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

Article

Accepted Version

Walker, N. D., Boyd, R., Watson, J., Kotz, M., Radford, Z., Readdy, L., Sibly, R. ORCID: https://orcid.org/0000-0001-6828-3543, Roy, S. ORCID: https://orcid.org/0000-0003-2543-924X and Hyder, K. (2020) A spatially explicit individual-based model to support management of commercial and recreational fisheries for European sea bass Dicentrarchus labrax. Ecological Modelling, 431. 109179. ISSN 0304-3800 doi: https://doi.org/10.1016/j.ecolmodel.2020.109179 Available at https://centaur.reading.ac.uk/91273/

It is advisable to refer to the publisher's version if you intend to cite from the work. See .

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

Nicola D. Walker[1,*], Robin Boyd[2], Joseph Watson[3], Max Kotz[4], Zachary Radford[1], Lisa Readdy[1], Richard Sibly[3], Shovonlal Roy[2] and Kieran Hyder[1,5]

[1]Centre for Environment, Fisheries and Aquaculture Science, Lowestoft Laboratory, Lowestoft, NR33 0HT, UK

[2]Department of Geography and Environmental Science, University of Reading, Whiteknights, Reading, RG6 6AB, UK

[3]School of Biological Sciences, University of Reading, Whiteknights, Reading, RG6 6AB, UK

[4]Department of Environmental Science and Engineering, California Institute of Technology, Pasadena, CA 91125

[5]School of Environmental Sciences, University of East Anglia, Norwich Research Park, Norwich, Norfolk NR4 7TJ, UK

*Correspondence: nicola.walker@cefas.co.uk

Abstract

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

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

Keywords

1. Introduction

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

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

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

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

4

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

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

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

5

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

2. Material and methods

2.1. THE MODEL

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

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 1st January 1985 to the 31st 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℃ 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^{-1}; 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 choses 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 choses 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.

11

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).

2.2. MODEL TESTING

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.

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

14

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.

3. Results

3.1. MODEL TESTING

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).

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.

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

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

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

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

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

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

Estimating recruitment of fish stocks is notoriously difficult and may be influenced by several confounding factors in addition to the size of the spawning stock. Given the high influence of environmental conditions on survivability and growth of juveniles (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.

Acknowledgements

References

510 Augusiak, J., Van den Brink, P.J., Grimm, V., 2014. Merging validation and evaluation

511   of ecological models to "evaludation": A review of terminology and a practical

512   approach.   Ecol.   Modell.   280,   117–128.

513   https://doi.org/10.1016/j.ecolmodel.2013.11.009

514 Baranov, F.I., 1918. On the question on the biological basis of fisheries. Nauchn.

515   Issled. Ikhtiologicheskii Inst. Izv 1, 81–128.

516 Bartsch, J., Coombs, S.H., Reid, D., 2004. Simulation of mackerel (*Scomber*

517   *scombrus*) recruitment with an individual-based model and comparison with field

518   data.   Fish.   Ocean.   13,   380–391.   https://doi.org/10.1111/j.1365-

519   2419.2004.00306.x

520 Bento, E.G., Grilo, T.F., Nyitrai, D., Dolbeth, M., Pardal, M.Â., Martinho, F., 2016.

521   Climate influence on juvenile European sea bass (*Dicentrarchus labrax*, L.)

522   populations in an estuarine nursery: A decadal overview. Mar. Environ. Res. 122,

523   93–104. https://doi.org/10.1016/j.marenvres.2016.09.011

524 Beraud, C., Molen, J. Van Der, Armstrong, M., Hunter, E., Fonseca, L., Hyder, K.,

525   2018. The influence of oceanographic conditions and larval behaviour on

526   settlement success-the European sea bass *Dicentrarchus labrax* (L.). ICES J.

527   Mar. Sci. 75, 455–470. https://doi.org/10.1093/icesjms/fsx207

528 Boyd, R., Roy, S., Sibly, R., Thorpe, R., Hyder, K., 2018. A general approach to

529   incorporating spatial and temporal variation in individual-based models of fish

530   populations with application to Atlantic mackerel. Ecol. Modell. 382, 9–17.

531   https://doi.org/10.1016/j.ecolmodel.2018.04.015

532 Boyd, R.J., Sibly, R., Hyder, K., Walker, N., Thorpe, R., Roy, S., 2020. Simulating the

533   summer feeding distribution of Northeast Atlantic mackerel with a mechanistic

534   individual-based   model.   Prog.   Oceanogr.   183,   102299.

535   https://doi.org/10.1016/j.pocean.2020.102299

536 Bueno-Pardo, J., Petitgas, P., Kay, S., Huret, M., 2020. Integration of bioenergetics in

537   an individual-based model to hindcast anchovy dynamics in the Bay of Biscay.

538   ICES J. Mar. Sci. 77, 655–667. https://doi.org/10.1093/icesjms/fsz239

539 Claireaux, G., 2006. Effect of temperature on maximum swimming speed and cost of

540   transport in juvenile European sea bass (*Dicentrarchus labrax*). J. Exp. Biol. 209,

541   3420–3428. https://doi.org/10.1242/jeb.02346

542 de Pontual, H., Lalire, M., Fablet, R., Laspougeas, C., Garren, F., Martin, S., Drogou,

543   M., Woillez, M., 2019. New insights into behavioural ecology of European seabass

544   off the West Coast of France : implications at local and population scales. ICES

545   J. Mar. Sci. 76, 501–515. https://doi.org/10.1093/icesjms/fsy086

546 Doyle, T.K., Haberlin, D., Clohessy, J., Bennison, A., Jessopp, M., 2017. Localised

547   residency and inter- annual fidelity to coastal foraging areas may place sea bass

548   at risk to local depletion. Sci. Rep. 1–9. https://doi.org/10.1038/srep45841

549 European Commission, 2015a. COUNCIL REGULATION (EU) 2015/960 of 19 June

550   2015 amending Regulation (EU) 2015/104 as regards certain fishing

551   opportunities. Off. J. Eur. Union L157, 1–19.

