1   **Can we project changes in fish abundance and distribution in response to climate?**

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29

30 **Abstract**

31 Large scale and long-term changes in fish abundance and distribution in response to
32 climate change have been simulated using both statistical and process-based models.
33 However, national and regional fisheries management requires also shorter term
34 projections on smaller spatial scales, and these need to be validated against fisheries data.
35 A 26-year time series of fish surveys with high spatial resolution in the North East Atlantic
36 provides a unique opportunity to assess the ability of models to correctly simulate the
37 changes in fish distribution and abundance that occurred in response to climate
38 variability and change. We use a dynamic bioclimate envelope model forced by physical-
39 biogeochemical output from eight ocean models to simulate changes in fish abundance
40 and distribution at scales down to a spatial resolution of 0.5°. When comparing with these
41 simulations with annual fish survey data, we found the largest differences at the 0.5°
42 scale. Differences between fishery model runs driven by different biogeochemical models
43 decrease dramatically when results are aggregated to larger scales (e.g. the whole North
44 Sea), to total catches rather than individual species or when the ensemble mean instead
45 of individual simulations are used. Recent improvements in the fidelity of biogeochemical
46 models translate into lower error rates in the fisheries simulations. However, predictions
47 based on different biogeochemical models are often more similar to each other than they
48 are to the survey data, except for some pelagic species. We conclude that model results
49 can be used to guide fisheries management at larger spatial scales, but more caution is
50 needed at smaller scales.

51

Introduction

Anthropogenic greenhouse gas emissions and associated warming strongly changes ocean conditions, including temperature, salinity, ice cover, currents, oxygen, nutrients and seawater acidity. These physical-biogeochemical changes affect the distribution, abundance and productivity of phytoplankton, zooplankton and the fisheries that depend on them (Perry et al., 2005; Pörtner, 2010; Cheung et al., 2011; Simpson et al., 2011; Barange et al., 2014; Jennings and Collingridge, 2015; Fernandes et al., 2017; Maar et al., 2018; Lotze et al., 2019). Such changes are expected to continue during the 21st century under further global warming (IPCC, 2019) and have large implications for communities and industries that depend on marine species for food and income (Roessig et al., 2004; Cheung et al. 2012; Lam et al. 2012; Merino et al. 2012). A range of modelling approaches has been developed to project future changes in marine ecosystems and fisheries (e.g. Stock et al. 2011; Cheung et al. 2016). These models range from considering only the ocean physical dynamics and low trophic levels (Dunne et al., 2010; Butenschön et al. 2016; Yool et al. 2013) to high trophic levels of fisheries and conservation interest (Nielsen et al., 2018; Peck et al., 2018; Tittensor et al., 2018).

Species process-based bioclimate envelope models are commonly applied to study biological responses to global warming (Cheung et al., 2011; Jones et al. 2012). For example, the Dynamic Bioclimate Envelope Model (DBEM) is a combined mechanistic-statistical approach that has been applied to a large number of marine species globally. The DBEM projects changes in species distribution and abundance with explicit consideration of known mechanisms of population dynamics, dispersal (larval and adult) and ecophysiology, under changes in ocean temperature, salinity, oxygen, pH, upwelling, sea-ice extent and habitat type (Cheung et al. 2008; 2009, 2011). Simulations with the DBEM model show that high-latitude regions will experience high rates of species invasion while the tropics will have high rates of local extinction by the end of the 21st century under a high greenhouse gas emission scenario (Cheung et al., 2009; 2016). In addition, maximum catch potential is projected to decrease in the tropics while some high latitude regions may experience increases in potential catch because of changes in range and size of exploited marine species as well as changes in primary productivity under global warming (Cheung et al. 2010). Recently, the DBEM has been combined with a size-spectrum model (Jennings et al., 2008) to evaluate the effects of inter-specific interactions

84   in projecting species distribution (Fernandes et al., 2013a). Size spectrum theory
85   accounts for energy transfer from primary production to individuals of different body
86   sizes to estimate abundance/biomass and their flows in marine ecosystems (Jennings et
87   al. 2008). The resulting integrated SS-DBEM (size-spectrum and DBEM model) projected
88   slower fish species shifts than in models that did not account for energy limitation. The
89   SS-DBEM has also been applied to several conservation issues (Jones et al., 2013; Queiros
90   et al., 2015) as well as socio-economic assessments in the North East Atlantic (Mullon et
91   al., 2016; Fernandes et al., 2017; Queiros et al., 2016) and developing countries
92   (Fernandes et al., 2016). However, projections of future species and fishery distributions
93   at local scales are uncertain (Payne et al., 2016, Cheung et al. 2016, Frölicher et al. 2016).

