support**  
2 **management of commercial and recreational fisheries for**  
3 **European sea bass *Dicentrarchus labrax***

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18 **Abstract**

19 The European sea bass (*Dicentrarchus labrax*) is a slow growing and late maturing  
20 high value fish that is exploited by both commercial and recreational fisheries. In  
21 recent years, scientific assessments have shown a rapid decline in spawning stock

22 biomass around the UK attributed to poor recruitment (driven by environmental  
23 factors) and high fishing mortality. This resulted in significant reductions in the  
24 harvest of sea bass following technical measures implemented by the European  
25 Commission to conserve stocks. Individual-based models (IBMs) are simulations  
26 of individual ‘agents’ of organisms that interact with each other and their  
27 environment locally and have been shown to be effective management tools in  
28 many systems. Here, an IBM that simulates the population dynamics and spatial  
29 distribution of sea bass was developed to assess how technical management  
30 measures applied to subsets of the population impact the overall stock.  
31 Conventional stock assessment techniques were used to model the processes  
32 affecting population dynamics, while the spatial distribution was simulated using a  
33 combination of temperature preferences and information from tagging studies. The  
34 IBM was parameterised using existing knowledge from the literature and can mimic  
35 key assessment outputs used to inform management and advice on fishing  
36 opportunities. Utility of the IBM is demonstrated by simulating the population  
37 consequences of several key management scenarios based on those implemented  
38 by the European Commission, including short-term bans on pelagic trawling in  
39 spawning areas, commercial and recreational catch limits and increasing the  
40 minimum conservation reference size. The IBM has potential to complement the  
41 annual stock assessment in managing European sea bass because it models  
42 individual movement, environmental drivers and emergent spatial distribution,  
43 thereby providing enhanced predictions of management strategy outcomes that  
44 could inform spatial advice on fishing opportunities and policy.

## 45 **Keywords**

46 European sea bass; individual-based model; management; spatially explicit

## 47        **1. Introduction**

48        The Northern stock of European sea bass (*Dicentrarchus labrax*), covering the North  
49        Sea, English Channel, Celtic Sea and Irish Sea, is an important target for both  
50        commercial and recreational fisheries, with recreational fisheries responsible for over  
51        a quarter of the total catch (Hyder et al., 2018; Radford et al., 2018). The commercial  
52        fishery developed rapidly in the late 1970s (Pawson et al., 2005) and fishing mortality  
53        has increased since then reaching a maximum in 2013. As a result of fishing pressure  
54        and poor recruitment, the stock has declined drastically over the past decade and was  
55        estimated below management reference points in 2018 (ICES, 2018a). Emergency  
56        management measures were introduced in 2015 and legislation is becoming  
57        increasingly strict for both recreational and commercial fisheries, including restrictions  
58        on the amount of catch, such as daily bag limits on the number of fish taken per  
59        recreational fisher and monthly catch limits for commercial vessels, as well as spatial  
60        restrictions such as closed seasons and areas (European Commission, 2015a). To  
61        make decisions about which measures will be most effective, there is a need to explore  
62        the impact of these measures on the current population and make predictions about  
63        how they will affect the population in the future.

64        Sea bass in the northern stock are relatively slow growing, reaching up to 30 years of  
65        age and maturing at around 4 to 6 years (Pawson and Pickett, 1996). They have a  
66        complex lifecycle with a pelagic larval phase, juveniles then occupy nursery grounds,  
67        generally located within inshore areas, before joining the adult population. Mature sea  
68        bass follow extensive migrations between inshore summer feeding areas and winter  
69        pre-spawning and spawning areas. Movement between areas is rapid and occurs  
70        around April to May, at the end of spawning, and between October and December as  
71        females seek warmer water (Pawson et al., 2007, 1987). There is strong evidence that

72 feeding areas are specific to local populations (Doyle et al., 2017; Pawson et al., 2008),  
73 while spawning generally occurs in the Celtic and southern North Seas between  
74 February and June. The geographic extent of spawning is thought to be bounded by  
75 a minimum temperature of 9°C meaning it can expand as the season progresses and  
76 in warmer years (Pickett and Pawson, 1994). The pelagic phase lasts between 2 to 4  
77 months (Jennings and Ellis, 2015) during which time dispersal brings a proportion of  
78 the larvae to the vicinity of nursery grounds in estuaries, saltmarshes and other  
79 sheltered coastal sites (Beraud et al., 2018).

80 The Northern sea bass stock is assessed by the International Council for the  
81 Exploration of the Sea (ICES) using Stock Synthesis (SS3; Methot and Wetzel, 2013):  
82 an analytical size- and age-structured population model. In broad terms, SS3 includes:  
83 1) a population dynamics model, which simulates growth, mortality and recruitment; 2)  
84 an observation model which relates the population dynamics to available data; and 3)  
85 a statistical model which estimates parameters to maximise the goodness of fit  
86 between population model and data. Stock status is determined by comparing outputs  
87 from SS3 to reference points considered consistent with obtaining maximum  
88 sustainable yield (MSY, i.e. the largest long-term yield that can be taken without  
89 causing the stock to collapse) and keeping the stock within safe biological limits  
90 (termed precautionary reference points). Outputs from SS3 are used as a starting point  
91 to project the population effects of various catch scenarios, with the objective of setting  
92 catch advice for the following year (ICES, 2018a). SS3 includes a “multi-area”  
93 configuration, where a stock can be sub-divided into multiple geographical units  
94 (Methot and Wetzel, 2013). However, this implicit spatial structure is limited in its ability  
95 to forecast the consequences of spatially explicit management measures. A more  
96 appropriate approach for evaluating spatially explicit management measures is to

97 develop models that can make predictions about the distribution of a stock, and hence  
98 capture the localized effects of those measures on the appropriate subset of the  
99 population.

100 The most widely used approach for predicting spatial distributions of fish populations  
101 is with correlative species distribution models (SDMs; Robinson et al., 2017). SDMs  
102 relate the abundance and/or occurrence of fish to environmental variables and can be  
103 used to generate maps of habitat suitability. While habitat suitability is an important  
104 determinant of a stock's spatial distribution, the degree to which potential habitat can  
105 be utilised depends on constraints to movement such as physical barriers and  
106 dispersal capacities. One way to account for these constraints is by explicitly  
107 simulating the movement of individuals. This can be achieved using individual-based  
108 models (IBMs) where animal populations are represented by their constituent  
109 individuals in spatially explicit landscapes, and population dynamics and structure  
110 emerge from the actions of all individuals (Grimm and Railsback, 2005; van der Vaart  
111 et al., 2016). As well as allowing for explicit simulation of individual movements, IBMs  
112 can incorporate population dynamics models such as those in SS3 (e.g. growth and  
113 mortality modules). The difference is that the population dynamics go from being size-  
114 and/or age-based, to size-, age- and individual-based to allow for variability among  
115 individuals of the same age or size group. As such, IBMs are now widely used to  
116 simulate the spatial distribution of fish populations (e.g. Heinänen et al., 2018; Watkins  
117 and Rose, 2017), as well as population size and structure (Boyd et al., 2018, 2020;  
118 Bueno-Pardo et al., 2020; Politikos et al., 2015).

119 We present a spatially explicit IBM that simulates the population dynamics and spatial  
120 distribution of the Northern sea bass stock. The model landscape consists of dynamic  
121 maps of sea surface temperature (SST) that influence growth, movement, migrations

122 and spawning. Spatial distribution is simulated using a combination of known  
123 temperature preferences and extensive information from tagging studies. The  
124 population dynamics are based on conventional stock assessment techniques and are  
125 conditioned on SS3 parameterisations for the Northern sea bass stock. We compare  
126 the IBM's predictions of abundance, spawning (SSB) and total stock biomass (TSB)  
127 to those from SS3 and the predicted spatial distribution to independent data from  
128 commercial catches. Finally, we demonstrate the utility of the IBM by predicting the  
129 population consequences of several management scenarios, including: (1) short-term  
130 bans on pelagic trawling in offshore spawning areas; (2) commercial and recreational  
131 catch limits; and (3) increasing in the minimum conservation reference size (MCRS).  
132 The potential use of IBM in managing fishing opportunities for sea bass is discussed  
133 and avenues for further research and model developments highlighted.