552 European Commission, 2015b. COUNCIL REGULATION (EU) 2015/104 of 19

553   January 2015 fixing for 2015 the fishing opportunities for certain fish stocks and

554   groups of fish stocks, applicable in Union waters and, for Union vessels, in certain

555   non-Union waters, amending Regulation (EU) No 43. Off. J. Eur. Union L22, 1–

556   150.

557   European Commission, 2015c. COMMISSION IMPLEMENTING REGULATION (EU)

558   2015/1316 of 30 July 2015 derogating from Council Regulation (EC) No 850/98,

559   as regards the minimum conservation reference size for sea bass (Dicentrarchus

560   labrax). Off. J. Eur. Union L203, 9–10.

561   Fabens, A.J., 1965. Properties and fitting of the von Bertalanffy growth curve. Growth

562   29, 265–289.

563   Grimm, V., Augusiak, J., Focks, A., Frank, B.M., Gabsi, F., Johnston, A.S.A., Liu, C.,

564   Martin, B.T., Meli, M., Radchuk, V., Thorbek, P., Railsback, S.F., 2014. Towards

565   better modelling and decision support: Documenting model development, testing,

566   and analysis using TRACE. Ecol. Modell. 280, 129–139.

567   https://doi.org/10.1016/j.ecolmodel.2014.01.018

568   Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard,

569   J., Grand, T., Heinz, S.K., Huse, G., Huth, A., Jepsen, J.U., Jørgensen, C., Mooij,

570   W.M., Müller, B., Pe'er, G., Piou, C., Railsback, S.F., Robbins, A.M., Robbins,

571   M.M., Rossmanith, E., Rüger, N., Strand, E., Souissi, S., Stillman, R.A., Vabø, R.,

572   Visser, U., DeAngelis, D.L., 2006. A standard protocol for describing individual-

573   based and agent-based models. Ecol. Modell. 198, 115–126.

574   https://doi.org/10.1016/j.ecolmodel.2006.04.023

575   Grimm, V., Berger, U., DeAngelis, D.L., Polhill, J.G., Giske, J., Railsback, S.F., 2010.

576   The ODD protocol: A review and first update. Ecol. Modell. 221, 2760–2768.

577   https://doi.org/10.1016/j.ecolmodel.2010.08.019

578   Grimm, V., Railsback, S.F., 2005. Individual-based Modeling and Ecology. Princeton

579   University Press, Princeton.

580   Heinänen, S., Chudzinska, M.E., Brandi Mortensen, J., Teo, T.Z.E., Rong Utne, K.,

581   Doksæter Sivle, L., Thomsen, F., 2018. Integrated modelling of Atlantic mackerel

582   distribution patterns and movements: A template for dynamic impact

583   assessments. Ecol. Modell. 387, 118–133.

584   https://doi.org/10.1016/j.ecolmodel.2018.08.010

585 Hyder, K., Weltersbach, M.S., Armstrong, M., Ferter, K., Townhill, B., Ahvonen, A.,

586   Arlinghaus, R., Baikov, A., Bellanger, M., Birzaks, J., Borch, T., Cambie, G., de

587   Graaf, M., Diogo, H.M.C., Dziemian, Ł., Gordoa, A., Grzebielec, R., Hartill, B.,

588   Kagervall, A., Kapiris, K., Karlsson, M., Kleiven, A.R., Lejk, A.M., Levrel, H.,

589   Lovell, S., Lyle, J., Moilanen, P., Monkman, G., Morales-Nin, B., Mugerza, E.,

590   Martinez, R., O'Reilly, P., Olesen, H.J., Papadopoulos, A., Pita, P., Radford, Z.,

591   Radtke, K., Roche, W., Rocklin, D., Ruiz, J., Scougal, C., Silvestri, R., Skov, C.,

592   Steinback, S., Sundelöf, A., Svagzdys, A., Turnbull, D., van der Hammen, T., van

593   Voorhees, D., van Winsen, F., Verleye, T., Veiga, P., Vølstad, J.H., Zarauz, L.,

594   Zolubas, T., Strehlow, H. V., 2018. Recreational sea fishing in Europe in a global

595   context—Participation rates, fishing effort, expenditure, and implications for

596   monitoring and assessment. Fish Fish. 19, 225–243.

597   https://doi.org/10.1111/faf.12251

598 ICES, 2018a. Sea bass (*Dicentrarchus labrax*) in divisions 4.b–c , 7.a, and 7.d–h

599   (central and southern North Sea, Irish Sea, English Channel, Bristol Channel, and

600   Celtic Sea), in: Report of the ICES Advisory Committee. pp. 1–10.

601 ICES, 2018b. Report of the Working Group on Celtic Seas Ecoregion (WGCSE), 9-18

602   May 2018, Copenhagen, Denmark. ICES CM 2018/ACOM:13. 1887 pp.

603 ICES, 2018c. Report of the Benchmark Workshop on Seabass (WKBASS), 20-24

604   February 2017 and 21-23 February 2018, Copenhagen, Denmark. ICES CM

605   2018/ACOM:44. 283 pp.

606   ICES, 2012. Report of the Working Group on assessment of New MoU species

607   (WGNEW), 5-9 March 2012. ICES CM 2012/ACOM:20. 258 pp.