94

95   The model simulations are often not well constrained by observational data as the
96   available observations are limited in time and space. However, the availability of an
97   extensive compilation of data describing the distribution and abundance of North Sea
98   fishes from 1982 to 2007 (Simpson et al., 2011) provide us the opportunity to evaluate
99   the accuracy of projections of simulated fish abundance and distributions from the SS-
100 DBEM model. The data were collected by ICES co-ordinated bottom trawl surveys (ICES,
101 2012). We compare the data with simulations of fish abundance and distribution
102 conducted by linking multiple biogeochemical models and the SS-DBEM of commercial
103 fish populations. Thereby, we assess the likely reliability of future projections of fish
104 stocks under climate change and the impact of spread in ocean biogeochemistry
105 simulations on the fisheries projections. In addition, the combination of observation
106 based atmospheric boundary conditions and atmospheric boundary conditions from
107 Earth system models allows for an indication as to how the projections of fish abundance
108 and distribution are affected by the internal variability of these systems in contrast with
109 the more realistic variability from the reanalysis datasets. This understanding can be
110 applied when considering other ecological modelling approaches that occupy a similar
111 niche to SS-DBEM, many of which are the focus of inter-comparison efforts within the
112 international FISH-MIP initiative (Nielsen et al., 2018; Peck et al., 2018; Tittensor et al.,
113 2018; Heike et al., 2019).

114

Methods

We use output from three different ocean biogeochemical models (Table 1) to generate the environmental and biological conditions (temperature, salinity, oxygen, pH, currents and primary production) that drive the fish community model (size-spectrum dynamic bioclimate envelope model; SS-DBEM; Fernandes et al., 2013a). The ocean biogeochemical models are either run in fully coupled mode (i.e. coupled to a freely evolving atmosphere, land, and sea-ice model) or run in hindcast mode (i.e. ocean-only and forced at the ocean's surface with observed or model-derived atmospheric conditions). We use multiple versions with different horizontal resolution of the three ocean biogeochemical models to examine how an increase in spatial resolution and/or different ocean biogeochemical model output influences the SS-DBEM simulations (Table 1). Furthermore, runs for the same model are used to compare different generations of the same model and spatial resolutions. Fish distribution and abundance as simulated between 1982 to 2007 are compared with 26 years of data from fish surveys by European marine laboratories with a comparable spatial resolution (Simpson et al., 2011).

<u>Ocean biogeochemical models</u>

The choice of the biogeochemical model used to force the DBEM may have a significant effect on forecasts of fish species abundance and distribution, especially in shelf seas regions where predictions of the biogeochemical models can differ markedly. For this reason, we chose to force the SS-DBEM with a diverse suite of output from three different ocean biogeochemical models run under a range of different forcing modes in order to cover the impact of the major sources of uncertainty in the biogeochemical forcing on the fisheries mode. These forcing modes differ in the underlying model configuration used and, as a result, in their relationship with real-world patterns of temporal variability. The forcing modes used here are:

1. "Ocean-only hindcast mode", where an ocean-only model is driven by observationally-derived surface forcing at its air-sea interface. This mode necessarily includes real-world trends and patterns of variability. There are a number of methods available for creating the so-called reanalysis forcing used in this mode, and this study exploits model simulations using several different approaches.

2. "Fully-coupled mode", where the model configuration includes an atmospheric component that interacts dynamically with the ocean component. This mode includes temporally-varying factors such as radiatively-active gases, so should reproduce overall climate trends (e.g. global warming). But each fully coupled model will show variability between runs whereas the observed data represent a single realisation for each time point. For example, the real ocean experienced an El Niño in 1997-1998. The coupled simulations may have had a La Niña, El Niño or been neutral at this time. Only the averages and variances of this internal variability are consistent with the real world.