## 134 **2. Material and methods**

### 135 **2.1. THE MODEL**

136 Conventional stock assessment techniques and parameterisations were combined  
137 with hypotheses drawn from 20 years of tagging studies (Pawson et al., 2007, 1987)  
138 to construct a spatially explicit individual-based model (IBM) of sea bass dynamics.  
139 Here we provide a summary description of the IBM. A full description following the  
140 ODD (Overview, Design concepts, Details) protocol for describing individual- and  
141 agent based models (Grimm et al., 2010, 2006) is provided in a TRACE (TRANSPARENT  
142 and Comprehensive model Evaluation; Augusiak et al., 2014; Grimm et al., 2014;  
143 Schmolke et al., 2010) document forming the supplementary material. The IBM is  
144 implemented in NETLOGO version 5.3.1 (Wilensky, 1999).

#### 145 **2.1.1. Overview**



146 The model environment is composed of a grid landscape of 36 x 38 patches (grid  
147 cells), representing the area from 9°E to 9°W and 48°N to 57.5°N, where each group  
148 of four patches represents an ICES statistical rectangle (rectangles of 30 min latitude  
149 by 1 degree longitude used for gridding of data). Sea patches are characterised by  
150 dynamic variable sea surface temperature (SST; a key driver of sea bass dynamics;  
151 Pickett and Pawson, 1994; TRACE Section 4) and variables for patch type (coastal  
152 patches are those within an ICES rectangle that intersects land, offshore patches are  
153 all remaining sea patches, spawning patches are described in Section 2.1.3.1 and  
154 nursery patches are those south of 54°N intersecting land; Beraud et al., 2017; Kelley,  
155 1988), ICES division (4.b, 4.c, 7.a, 7.d, 7.e or 7.fg) and region (North Sea, English  
156 Channel, Celtic Sea or Irish Sea). ICES divisions and regions are mutually exclusive  
157 while patch types are not, as all nursery patches are coastal, and all spawning patches  
158 are offshore (Figure 1). For simplicity, we assume the population is closed to  
159 migrations outside the model domain.

160 To render model run times tractable, the sea bass population is modelled with super-  
161 individuals (hereafter termed individuals) each of which represents many fish with  
162 identical state variables (Scheffer et al., 1995). Individuals are characterised by the  
163 number of fish represented, age, cohort age (integer age of the year class), life stage  
164 (juvenile < 6 years or adult/mature aged 6+), length, weight, location, swimming speed  
165 and daily direction changes, spawning trigger and counter, mortality rates (natural,  
166 commercial inshore and offshore- and recreational-fishing) and the division they have  
167 an affinity to feed in. Sea bass variables and processes are described further in  
168 Section 2.1.3.

169 The model runs in daily time steps from 1<sup>st</sup> January 1985 to the 31<sup>st</sup> December 2014,  
170 just prior to the implementation of emergency management measures in 2015. In each

171 time step, individuals follow five main processes, all constructed from several  
172 submodels: *growth, mortality, movement, aging and reproduction*. Figure 2 provides a  
173 conceptual overview of the processes and submodels represented in the IBM.

### 174 **2.1.2. Initialisation**

175 The population is initialised using numbers-at-age data estimated for 1985 (ICES,  
176 2018b; TRACE Section 3) apportioned into ten super-individuals per cohort (year  
177 class). Individuals in the juvenile life-stage that are less than four years old are  
178 distributed randomly in nursery patches, juveniles 4–6 years in coastal patches and  
179 the adult life-stage in pre-spawning areas (coastal patches in division 7.e; Figure 1).  
180 Each mature individual is assigned a random ICES division for which it has an affinity  
181 to feed.

### 182 **2.1.3. Processes**

183 Here we describe the model processes. Detailed descriptions of submodels,  
184 parameters, input data and underlying assumptions are provided in the TRACE  
185 document. Aside from *patch updates* (Section 2.1.3.1) the following processes relate  
186 to sea bass individuals and, unless otherwise stated, are executed daily in the  
187 following order:

#### 188 **2.1.3.1. Patch updates**

189 The SST of patches are updated monthly using data from the Operational Sea Surface  
190 Temperature and Sea Ice Analysis data set (OSTIA; <http://marine.copernicus.eu/> )  
191 averaged over the month. Between February–May any offshore patches south of 54°N  
192 with an SST value between 9–15°C are assigned as spawning patches (Beraud et al.,  
193 2018; Kelley, 1988; Thompson and Harrop, 1987).

194        2.1.3.2.    *Growth*

195    Each individual increases its length according to Fabens (1965) manipulation of the  
196    von Bertalanffy growth equation adjusted for the effects of temperature on growth  
197    (TRACE Section 2). The mean weight of fish within an individual is calculated from  
198    length following the allometric equation. Both equations are parameterised with the  
199    same parameter values used in the stock assessment (ICES, 2018b).

200        2.1.3.3.    *Mortality*

201    The number of fishes within an individual decline exponentially due to natural and  
202    fishing mortality. Natural mortality occurs due to factors such as predation and disease  
203    and is taken as a fixed instantaneous rate of 0.24 (year<sup>-1</sup>; ICES, 2018b; TRACE  
204    Section 3) converted to a daily rate.

205    Commercial fisheries operating in the Northern management unit are considered to  
206    have two distinct components catching different subsets of the population throughout  
207    their life and migration cycles: (1) offshore fisheries on pre-spawning and spawning  
208    bass; and (2) small-scale inshore fisheries catching immature bass and mature bass  
209    returning to coastal feeding areas (ICES, 2012). Partial fishing mortality estimates by  
210    age and metier derived from the stock assessment outputs (ICES, 2018b) were  
211    therefore aggregated to give annual fishing mortality rates-at-age for three broad  
212    fleets: commercial inshore, commercial offshore and recreational (TRACE Section 3).  
213    Fishing mortality varies across patches such that when an individual occupies an  
214    inshore patch only the commercial inshore and recreational fishing mortality rates are  
215    applied, and when an individual occupies an offshore patch only the offshore fishing  
216    mortality rate is applied. Commercial fishing mortality rates are raised to account for  
217    the fact that fishing does not occur all year round. The commercial offshore fleet is

218 assumed to operate predominantly between November and April (ICES, 2012) and  
219 the commercial inshore fleet between April and November. The total fishing mortality  
220 applied to individuals is then the sum of fishing mortality from the relevant fleets  
221 converted to a daily rate. Any individuals with less than one fish after applying natural  
222 or fishing mortality die and are removed from the simulation.

#### 223 2.1.3.4. *Movement*

224 The sustained swimming speed of individuals is calculated from length and the aspect  
225 ratio of the caudal fin (Sambilay Jr, 1990), and is adjusted for the effects of temperature  
226 on swimming speed (TRACE Section 2). Speeds in kilometres per hour are converted  
227 to patches per day assuming 12 hours swimming per day. The number of times  
228 individuals change direction is taken as the smallest integer such that quotient of  
229 speed and the number of direction changes is less than 0.25, chosen to minimise  
230 overlap of individuals and land without restricting movement (TRACE Section 3).

231 Mature individuals follow two types of migration based on hypotheses drawn from 20  
232 years of mark-recapture studies conducted around England and Wales, and  
233 corroborated by recent electronic data storage tag (DST) experiments: spawning  
234 migrations to offshore regions and feeding migrations to coastal divisions (Figure 1  
235 and Figure 3). Pawson et al. (2007, 1987) hypothesised that these seasonal migrations  
236 are a function of temperature. Adult bass migrate to pre-spawning areas in the western  
237 English Channel between October and December as females seek water warmer than  
238 9°C. Spawning then starts offshore in the Celtic Sea and western English Channel  
239 from February and spreads east as the water attains 9°C (Thompson and Harrop,  
240 1987). It was inferred that spent fish moved to specific feeding grounds around April  
241 to May after spawning (Pawson and Pickett, 1996). Movement between areas

242 appeared rapid (de Pontual et al., 2019) with most migrations being made along the  
243 coast (Pickett and Pawson, 1994). Here, the migration submodels incorporate both  
244 directed movements towards a destination (migratory) and random localised  
245 movements (non-migratory) once the destination has been reached.