608   Jennings, S., Ellis, J.R., 2015. Bass (Moronidae), in: Heesen, H.J.L., Daan, N., Ellis,

609   J.R. (Eds.), Fish Atlas of the Celtic Sea, North Sea, and Baltic Sea: Based on

610   International Research Vessel Data. KNNV Publishing, The Netherlands, pp.

611   324–327.

612   Kelley, D.F., 1988. The importance of estuaries for sea-bass, *Dicentrarchus labrax*

613   (L.). J. Fish Biol. 33, 25–33. https://doi.org/10.1111/j.1095-8649.1988.tb05555.x

614   Methot, R.D., Wetzel, C.R., 2013. Stock synthesis: A biological and statistical

615   framework for fish stock assessment and fishery management. Fish. Res. 142,

616   86–99. https://doi.org/10.1016/j.fishres.2012.10.012

617   MMO, 2018. Marine Management Organisation - Latest dataset - UK and foreign

618   vessels landings by UK port and UK vessel landings abroad: 2014, 2015, 2016

619   and 2017 (year to date) - GOV.UK [WWW Document].

620   O'Neill, R., Ó Maoiléidigh, N., McGinnity, P., Bond, N., Culloty, S., 2018. The novel

621   use of pop-off satellite tages (PSATs) to investigate the migratory behaviour of

622   European sea bass *Dicentrarchus labrax*. J. Fish Biol. 92, 1404–1421.

623   https://doi.org/10.1111/jfb.13594

624   Pawson, M.G., Brown, M., Leballeur, J., Pickett, G.D., 2008. Will philopatry in sea

625   bass, *Dicentrarchus labrax*, facilitate the use of catch-restricted areas for

626   management of recreational fisheries? Fish. Res. 93, 240–243.

627   https://doi.org/10.1016/j.fishres.2008.03.002

628 Pawson, M.G., Pickett, G.D., 1996. The Annual Pattern of Condition and Maturity in

629 Bass, *Dicentrarchus Labrax*, in Waters Around England and Wales. J. Mar. Biol.

630 Assoc.   United   Kingdom   76,   107–125.

631 https://doi.org/10.1017/S0025315400029040

632 Pawson, M.G., Pickett, G.D., Kelley, D.F., 1987. The distribution and migrations of

633 bass, *Dicentrarchus labrax* L., in waters around England and Wales as shown by

634 tagging.   J.   Mar.   Biol.   Assoc.   United   Kingdom   67,   183–217.

635 https://doi.org/10.1017/S0025315400026448

636 Pawson, M.G., Pickett, G.D., Leballeur, J., Brown, M., Fritsch, M., 2007. Migrations,

637 fishery interactions, and management units of sea bass (*Dicentrarchus labrax*) in

638 Northwest   Europe.   ICES   J.   Mar.   Sci.   64,   332–345.

639 https://doi.org/10.1093/icesjms/fsl035

640 Pawson, M.G., Pickett, G.D., Smith, M.T., 2005. The role of technical measures in the

641 recovery of the UK sea bass (*Dicentrarchus labrax*) fishery 1980-2002. Fish. Res.

642 76, 91–105. https://doi.org/10.1016/j.fishres.2005.06.006

643 Pickett, G.D., Kelley, D.F., Pawson, M.G., 2004. The patterns of recruitment of sea

644 bass, *Dicentrarchus labrax* L. from nursery areas in England and Wales and

645 implications   for   fisheries   management.   Fish.   Res.   68,   329–342.

646 https://doi.org/10.1016/j.fishres.2003.11.013

647 Pickett, G.D., Pawson, M.G., 1994. Sea bass biology, exploitation and conservation.

648 Chapman and Hall, London.

649 Politikos, D., Somarakis, S., Tsiaras, K., Giannoulaki, M., Petihakis, G., Machias, A.,

650 Triantafyllou, G., 2015. Simulating anchovy's full life cycle in the northern Aegean

651 Sea (eastern Mediterranean): A coupled hydro-biogeochemical-IBM model. Prog.

652   Oceanogr. 138, 399–416. https://doi.org/10.1016/j.pocean.2014.09.002

653 Punt, A.E., Butterworth, D.S., de Moor, C.L., De Oliveira, J.A.A., Haddon, M., 2016.

654   Management strategy evaluation: Best practices. Fish Fish. 17, 303–334.

655   https://doi.org/10.1111/faf.12104

656 Quayle, V.A., Righton, D., Hetherington, S., Pickett, G., 2009. Observations of the

657   Behaviour of European Sea Bass (*Dicentrarchus labrax*) in the North Sea,

658   Tagging and Tracking of Marine Animals with Electronic Devices, Reviews:

659   Methods and Technologies in Fish Biology and Fisheries. Springer Netherlands,

660   Dordrecht. https://doi.org/10.1007/978-1-4020-9640-2

661 Radford, Z., Hyder, K., Zarauz, L., Mugerza, E., Ferter, K., Prellezo, R., Strehlow, H.V.,

662   Townhill, B., Lewin, W.-C., Weltersbach, M.S., 2018. The impact of marine

663   recreational fishing on key fish stocks in European waters. PLoS One 13,

664   e0201666. https://doi.org/10.1371/journal.pone.0201666

665 Robinson, N.M., Nelson, W.A., Costello, M.J., Sutherland, J.E., Lundquist, C.J., 2017.

666   A Systematic Review of Marine-Based Species Distribution Models (SDMs) with

667   Recommendations   for   Best   Practice.   Front.   Mar.   Sci.   4,   1–11.

668   https://doi.org/10.3389/fmars.2017.00421

669 Sainsbury, N.C., Genner, M.J., Saville, G.R., Pinnegar, J.K., O'Neill, C.K., Simpson,

670   S.D., Turner, R.A., 2018. Changing storminess and global capture fisheries. Nat.

671   Clim. Chang. 8, 655–659. https://doi.org/10.1038/s41558-018-0206-x

672 Sambilay Jr, V., 1990. Interrelationships between swimming speed, caudal fin aspect

673   ratio and body length of fishes. Fishbyte 8, 16–20.