3. "Coupled-forced ocean-only mode", where an ocean-only model is driven by surface forcing derived from a fully-coupled model. This mode is similar to the first mode, but uses surface forcing output from a model running in the second mode rather than observationally-derived forcing. As such, it may reproduce observed long-term trends, but not specific temporal variability. This approach is typically used where projection simulations into the future with relatively high ocean model resolution or model downscaling are required (Yool et al., 2015).

165 Note that both ocean-only and coupled modes have limitations in the context of decadal-
166 scale simulations: the forced ocean-only mode excludes any feedbacks between ocean
167 and atmosphere (and the associated uncertainties), while the fully-coupled mode and
168 coupled-forced ocean-only mode generate less directly-comparable data with present
169 day conditions (particularly when phasing of internal variability is relevant). The use of
170 a coupled prediction system as used in the WCRP Decadal Climate Prediction Project
171 could reduce these shortcoming, however, these systems currently focus on physical
172 climate and exclude biogeochemical components.

173

174 Table1 summarises the models from which output has been used to force the SS-DBEM
175 model.

Name of model run	Horizontal ocean resolution	Forcing mode (Forcing dataset)
GFDL-hindcast	1°	Hindcast (CORE2 reanalysis)
GFDL-coupled	1°	Fully coupled
GFDL-coupled-esm2m	1°	Fully coupled
MEDUSA-coupled-forced	1°	Coupled-forced (HadGEM2-ES)
ERSEM-hindcast-lowres	0.25°	Hindcast (DFS 4.1)
ERSEM-hindcast-lowres2	0.25°	Hindcast (DFS 5)
ERSEM-hindcast-highres	0.125°	Hindcast (ERA 40 & ECMWF)

176 Table 1. Characteristics of the different ocean biogeochemical simulations used in this study.

177

178 The models are:

179 1) The National Oceanographic and Atmospheric Administration (NOAA) and
180 Geophysical Fluid Dynamic Laboratory (GFDL) Earth System Model. GFDL is a
181 global model where: 1) GFDL CM2.1 is using MOM4 for its physics (Delworth et al.
182 2006) and TOPAZv0 for its biogeochemistry (Henson et al., 2010); and 2) GDFL
183 ESM2M is using MOM4p1 for its physics and TOPAZv2 for its biogeochemistry
184 (Dunne et al., 2010; 2012; 2013). TOPAZ simulates the cycling of carbon, nitrogen,
185 phosphorus, silicon, iron, oxygen, alkalinity and lithogenic material, and includes
186 three phytoplankton functional groups and one zooplankton. In this work the
187 GFDL CM2.1 is run in both hindcast and fully-coupled modes, whereas GFDL
188 ESM2M is run in fully coupled mode. The hindcast run here uses boundary
189 conditions of bulk air properties, incoming fluxes of radiation and freshwater, and

190   surface wind stress as prescribed by the observationally-derived CORE-2

191   reanalysis product (Large & Yeager, 2009).

192 2) The European Regional Seas Ecosystem Model (ERSEM, Butenschön et al. 2016)

193   coupled to the NEMO ocean model (low resolution; Madec, 2008) and the

194   POLCOMS ocean model (high resolution; Holt et al., 2001). Hindcast mode

195   simulations are used in this study both at different resolutions and under different

196   observationally-derived atmospheric boundary forcing including DFS 4.1

197   (Brodeau et al., 2010), ERA 40 & ECMWF (Uppala et al., 005) and DFS 5 (Brodeau

198   et al., 2010). ERSEM is a biogeochemical model for the lower trophic levels of the

199   pelagic and benthic ecosystem, and uses a functional-groups approach that

200   incorporates four phytoplankton, three zooplankton and bacterioplankton to

201   simulate decoupled carbon and nutrient dynamics (Blackford et al., 2004;

202   Butenschön, 2016). All ERSEM models here are regional models where the highres

203   simulation is a regional set-up for the North-West European Shelf with details on

204   the configuration, initial conditions, boundary conditions and forcings are

205   available in (Holt et al. 2012). The two ERSEM lowres simulations are from a

206   NEMO-ERSEM configuration for the Atlantic Ocean at 0.25 degree (further details

207   in Memery and Allen, 2011; Allen et al., 2014). The two different versions of this

208   system reflect an update in model parametrisation and atmospheric forcing and

209   forecasting performance differences between using higher and lower results. Both

210   versions were included in the analysis in order to investigate how the resulting

211   changes propagate to the higher trophic level model.