246 Within the IBM, spawning migrations occur from October to May and are triggered by  
247 temperature either when a mature individual neighbours a spawning patch (see  
248 Section 2.1.3.1) or the patch occupied has an SST below 9°C (Figure 3a). Once a  
249 spawning migration has been triggered, the individual follows a decision hierarchy that  
250 transports it along the coast towards the western English Channel (division 7.e in  
251 Figure 1), moving offshore if and when neighbouring a spawning patch (Figure 3b;  
252 TRACE Figure 4). To do this, each 'step' the individual chooses a neighbour patch  
253 based on patch type and direction, preferentially: (1) moving towards an offshore  
254 spawning neighbour and if no such neighbour exists (2) moving towards a coastal  
255 neighbour on route to division 7.e (Figure 3b). Movement offshore therefore occurs in  
256 the Celtic Sea and English Channel but can also occur in other areas when  
257 temperature conditions are satisfied. Once offshore, the individual moves randomly  
258 within spawning patches until assumed spent after spawning, which occurs either after  
259 spending 60 days offshore or on 1 June, whichever occurs first (Figure 3a).

260 When a mature individual is not following a spawning migration, it defaults to a feeding  
261 migration, which transports the individual to the coastal division it has an affinity to  
262 feed in. Each 'step' the individual again chooses a neighbour patch based on patch type  
263 and direction where, assuming the individual starts offshore, the migration broadly  
264 follows: (1) move directly towards the coast then (2) move towards a coastal neighbour  
265 on route to the correct region and division (Figure 3b; TRACE Figure 5). The individual  
266 moves randomly once it has reached its assigned feeding division.

267 Evidence from tagging studies suggest that juveniles remain within discrete nursery  
268 grounds for the first few years of life and disperse primarily during the adolescent  
269 phase (Pickett et al., 2004; Pickett and Pawson, 1994). Juvenile individuals therefore  
270 follow a random walk constrained to discrete nursery areas (brown patches in Figure  
271 1) when aged less than four years and widen their movements to all coastal patches  
272 (green and brown patches in Figure 1) when aged four to six.

#### 273 2.1.3.5. *Aging*

274 Juvenile individuals become sexually mature at six years (TRACE Section 4). Given  
275 sea bass disperse primarily during the adolescent phase, individuals adopt the division  
276 occupied at the time of maturity as the coastal division for which they have an affinity  
277 to feed, which may not be the same as the parent stock or close to their nursery ground  
278 (Pickett et al., 2004; Pickett and Pawson, 1994).

#### 279 2.1.3.6. *Reproduction*

280 Newly recruited fish enter the model in June–September (Jennings and Ellis, 2015).  
281 Ten juvenile individuals enter the IBM each year with the number of individuals  
282 entering in a month being proportional to the number of spawning individuals (mature  
283 individuals occupying offshore patches) earlier in the year (Figure 4A). Recruiting  
284 individuals are distributed in coastal divisions according to the distribution of spawning  
285 individuals via connectivity probabilities derived from a particle tracking IBM coupled  
286 with hydrodynamics (Beraud et al., 2018; TRACE Section 3; Figure 4B). Given the  
287 lack of stock-recruitment relationship for sea bass (see Section 4), the number of fish  
288 represented by recruiting individuals is taken as the number of age 0 fish from the  
289 ICES numbers-at-age data (ICES, 2018b). Each individual is assumed 100 days old  
290 when it settles in a nursery area (Beraud et al., 2018; Jennings and Ellis, 2015).

## 291        **2.2. MODEL TESTING**

### 292        **2.2.1. Conditioning and validation**

293        To check conditioning of the population dynamics, numbers, spawning stock biomass  
294        (SSB) and total stock biomass (TSB) from the IBM were compared to the same  
295        quantities from the stock assessment (ICES, 2018b), which represents the best  
296        available knowledge on status of the stock. To account for stochasticity, the IBM was  
297        run ten times and differences between median IBM output and the assessment  
298        quantified. Cohort (integer) ages were fed into calculations of biomass to account for  
299        the differing temporal resolution of the IBM and stock assessment.

300        In the absence of a suitable survey (see Section 4), spatial patterns from a single run  
301        of the IBM were compared to commercial catch data for 2009–2014 from the Scientific,  
302        Technical and Economic Committee for Fisheries (STECF;  
303        <https://stecf.jrc.ec.europa.eu/>). Equivalent catches from the IBM were calculated using  
304        the standard equation (Baranov, 1918; TRACE Section 2) for commercial inshore and  
305        commercial offshore fleets.

### 306        **2.2.2 Sensitivity analysis**

307        Local sensitivity analyses were conducted to explore how sensitive IBM outputs were  
308        to changes in model parameters and inputs. To assess temporal sensitivity, five  
309        simulations were performed for 10% increases and decreases in each model  
310        parameter, holding all other parameters at their baseline values, and compared to five  
311        baseline simulations. Median numbers and biomasses were averaged over the time-  
312        series, with the result of each perturbation presented as a percentage of the baseline.  
313        Spatial sensitivity was assessed similarly, but with a single run of the IBM providing  
314        replicates at each parameter level and results taken over the last five years. The

315 spatial distribution of the catch for each perturbation is approximated and summarised  
316 by the centre of gravity (Woillez et al., 2007) while the mean correlation coefficient  
317 between perturbed and baseline catch quantifies the degree of change in spatial  
318 pattern with each perturbation.

### 319 **2.3. MODEL APPLICATIONS**

320 To demonstrate potential for management, the IBM was projected forward under a  
321 range of management strategies based on those implemented by the European  
322 Commission in 2015 and 2016. As future conditions are unknown, scenarios were  
323 explored based on current environmental conditions and fishing practices: (1) SST  
324 data for 2015–2016 were obtained from the OSTIA database while SST data for  
325 subsequent years were taken as the average of 2014–2016, (2) recruitment was taken  
326 as the 25%, 50% and 75% quantile of recruitment estimates from the assessment  
327 (ICES, 2018b), (3) natural mortality was assumed constant at 0.24 and (4) unless  
328 otherwise stated, fishing level and exploitation pattern for each fleet was assumed the  
329 same as in 2014; the last year prior to implementation of management measures.

330 Management strategies for forward projections included: (1) a short-term ban on  
331 trawling in offshore areas; (2) commercial and recreational catch limits and restrictions;  
332 and (3) an increase in the minimum conservation reference size (MCRS) (Table 1). All  
333 scenarios were implemented by adjusting the fishing mortality rates applied to the  
334 appropriate individuals based on length or location in relation to a fleet restriction. For  
335 simplicity, we do not consider redistribution of fishing mortality from individuals that  
336 are protected by a management scenario to those that are not.

337 The IBM was run ten times for each management scenario and a series of constant  
338 fishing mortalities. A set of hindcast simulations provided the starting point for



339 projections and ensured performance was not influenced by initial conditions.  
340 Management strategies were evaluated based on mean SSB in: (1) the first 10 years  
341 of projections to inform on short-term recovery; and (2) the last 10 years of projections  
342 to inform on long-term stock status, i.e. once equilibrium has been reached.

### 343 **3. Results**

#### 344 **3.1. MODEL TESTING**

##### 345 ***3.1.1. Conditioning and validation***

346 Abundances from the IBM and stock assessment match well with almost perfect  
347 correlation and low root-mean square (RMS) difference (Table 2; Figure 5), largely  
348 due to conditioning of the IBM on the SS3 assessment. Biomass patterns match well  
349 but with differences for SSB due to differences in the way maturity is modelled (length-  
350 based in SS3 and age-based in the IBM). The IBM estimates TSB to be an average  
351 of 6% lower over the time series than the assessment because SS3 uses an  
352 alternative parameterisation of the von Bertalanffy growth equation (Methot and  
353 Wetzel, 2013; TRACE Section 6). This perceived bias is somewhat concealed for SSB  
354 due to the differences in modelling maturity.

355 The IBM correctly predicts the majority of catch is taken in the English Channel (ICES  
356 divisions 7.d-e) with a correlation of 0.32 ( $p < 0.01$ ) between mean catch from the IBM  
357 and STECF data over the whole stock area (Figure 6; 0.24–0.40 over individual years;  
358 TRACE Section 8). The IBM tends to overestimate catch in the Celtic (7.f-h) and Irish  
359 (7.a) Seas and underestimate catch in the North Sea (4.b-c; Figure 7; see Section 4).

##### 360 ***3.1.2. Sensitivity analysis***

361 Sensitivity of abundance and biomasses to most parameter values and inputs was  
362 low, with 10% changes in these quantities mostly resulting in changes of <10% in

363 model outputs (Table 3). Biomasses were sensitive to the von Bertalanffy growth and  
364 length-weight parameters, known with some confidence, and all three outputs showed  
365 some sensitivity to natural mortality. Of the stock assessment inputs, IBM outputs were  
366 most sensitive to recruitment and least sensitive to commercial offshore fishing  
367 mortality (see Section 4). Spatial distribution and pattern were most sensitive to the  
368 aspect ratio of the caudal fin and rate coefficient of the growth equation, both of which  
369 contribute to calculation of swimming speed (TRACE Section 2). However, for both  
370 metrics the effects were small with the displacement in centre of gravity less than the  
371 length of a patch for most perturbations (mean = 18 km; maximum = 55 km for a 10%  
372 increase in the rate coefficient; TRACE Section 7) and the correlation between  
373 perturbed and baseline catch remaining above 0.8 (Table 3).