674 Scheffer, M., Baveco, J.M., DeAngelis, D.L., Rose, K.A., van Nes, E.H., 1995. Super-

675   individuals a simple solution for modelling large populations on an individual

676   basis. Ecol. Modell. 80, 161–170. https://doi.org/10.1016/0304-3800(94)00055-M

677 Schmolke, A., Thorbek, P., DeAngelis, D.L., Grimm, V., 2010. Ecological models

678   supporting environmental decision making: A strategy for the future. Trends Ecol.

679   Evol. 25, 479–486. https://doi.org/10.1016/j.tree.2010.05.001

680 Shin, Y., Cury, P., 2001. Exploring fish community dynamics through size-dependent

681   trophic interactions using a spatialized individual-based model. Aquat. Living

682   Resour. 14, 65–80. https://doi.org/10.1016/S0990-7440(01)01106-8

683 Thompson, B.M., Harrop, R.T., 1987. The distribution and abundance of bass

684   (*Dicentrarchus labrax*) eggs and larvae in the English Channel and Southern

685   North Sea. J. Mar. Biol. Assoc. United Kingdom 67, 263.

686   https://doi.org/10.1017/S0025315400026588

687 van der Vaart, E., Beaumont, M.A., Johnston, A.S.A., Sibly, R.M., 2015. Calibration

688   and evaluation of individual-based models using Approximate Bayesian

689   Computation. Ecol. Modell. 312, 182–190.

690   https://doi.org/10.1016/j.ecolmodel.2015.05.020

691 van der Vaart, E., Johnston, A.S.A., Sibly, R.M., 2016. Predicting how many animals

692   will be where : How to build , calibrate and evaluate individual-based models.

693   Ecol. Modell. 326, 113–123. https://doi.org/10.1016/j.ecolmodel.2015.08.012

694 Walker, N.D., Maxwell, D.L., Le Quesne, W.J.F., Jennings, S., 2017. Estimating

695   efficiency of survey and commercial trawl gears from comparisons of catch-ratios.

696   ICES J. Mar. Sci. 74, 1448–1457. https://doi.org/10.1093/icesjms/fsw250

697 Watkins, K.S., Rose, K.A., 2017. Simulating individual-based movement in dynamic

698 environments. Ecol. Modell. 356, 59–72.
699 https://doi.org/10.1016/j.ecolmodel.2017.03.025

700 Wilensky, U., 1999. NetLogo. Centre for Connected Learning and Computer-based
701 Modelling. Northwestern University, Evanstonm IL.
702 http://ccl.northwestern.edu/netlogo/

703 Woillez, M., Fablet, R., Ngo, T.T., Lalire, M., Lazure, P., de Pontual, H., 2016. A HMM-
704 based model to geolocate pelagic fish from high-resolution individual temperature
705 and depth histories: European sea bass as a case study. Ecol. Modell. 321, 10–
706 22. https://doi.org/10.1016/j.ecolmodel.2015.10.024

707 Woillez, M., Poulard, J.-C., Rivoirard, J., Petitgas, P., Bez, N., 2007. Indices for
708 capturing spatial patterns and their evolution in time, with application to European
709 hake (Merluccius merluccius) in the Bay of Biscay. ICES J. Mar. Sci. 64, 537–
710 550. https://doi.org/10.1093/icesjms/fsm025

Supporting information

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

Scenario	Description	Implementation
Constant fishing mortality		
F=0	No fishing	Multiplier of 0 applied to Fs of all individuals (fishing mortality switched off)
$F=F_{MSY}$	F_{4-15} = 0.203 (ICES, 2018c)	Multiplier of 0.781 applied to Fs of all individuals $$\frac{0.203}{F(2014)_{4-15}} = 0.781$$
$F=F$(2014)	$F=F$(2014)	Multiplier of 1 applied to Fs of all individuals
Management scenarios		
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. $$F_{tar}\begin{cases} F_{MSY}, & SSB \geq MSY\ B_{trigger} \\ F_{MSY} \times \dfrac{SSB}{MSY\ B_{trigger}}, & SSB < MSY\ B_{trigger} \end{cases}$$ 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). 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' (%)
Numbers	1.00	0.68	-0.49	0.47
SSB	0.93	8.32	0.39	8.31
TSB	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+
Growth												
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
Weight												
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
Swimming												
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
Mortality												
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
Stock assessment inputs												
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

720

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%
Constant fishing mortality						
$F=0$	**16511**			**42129**		
$F=F_{MSY}$	**8670**			**12813**		
$F=F(2014)$	**7507**			**10148**		
Management scenarios						
Offshore ban	**7745**	7072	8218	**10653**	5700	14133
Increase MCRS	**8676**	7813	9282	**13155**	7038	17451
Recreational limits	**8224**	7513	8723	**11726**	6272	15556
Catch & release	**8421**	7699	8929	**12196**	6524	16179
Commercial limit	**9035**	8266	9568	**12743**	7498	16734

725   Table 4: Results of projections under constant *F* and management strategies. Rxx% 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.