212 3) The MEDUSA biogeochemical model (Yool et al., 2013a, 2013b) coupled to the

213   NEMO ocean model. Output from a coupled-forced ocean-only mode simulation is

214   used here, with the forcing derived from a CMIP5 simulation of the HadGEM2-ES

215   ESM (Collins et al., 2011). MEDUSA is lower complexity model, with two

216   phytoplankton, two zooplankton, three nutrients (N, Fe, Si) and slow-/fast-sinking

217   detritus compartments (Yool et al. 2013a).

218 In terms of biogeochemical complexity, MEDUSA is the simplest model considered here,

219 ERSEM is the more complex, with GFDL intermediate. Note that different versions of the

220 GDFL and ERSEM models were used here as well as different simulation configurations.

221   These differences relate to model evolution and improvement, including parameter

222   updates and the use of different spatial resolutions.

223

224   <u>Fish model</u>

225

226   The size-spectrum dynamic bioclimate envelope model (SS-DBEM) described in

227   Fernandes et al. (2013a) is used to simulate changes in abundance and distribution of fish

228   species. The SS-DBEM projects changes in species distribution and abundance with

229   explicit consideration of known mechanisms (Table 2) of population dynamics, dispersal

230   (larval and adult) and ecophysiology, under changes in ocean temperature, salinity,

231   upwelling, sea-ice extent and habitats (Cheung et al. 2011), and species interactions

232   based on size-spectrum theory and habitat suitability (Fernandes et al., 2013a). In SS-

233   DBEM, current distributions of the studied species are first estimated based on habitat

234   suitability (Close et al. 2006). This is done based on a global dataset of observed

235   abundance data from Cheung et al. (2008; available at fishbase.org which redirects to

236   maps hosted at aquamaps.com) overlaid with environmental data (temperature, salinity,

237   oxygen and pH at sea surface for pelagic species and at sea bottom for demersal species

238   as well as depth and distance to ice) from biogeochemical models described above. It is

239   assumed that the carrying capacity of each species in each area is partly dependent on

240   the inferred preference profiles which depend on the projected biogeochemical

241   conditions (e.g. temperature, salinity, pH and currents) but limited by primary

242   production. Simultaneously, the model considers each species' physiological preferences

243   and tolerances to temperature, and sensitivity of key parameters determining the

244   species' mechanisms (mortality, growth and length-weight relationship). Natural

245   mortality rate is estimated from an empirical equation (Pauly, 1980) which considers

246   weight, growth and temperature. The model growth algorithm (Cheung et al., 2011) is

247   derived from the von Bertalanffy growth function (VBGF; von Bertalanffy, 1951). Therein,

248   growth is viewed as the difference between anabolic and catabolic processes. The

249   temporal and spatial patterns of pelagic larval dispersal (Cheung et al., 2008) are

250   modelled by a two-dimensional advection-diffusion equation (Sibert et al. 1999; Gaylord

251   & Gaines 2000; Hundsdorfer & Verwer, 2003). Adult dispersal is calculated from the

252   dispersal or movement rate using an algorithm employed in an Eulerian spatial

253   ecosystem simulation model (Walters et al. 1999).

254 Table 2. Table summarizing main equations and parameters to consider the species

255 mechanisms in SS-DBEM. Further details are given in the associated references.

Mechanism	Equation	Parameters
Growth = anabolism – catabolism (Pauly 2010; Cheung et al., 2011)	$G = HW^a - kW$ $H = g[O_2] * e^{-j1/T}$ $k = h[H^+] * e^{-j2/T}$	H = anabolism coefficient k = catabolism coefficient W = body weight a = anabolism exponent (0.5 to 0.95) W_∞ = asymptotic weight The coefficients g and h were derived from the average W_1, K, and environmental temperature (T) of the species reported in the literature.
Length-Weight	$W = a * L^b$	W = weight L = length
Size-spectrum production (Jennings et al., 2008; Fernandes et al., 2013)	$P = exp (25.22 - E/kT) * W^{0.76}$	E = activation energy of metabolism k = Boltzmann's constant T = temperature in Kelvin (°C+273)
Intrinsic population growth rate (Hilborn & Walters,1992)	$G = r * A * (1 - (A/KC))$	r = intrinsic rate of population increase A = the relative abundance KC = population carrying capacity
Larval dispersal (Hundsdorfer & Verwer 2003; Cheung et al., 2008)		D = diffusion parameter (u, v) = velocity parameters LAV = larvae recruitment
Adult movement	$Cm * h^{-1}$	Cm = centimetre h = hour
Natural mortality	$M = -0.4851 - 0.0824 * log(Winf) + 0.6757 * log (K) + 0.4687 * log(T)$	Winf = asymptotic weight K = von Bertalanffy growth parameter T = average water temperature in the animal's range.