### 374 **3.2. MODEL APPLICATIONS**

375 Forward projections under constant fishing mortality showed median SSB to  
376 equilibrate after approximately 25 years (Figure 8), informing the choice of a 35-year  
377 projection period.

378 Even with the associated reductions in fishing mortality, management scenario  
379 trajectories show SSB to continue its decrease in the first years of the projection  
380 because the year classes reaching maturity are not large enough to replace losses  
381 from the existing spawning stock. The future recruitment assumption begins to impact  
382 the spawning stock in 2021, from which time age structure improves and SSB  
383 increases to equilibrium (Figure 9). Results show setting commercial limits to be the  
384 most effective strategy for short-term rebuilding of the spawning stock and increasing  
385 the MCRS to be the most effective strategy for long-term health (Table 4), which is  
386 unsurprising given that these strategies are applied throughout the management area

387 and potentially protect a larger proportion of the stock. We note that our median  
388 recruitment assumption is larger than any recruitment observed since 2009 and likely  
389 contributes to long-term success of the increase in MCRS because there are more  
390 smaller individuals to protect once the age structure of the stock improves.

#### 391 **4. Discussion**

392 The IBM was conditioned on the stock assessment, which represents the best  
393 available knowledge on status of the Northern sea bass stock. It can mimic the  
394 population dynamics component of SS3 and, given appropriate catchability  
395 parameters, could also produce simulated observations in a manner similar to SS3.  
396 Where the IBM falls short is in the ability to statistically fit such modelled observations  
397 to data from commercial fishing fleets or fishery-independent surveys, and for this  
398 reason cannot substitute SS3 for the annual stock assessment. Rather, the IBM has  
399 potential to complement SS3 because it models the movement and distribution of sea  
400 bass, essential for predicting the population consequences of spatial management  
401 strategies.

402 Model validation has taken the 'pattern-oriented approach' (Grimm and Railsback,  
403 2005). While it would be attractive to use objective methods such as approximate  
404 Bayesian computation (van der Vaart et al., 2016, 2015) these will be challenging to  
405 implement because of long model run times (~10 minutes).

406 Pawson et al. (1987) formulated hypotheses on the movement and migrations of sea  
407 bass from data for 5959 fish tagged around England and Wales, with a follow-on  
408 exercise for a further 4959 fish confirming the validity of the hypothesis 20 years later  
409 (Pawson et al., 2007). Without knowledge on the mechanisms informing these large-  
410 scale migrations, our submodels simulate these hypothesised movements based on

411 a set of empirical rules. Recent studies deploying electronic data storage tags (DSTs)  
412 confirm the migratory nature of sea bass and have the potential to further elucidate  
413 this behaviour (de Pontual et al., 2019; O'Neill et al., 2018; Quayle et al., 2009). In  
414 particular, DSTs record both the temperature and depth experienced by fish at regular  
415 intervals, making it possible to geolocate and reconstruct movement trajectories  
416 (Woillez et al., 2016) that could inform a statistical movement model within the IBM.  
417 However, DST returns to date are low and, given specific DST release sites and high  
418 fidelity of sea bass to localised feeding areas (Doyle et al., 2017; Pawson et al., 2008),  
419 likely do not contain sufficient information on all local populations in the management  
420 area we consider. Temperature triggers in the IBM allow some modelling of  
421 behavioural traits and provide mechanisms for responding to changes in sea surface  
422 temperature, e.g. delayed spawning in warmer years and increased spawning in the  
423 southern North Sea (Pawson et al., 2007); however, as DST returns increase, it would  
424 be desirable to devise fully mechanistic movement submodels.

425 Some IBMs for small pelagic species relate movement to an underlying distribution of  
426 food via satellite measurements of chlorophyll or model based estimates of  
427 zooplankton (Boyd et al., 2020; Politikos et al., 2015). However, the distribution of sea  
428 bass is not as closely related to primary production and the plankton due to its higher  
429 trophic level and exploitation of many different food sources.

430 Ideally, the spatial aspect of the IBM would be validated against data from a fishery-  
431 independent survey providing an unbiased estimator of the underlying population.  
432 However, sea bass are not captured well by survey gears (Walker et al., 2017) and  
433 surveys that do capture bass either only target recruits or cover just a small portion of  
434 the stock area (ICES, 2018c). Without a suitable survey, we take reported catch as a  
435 proxy for the underlying distribution. However, the distribution of fishing effort does not

436 necessarily match the underlying distribution of fish. In recent years the majority of  
437 monthly sea bass landings in the UK are from ports in the English Channel and from  
438 under 10m vessels (MMO, 2018). These smaller vessels are likely to travel a limited  
439 distance from port to fishing grounds, creating a limited area from which bass captures  
440 are reported. Additionally, socio-economic factors, weather and legislation influence  
441 when and where vessels fish (Sainsbury et al., 2018). This combination of factors may  
442 provide explanation for the discrepancies between IBM and STECF catch data,  
443 especially in the Celtic sea. We note that, beyond splitting annual fishing mortality  
444 rates between fleets, effort is not modelled explicitly in this study and the current focus  
445 is modelling the spatiotemporal distribution of the population rather than regenerating  
446 catch. While it would be desirable to spatialise fishing mortality, time-series of reliable  
447 fishing effort data are lacking. Most smaller boats employ a variety of gears and take  
448 small amounts of sea bass as bycatch, meaning that fishing effort is not directly  
449 proportional to the fishing mortality exerted on sea bass.

450 Experimental studies on swimming speeds of bass focused on juveniles (e.g.  
451 Claireaux, 2006). Without information for adults we assume a generic equation  
452 parameterised for sea bass (Sambily Jr, 1990). This coupled with direct movement  
453 (Pickett and Pawson, 1994), results in rapid migration of individuals to spawning areas  
454 in the Celtic Sea and English Channel and increased settlement of juveniles in coastal  
455 divisions with high connectivity to these areas, likely contributing to the overestimation  
456 of catch in divisions 7.a,f-g.

457 Estimating recruitment of fish stocks is notoriously difficult and may be influenced by  
458 several confounding factors in addition to the size of the spawning stock. Given the  
459 high influence of environmental conditions on survivability and growth of juveniles  
460 (Bento et al., 2016) there is no clear stock-recruitment (S-R) relationship for European

461 sea bass. The SS3 assessment uses a Beverton-Holt S-R with high steepness,  
462 mimicking a segmented regression that gives average recruitment with high  
463 uncertainty (ICES, 2018c). Given the apparent lack of S-R for sea bass, we used the  
464 assessment estimates as input to the IBM, and project the quantiles of these estimates  
465 when testing management strategies. This approach suggests that age structure of  
466 the stock may be important in determining how well a management strategy performs  
467 and highlights the importance of modelling recruitment. Furthermore, decoupling  
468 recruitment from the modelled spawning stock likely contributed to the low sensitivity  
469 of model outputs to offshore fishing mortality and poor performance of an offshore  
470 fishing ban. This is because any benefits from protecting the mature portion of the  
471 stock from their highest source of fishing mortality are not realised in modelled  
472 recruitment.

473 An interesting possibility is that the IBM could be used to predict recruitment without  
474 an S-R. Recruitment can be broadly decomposed into the number of eggs produced  
475 by the spawning stock and the number of eggs that survive. There have been several  
476 attempts to represent these processes with IBMs, often using a bioenergetics-based  
477 approach (Bartsch et al., 2004; Boyd et al., 2018; Bueno-Pardo et al., 2020; Politikos  
478 et al., 2015; Shin and Cury, 2001). When predictions of egg production and early  
479 survival are combined, it is possible to obtain emergent predictions of recruitment.

480 Spawning stock biomass (SSB) is an important metric for determining the state of fish  
481 stocks and informing on management actions. The fact our IBM can mimic estimates  
482 of SSB that are robust to uncertainty in parameter values make it an ideal tool for  
483 testing the performance of fishing strategies and informing management. In particular,  
484 our study includes many elements of a shortcut management strategy evaluation  
485 (MSE; Punt et al., 2016) in that we model population dynamics, observations (e.g.