728
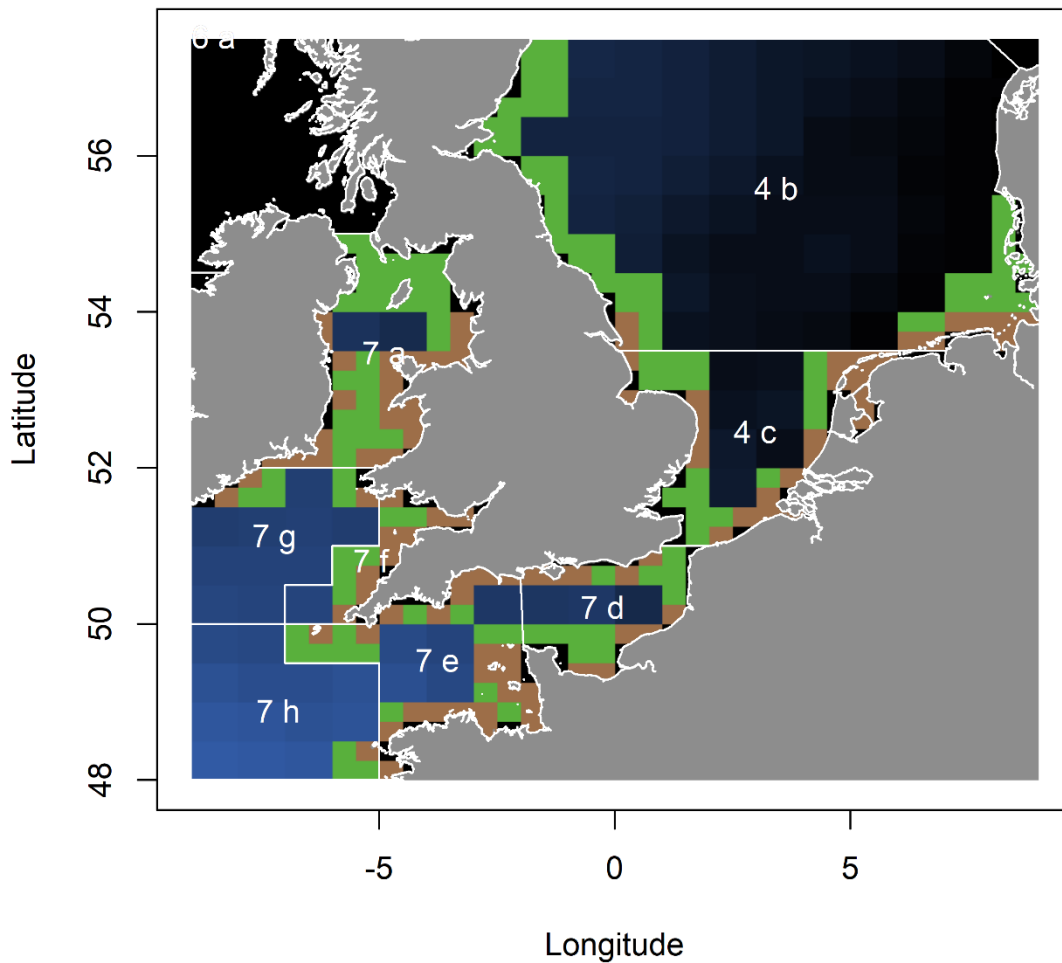
Figure 1: The model interface at set-up (1st January 1985). Coastal patches are represented in green,
nursery patches (also coastal) in brown and offshore patches in blue (with the blue gradient from dark
to light representing increasing SST; monthly averages). ICES divisions spanning the northern
assessment unit are superimposed. Regions for offshore spawning are defined as follows: North Sea
= 4.b-c; English Channel = 7.d-e, Celtic Sea = 7.f-h and Irish Sea = 7.a.
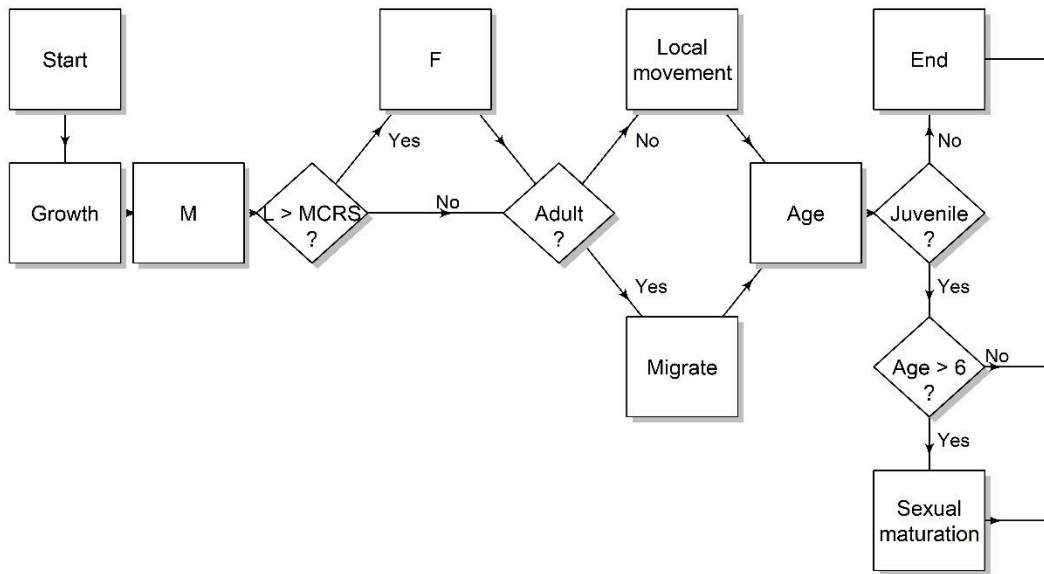
734

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.

738

a) migration schedule

b) migration route
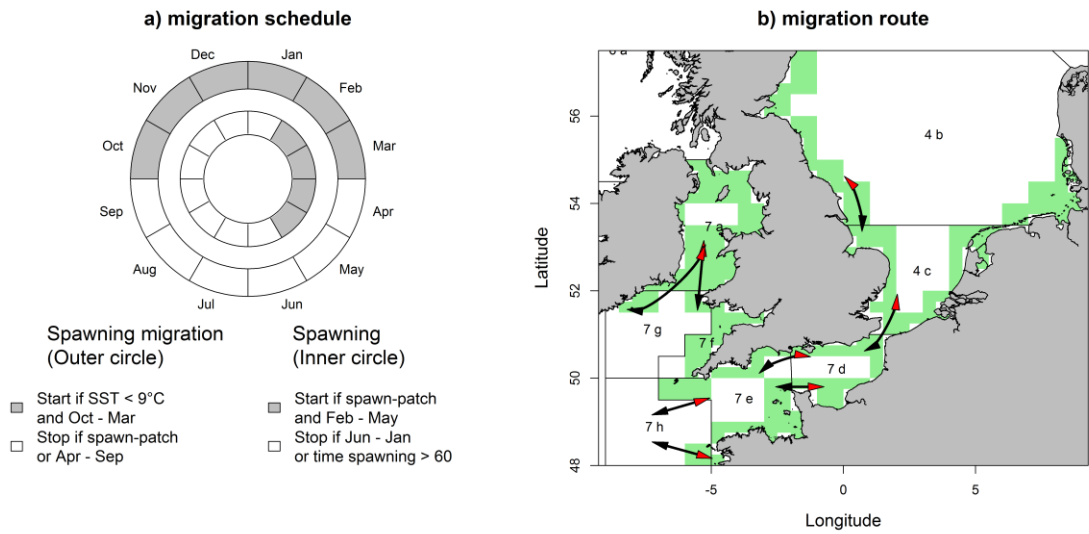
739

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.
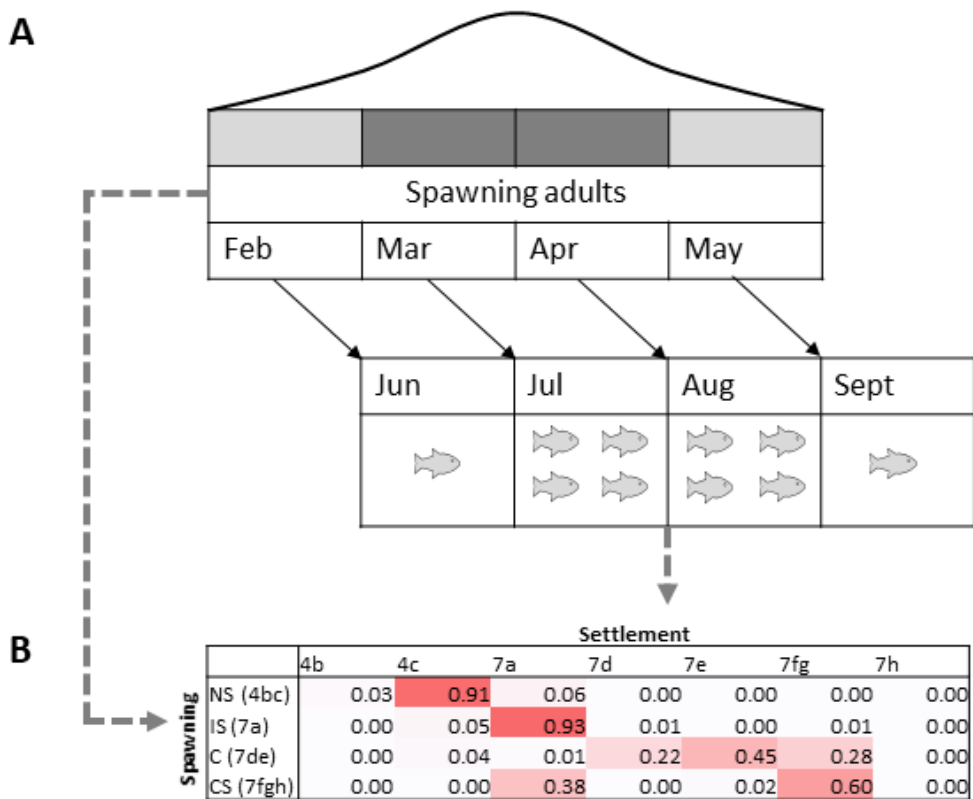
Figure 4: Schematic showing how the spatiotemporal distribution of recruiting individuals follows from the spatiotemporal distribution of spawning individuals. A: Ten individuals enter the IBM proportional to the number of spawning individuals in the corresponding month. B: Connectivity between offshore spawning regions and coastal settlement divisions. Each cell gives the probability of settling in a coastal division given the distribution of spawning individuals in offshore regions the corresponding month. Shading represents the strength of connectivity. Modified from Beraud et al. (2017).
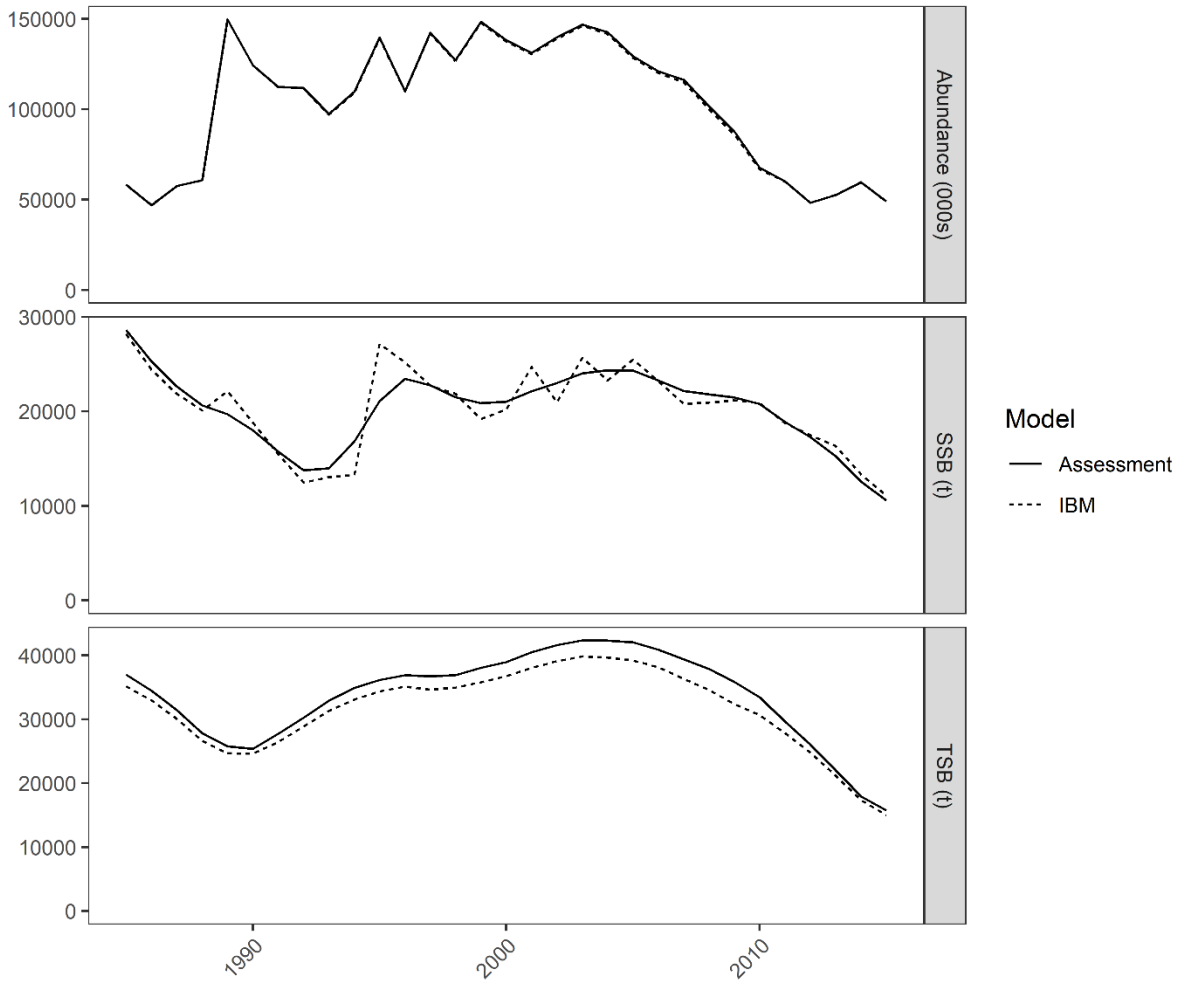
754