486 catch) and implementation of management strategies without performing an  
487 assessment within our simulations. However, given long model run times, it would be  
488 difficult to consider the full range of uncertainties typically modelled in an MSE. Given  
489 the current status of the stock, we focused on performance statistics related to  
490 recovery and long-term health, but the IBM could be used to assess other aspects of  
491 performance such as yield maximisation, risk reduction and TAC (total allowable  
492 catch) stability.

493 This first implementation of the IBM offers a tool to assess how technical measures  
494 applied to subsets of the population, through fleet or spatial restrictions, may impact  
495 the stock. For example, our management simulations suggest technical measures  
496 applied throughout the management area, such as an increase in MCRS or limits for  
497 commercial fleets, are more effective than localised measures, such as inshore  
498 recreational restrictions or bans on offshore trawling. Our movement and recruitment  
499 assumptions limit the validity of the model to past and current environmental  
500 conditions; further research into these areas would increase robustness of predictions  
501 in novel environmental conditions and reliability of management strategy outcomes.

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## 711 **Supporting information**

712 Additional Supporting Information may be found in the online version of this article.



Scenario	Description	Implementation
<b>Constant fishing mortality</b>		
$F=0$	No fishing	Multiplier of 0 applied to $F_s$ of all individuals (fishing mortality switched off)
$F=F_{MSY}$	$F_{4-15} = 0.203$ (ICES, 2018c)	Multiplier of 0.781 applied to $F_s$ of all individuals $\frac{0.203}{F(2014)_{4-15}} = 0.781$
$F=F(2014)$	$F=F(2014)$	Multiplier of 1 applied to $F_s$ of all individuals
<b>Management scenarios</b>		
Offshore ban	Short-term ban on pelagic trawling to protect the spawning stock (European Commission, 2015b)	Commercial offshore fishing mortality switched off between 1 Jan-30 Apr each year ( $F_{Co}=0$ )
Increase MCRS	Increase in the minimum size from 36 to 42 cm (European Commission, 2015c)	Fishing mortality on individuals <42 cm switched off
Recreational limits	Six months no take followed by 1 fish bag limit	Multiplier of 0.282 applied to recreational fishing mortalities ( $F_{Ri}$ ) (this annual multiplier accounts for both management measures; see ICES, 2018c)
Catch & release	All fish caught recreationally are released	Multiplier of 0.099 applied to recreational fishing mortalities ( $F_{Ri}$ ) (ICES, 2018c)
Commercial limit	Monthly catch limits for commercial fleets (European Commission, 2015a)	Target fishing mortality is set following a simple harvest control rule (ICES, 2018a), converted to commercial catch with the standard Baranov equation and divided by 12. $F_{tar} \begin{cases} F_{MSY}, & SSB \geq MSY B_{trigger} \\ F_{MSY} \times \frac{SSB}{MSY B_{trigger}}, & SSB < MSY B_{trigger} \end{cases}$ Commercial inshore and offshore fishing mortality switched off for the remainder of the month once limit is exceeded ( $F_{Co}$ & $F_{Ci}$ ).

713 Table 1: Forward projections conducted with the IBM including both constant fishing mortality and management scenarios. Description refers to the ‘real life’  
714 management actions while Implementation describes the settings used to simulate the scenario within the IBM. Management scenarios are based on those  
715 implemented by the European Commission in 2015/16 ([https://ec.europa.eu/fisheries/cfp/fishing\\_rules/sea-bass\\_en](https://ec.europa.eu/fisheries/cfp/fishing_rules/sea-bass_en)).  $F_{MSY}=0.203$  and  $MSY B_{trigger}=13465$   
716 tonnes are reference points used in the management of the northern stock of sea bass

	$r$	$E$ (%)	$\bar{E}$ (%)	$E'$ (%)
<b>Numbers</b>	1.00	0.68	-0.49	0.47
<b>SSB</b>	0.93	8.32	0.39	8.31
<b>TSB</b>	1.00	6.17	-5.73	2.30

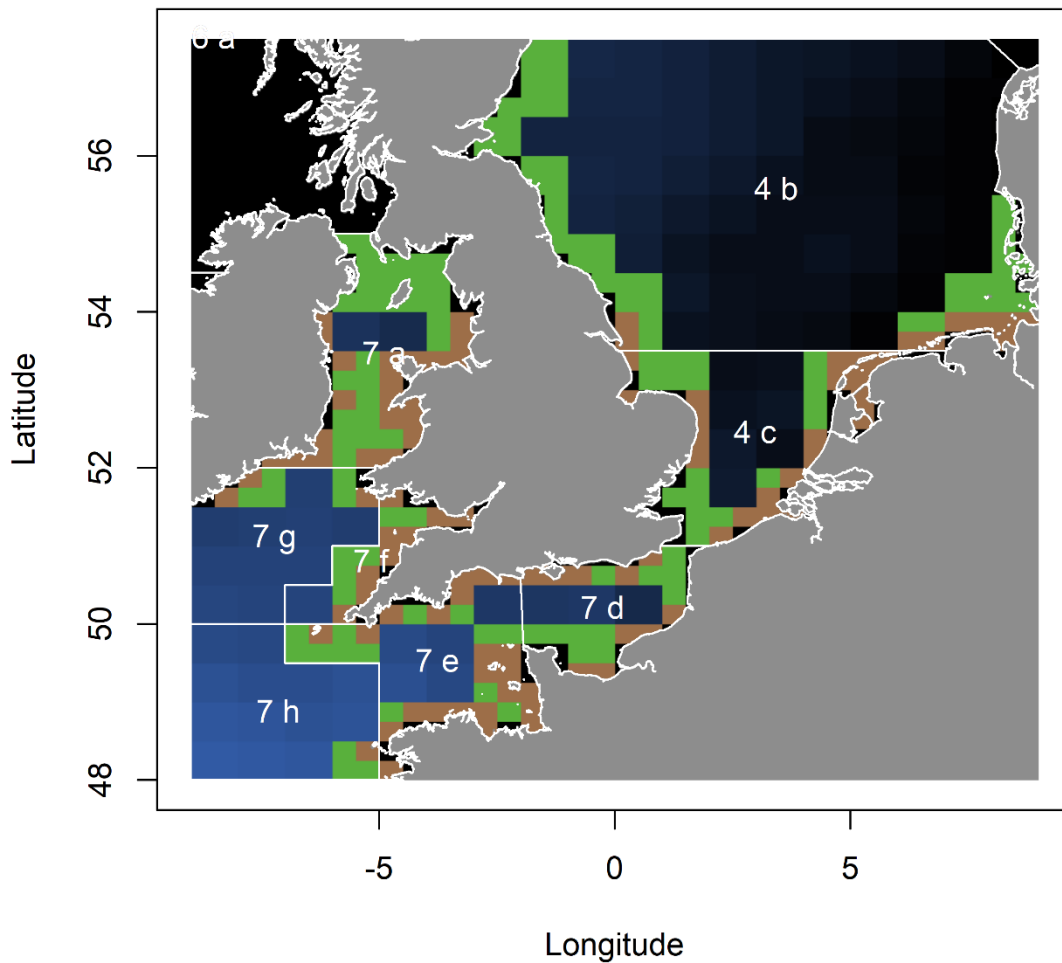
717 Table 2: Correlation coefficient ( $r$ ) and normalised RMS difference ( $E$ ) resolved into bias ( $\bar{E}$ ) and  
718 variability ( $E'$ ) components for IBM outputs compared to those of the stock assessment for the hindcast  
719 period (1985–2014).