755   Figure 5: Abundance, SSB and TSB as estimated by the stock assessment and IBM.
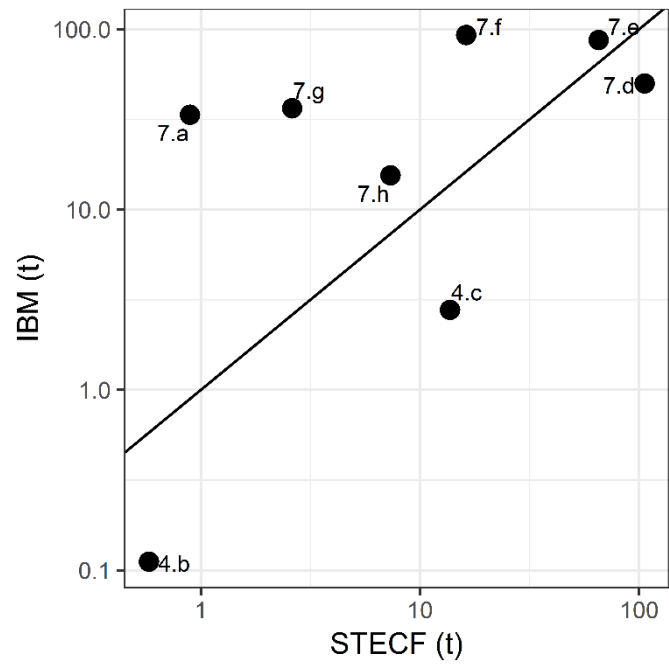
756
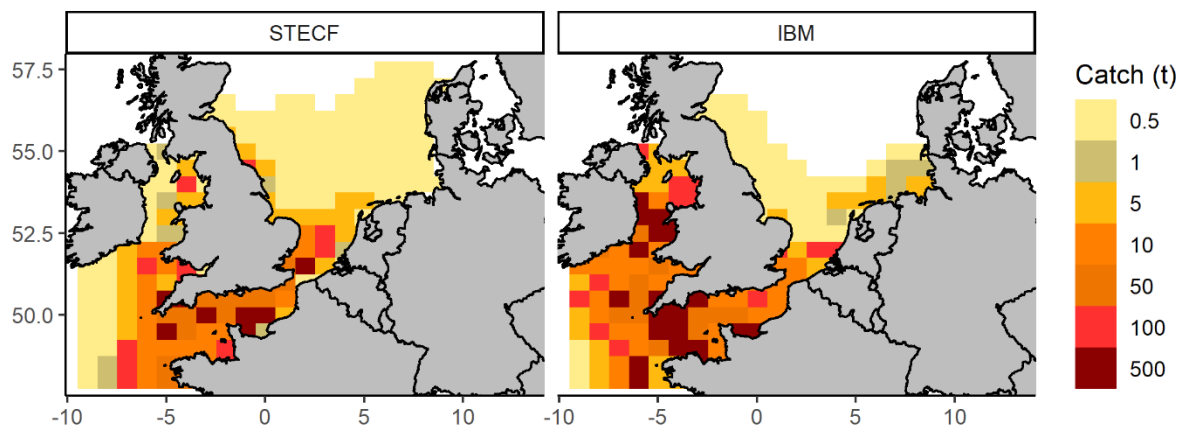
757

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.

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.

765

766
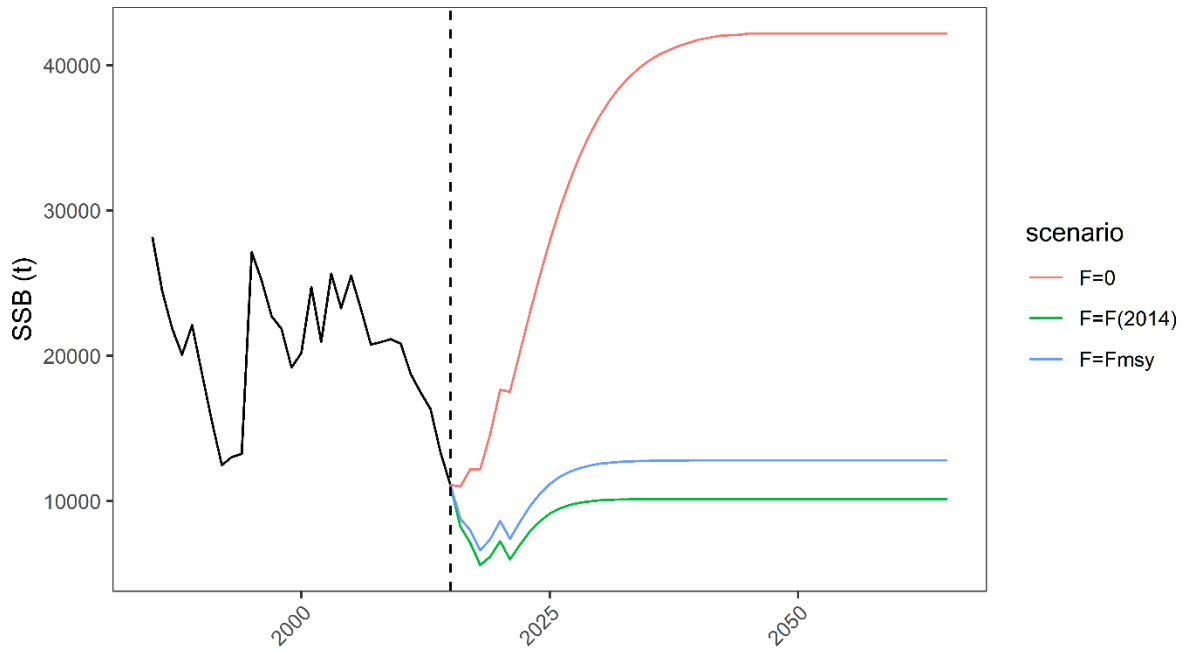
Figure 8: Forward 50-year projections of SSB (tonnes) under constant fishing mortality: F=0, F=F_{MSY}=0.203 (a reference for northern sea bass) and F=F(2014)=0.260. The black line shows the median of 10 hindcast simulations, the coloured lines the median for future projections and the dashed line the start of the projection period.

771
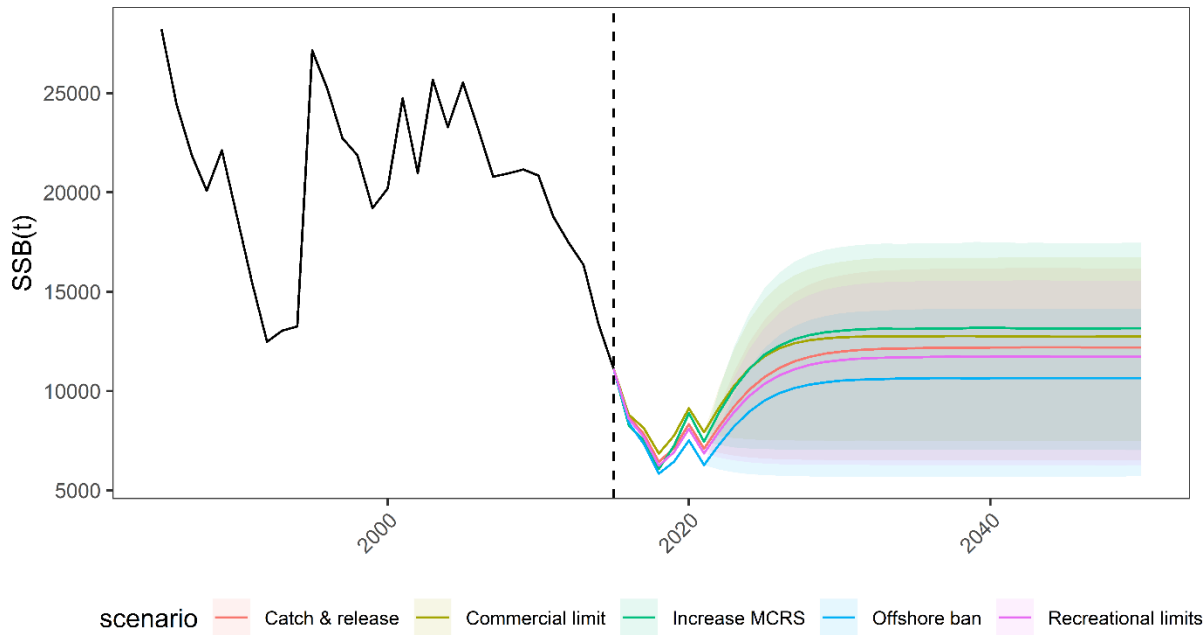
772

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