Parameter	Value	Quality	N-	N+	SSB-	SSB+	TSB-	TSB+	d-	d+	r-	r+
<b>Growth</b>												
Asymptotic length ( $L_{\infty}$ )	84.55	4	0.0	0.0	-26.8	32.8	-26.8	32.8	10.1	10.0	0.92	0.90
Growth rate coefficient ( $k$ )	0.096699	4	0.0	0.0	-17.4	17.9	-19.2	20.5	29.8	55.4	0.89	0.84
Age at length 0 ( $t_0$ )	-0.73	4	0.0	0.0	-1.4	1.4	-2.5	2.6	14.7	21.6	0.91	0.92
Activation energy ( $E_g$ )	5.2E-21	1	0.0	0.0	0.0	0.0	0.0	0.0	20.9	6.5	0.91	0.93
Reference temperature ( $T_g$ )	12	1	0.0	0.0	0.0	0.0	0.0	0.0	22.1	21.2	0.91	0.91
<b>Weight</b>												
Length-weight parameter ( $a$ )	1.3E-05	4	---	---	-10.0	10.1	-10.0	10.1	12.9	9.6	0.87	0.91
Length-weight parameter ( $b$ )	2.969	4	---	---	-68.8	221.4	-66.6	203.3	11.6	23.1	0.92	0.90
<b>Swimming</b>												
Aspect ratio of the caudal fin ( $A$ )	1.76	2	0.0	0.0	0.1	0.1	0.1	0.1	31.2	29.0	0.89	0.89
Activation energy ( $E_s$ )	5.03E-21	2	0.0	0.0	0.0	0.0	0.0	0.0	8.0	38.4	0.91	0.90
Activation temperature ( $T_s$ )	6	2	0.0	0.0	0.0	0.0	0.0	0.0	16.3	1.7	0.92	0.92
Swimming hours ( $h$ )	12	1	0.0	0.0	0.0	0.1	0.0	0.0	13.4	23.5	0.90	0.89
Maximum patch direction ( $P_{max}$ )	0.25	1	0.0	0.0	-0.1	0.1	0.0	0.1	15.4	33.2	0.91	0.89
<b>Mortality</b>												
Natural mortality ( $M$ )	0.24	2	6.3	-5.5	19.2	-15.4	15.5	-12.8	14.1	31.3	0.90	0.87
<b>Stock assessment inputs</b>												
Commercial inshore mortality ( $F_{Ci}$ )	1	3	0.5	-0.5	3.9	-3.5	2.6	-2.4	23.5	9.9	0.88	0.90
Commercial offshore mortality ( $F_{Co}$ )	1	3	0.0	0.0	0.3	-0.4	0.2	-0.3	13.1	8.1	0.90	0.92
Recreational mortality ( $F_{Ri}$ )	1	3	0.3	-0.3	2.0	-1.9	1.3	-1.3	7.7	11.7	0.92	0.91
Recruitment ( $R$ )	1	3	-9.3	9.3	-6.9	6.9	-7.7	7.7	16.4	10.7	0.92	0.92

721 Table 3: Sensitivity of abundance (N), spawning stock biomass (SSB), total stock biomass (TSB), spatial distribution (d) and spatial pattern (r) to 10% decreases  
722 (-) and increases (+) in model parameters and inputs. Model abundance and biomasses are quantified by percentage difference, spatial distribution by  
723 displacement of the centre of gravity (km) and spatial pattern by correlation coefficient with a baseline run. Quality gives the estimated quality of empirical  
724 knowledge used to set each parameter value: 5 means high certainty while 1 means low certainty (TRACE Section 3).

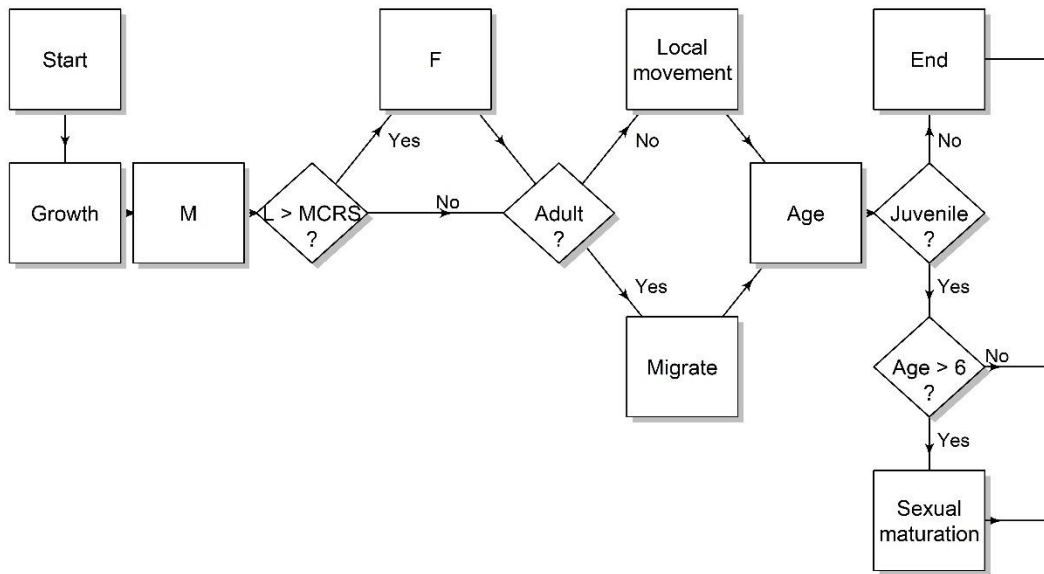
	Mean SSB (tonnes)					
	Short term (2015–2024)			Long term (2041–2050)		
Scenario	R50%	R25%	R75%	R50%	R25%	R75%
<b>Constant fishing mortality</b>						
$F=0$	<b>16511</b>			<b>42129</b>		
$F=F_{MSY}$	<b>8670</b>			<b>12813</b>		
$F=F(2014)$	<b>7507</b>			<b>10148</b>		
<b>Management scenarios</b>						
Offshore ban	<b>7745</b>	7072	8218	<b>10653</b>	5700	14133
Increase MCRS	<b>8676</b>	7813	9282	<b>13155</b>	7038	17451
Recreational limits	<b>8224</b>	7513	8723	<b>11726</b>	6272	15556
Catch & release	<b>8421</b>	7699	8929	<b>12196</b>	6524	16179
Commercial limit	<b>9035</b>	8266	9568	<b>12743</b>	7498	16734

725 Table 4: Results of projections under constant  $F$  and management strategies.  $R_{xx}\%$  relate to assumed  
726 recruitment, with the median highlighted in bold for each scenario. Mean SSB is the mean of the median  
727 SSB across replicates for the given projection period.



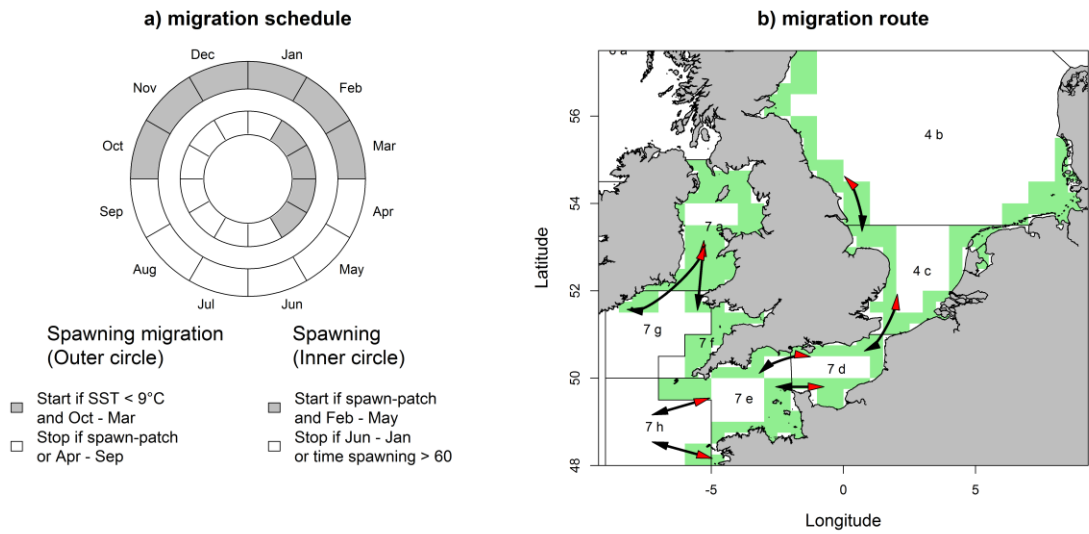
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729 Figure 1: The model interface at set-up (1<sup>st</sup> January 1985). Coastal patches are represented in green,  
 730 nursery patches (also coastal) in brown and offshore patches in blue (with the blue gradient from dark  
 731 to light representing increasing SST; monthly averages). ICES divisions spanning the northern  
 732 assessment unit are superimposed. Regions for offshore spawning are defined as follows: North Sea  
 733 = 4.b-c; English Channel = 7.d-e, Celtic Sea = 7.f-h and Irish Sea = 7.a.



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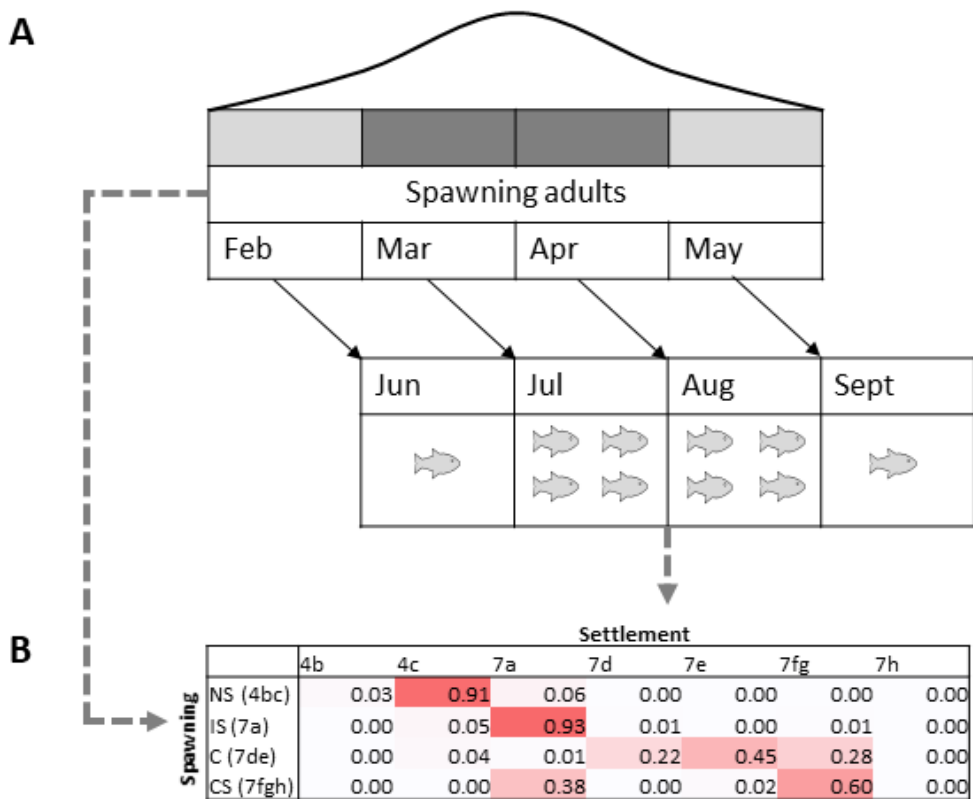
735 Figure 2: Conceptual model showing the processes that individuals follow each daily time-step. M is  
 736 natural mortality, F is fishing mortality (including commercial inshore and offshore and recreational), L  
 737 is length and MCRS is the minimum conservation reference size.



739

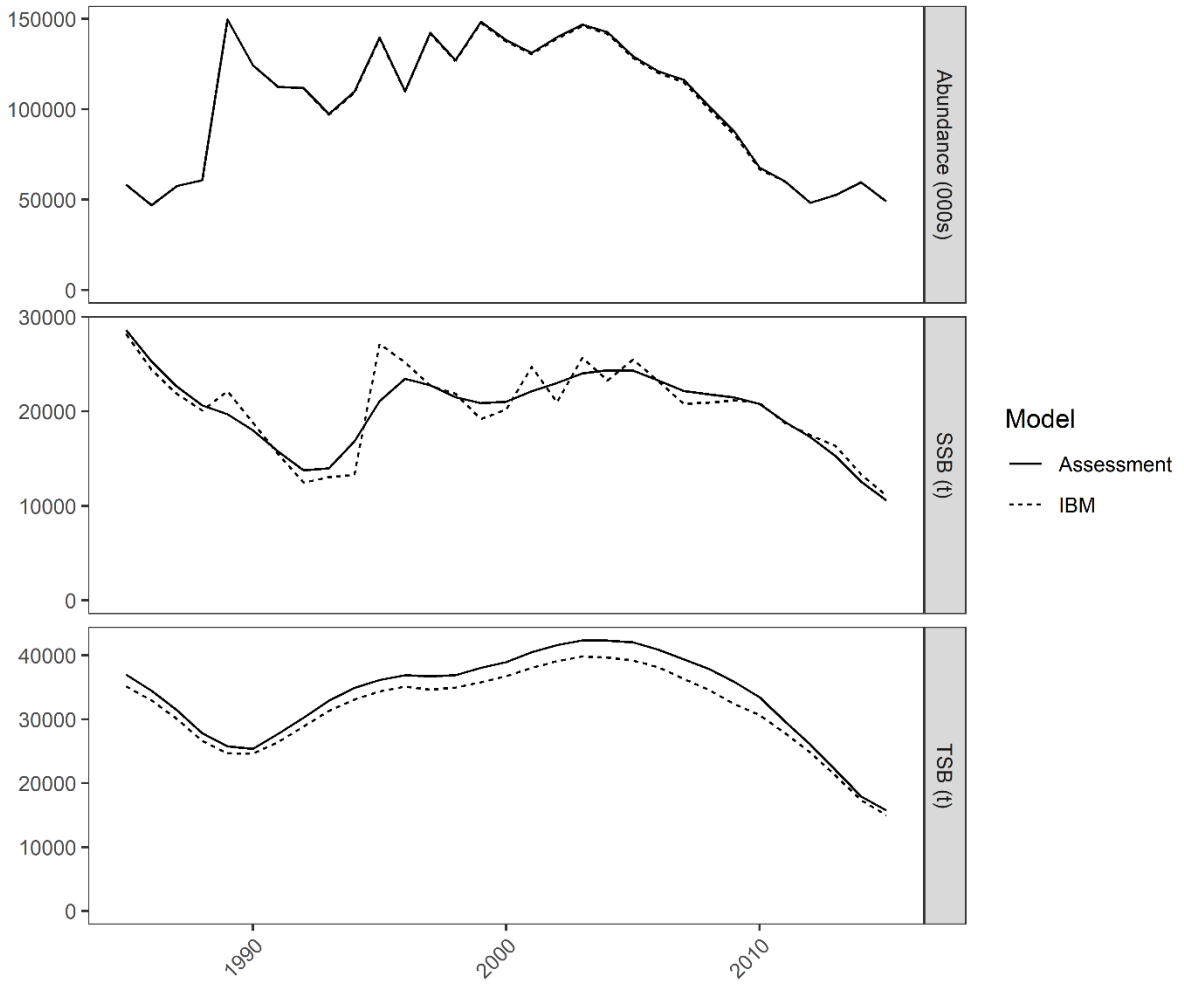
740 Figure 3: (a) Schedule for spawning migrations. Outer circle: migration to (pre-)spawning areas is  
 741 triggered by SST and can take place between October and March. Inner circle: spawning takes place  
 742 within offshore spawning patches appearing February–May. b) Mature individuals migrate following the  
 743 hypotheses of Pawson et al. (1987, 2007). Arrows show movement around the coast to and from the  
 744 English Channel and Celtic Sea (although movement offshore can occur anywhere temperature  
 745 conditions are satisfied) with black arrow heads representing the spawning migration and red arrow  
 746 heads the feeding migration.





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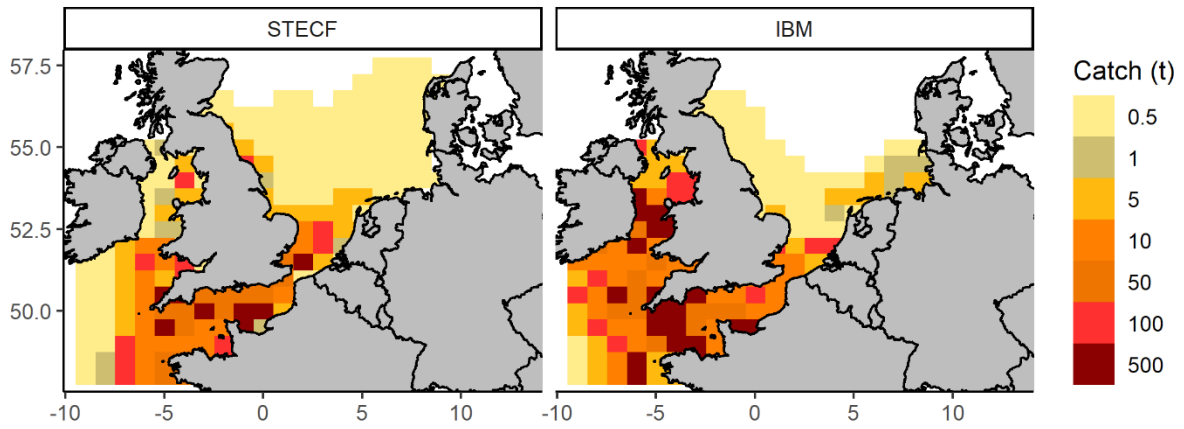
748 Figure 4: Schematic showing how the spatiotemporal distribution of recruiting individuals follows from  
 749 the spatiotemporal distribution of spawning individuals. A: Ten individuals enter the IBM proportional to  
 750 the number of spawning individuals in the corresponding month. B: Connectivity between offshore  
 751 spawning regions and coastal settlement divisions. Each cell gives the probability of settling in a coastal  
 752 division given the distribution of spawning individuals in offshore regions the corresponding month.  
 753 Shading represents the strength of connectivity. Modified from Beraud et al. (2017).



754

755 Figure 5: Abundance, SSB and TSB as estimated by the stock assessment and IBM.

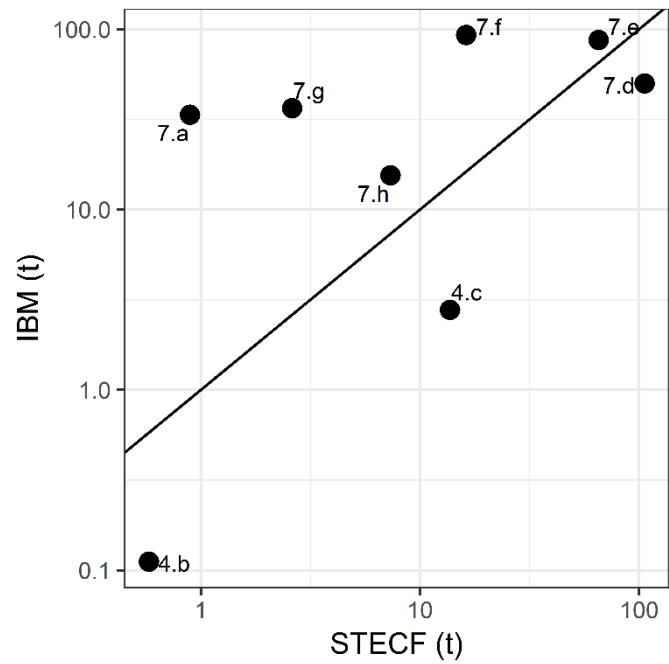
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758 Figure 6: Comparison of mean catch from 2009–2014 as recorded in the STECF database and  
759 estimated by the IBM. Only non-zero catches are plotted because effort is not explicitly represented in  
760 the IBM.

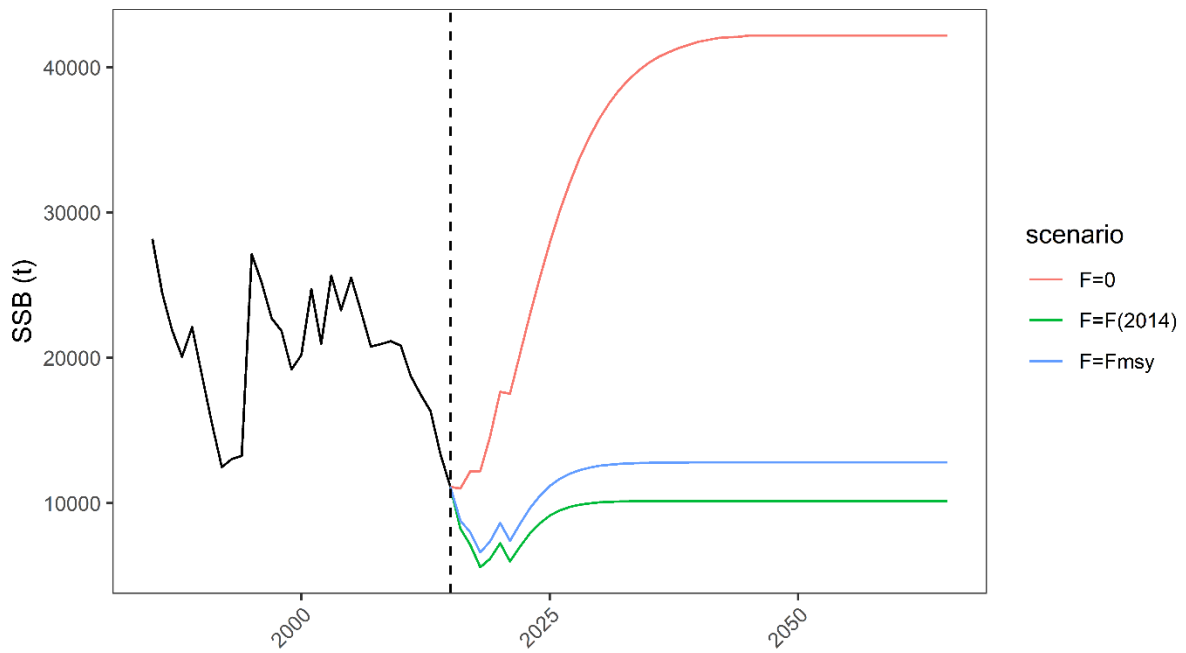
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763 Figure 7: Comparison of mean catch by ICES division from 2009–2014 as recorded in the STECF  
764 database and estimated by the IBM. See Figure 1 for a map of ICES divisions.

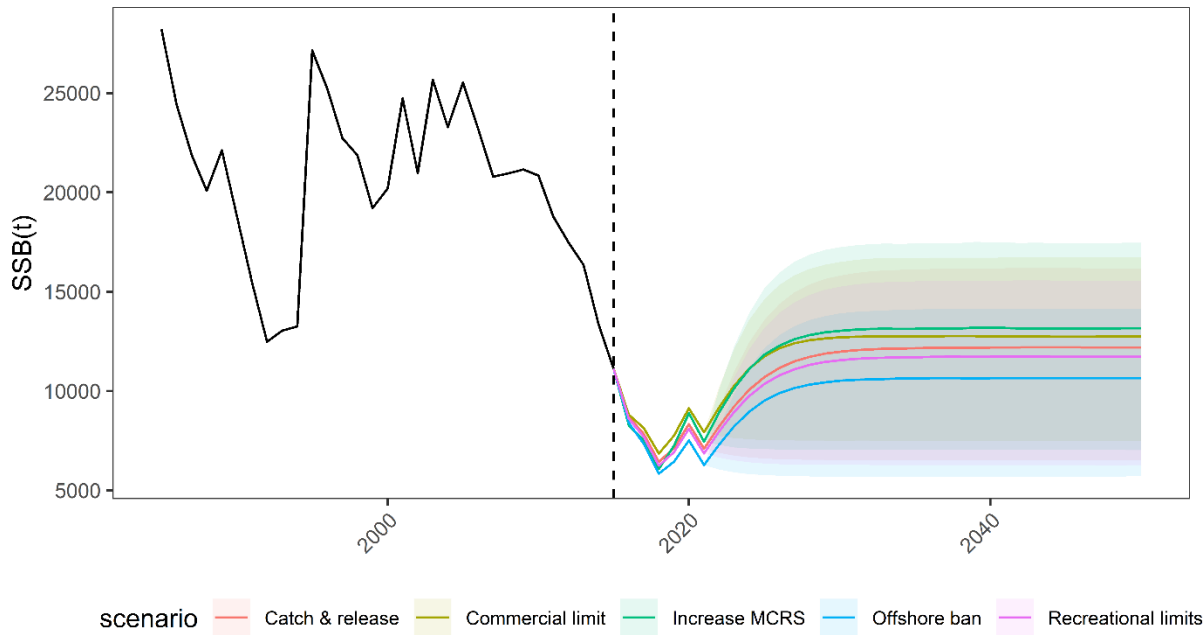
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766

767 Figure 8: Forward 50-year projections of SSB (tonnes) under constant fishing mortality:  $F=0$ ,  
768  $F=F_{MSY}=0.203$  (a reference for northern sea bass) and  $F=F(2014)=0.260$ . The black line shows the  
769 median of 10 hindcast simulations, the coloured lines the median for future projections and the dashed  
770 line the start of the projection period.

771



772

773 Figure 9: Projections under the management scenarios described in Table 1. The black line shows the  
774 median of 10 hindcast simulations, the coloured lines and shaded regions median SSB under different  
775 recruitment assumptions (median and 25-75% quantiles respectively) and the dashed line the start of  
776 the projection period.

777