256
257 The SS component of the model addresses resource competition between different

258 species co-occurring in any given cell by comparing the biomass that can be supported in

259 the cell, as determined from primary production and the size-spectrum model, with the

260 energy demanded by the abundance of the species predicted to inhabit this cell. This

261 allocation is based on habitat suitability considerations and a generic group (other

262 species) that can also compete for energy particularly if there is a surplus is available

263 (Fernandes et al 2013a). If the energy demanded by all species in the cell exceeds the

264 energy available, then the model allocates available energy to each species in proportion

265 to its energy demands. If the energy demanded by all the species is lower than the energy
266 available, the surplus energy is allocated according to the proportional energy demand of
267 the species present. The rate at which this energy can be assimilated is limited by
268 constraints on species' growth rates as described in Fernandes et al (2013a).

269

270 The model can consider fishing pressure in relation to maximum sustainable yield
271 (MSY). MSY is defined as the highest average theoretical equilibrium catch that can be
272 continuously taken from a stock under average environmental conditions (Hilborn &
273 Walters, 1992). Based on a simple logistic population growth function and under
274 equilibrium conditions, MSY can be defined as:

275

276 $MSY = B\infty * intR / 4$

277

278 where intR is the intrinsic rate of population increase and B∞ is the biomass at carrying
279 capacity (Schaefer, 1954; Sparre and Venema, 1992). In our application, the intR values
280 are calculated based on natural mortality (Pauly 1980; Cheung et al., 2008). This is an
281 approximation and not as reliable as estimates of biomass using survey-based methods
282 (McAllister et al. 2001; Pauly et al., 2013). However, these estimates have proven to be
283 significantly correlated with those from aggregated stock assessments (Froese et al.,
284 2012; Fernandes et al., 2013). This fishing mortality is applied uniformly across all the
285 cells according to scenarios of fishing (e.g. 0.8 or 1.2 times MSY) and do not aims to
286 reproduce exact past fisheries effort distribution. Therefore, in this work no fishing
287 mortality scenario was activated in the model projections. Future work based on catch
288 and fishing effort reconstructions (Watson et al., 2017; Taconet et al., 2019) may allow
289 estimates of historical non-uniform fishing mortality to be included in models.

Fisheries survey data

291 Eleven standardised and long-term fisheries surveys from 1982 to 2007 covering all year

292 seasons (Simpson et al., 2011) were used to validate the model (Fig. 1). These surveys

293 (AFBI Iris Sea Q3, AFBI Irish Sea Q1, CEFAS Celtic Sea, CEFAS Eastern Channel, CEFAS

294 Irish Sea, CEFAS North Sea, CEFAS Western Channel, FRS NW Scotland Q1, FRS NW

295 Scotland Q4, ICES IBTS North Sea Q1, MBA Western Channel) were collated by Simpson

296 et al. (2011) and now available at ICES DATRAS online database (www.ices.dk/marine-

297 data/data-portals/Pages/DATRAS.aspx). To control for the differing effort between

298 surveys, the swept area for each haul (over 22 000 hauls with six different gears) was

299 calculated using estimates of wing-spread for Grande Ouverture Verticale trawls from

300 Fraser et al. (2007):

301

302 Area swept = $(((6.85 * (\log10(depth))) + 5.89) * distance) / 10^6$

303

304 Where area swept is in km2, and depth and distance are in meters. A tow speed of 4 knots

305 (7.4 km h^{-1}) was assumed for the duration of the haul, except for data from the Celtic sea

306 collected by Agri-Food and Biosciences Institute, Belfast, UK, where the data were

307 originally provided as number of individuals per 3 nautical miles (~5.6 km). The 10^6

308 scaling converts from m^2 to km^2.

309

310 Catchability estimates (Table 3) were used to provide more robust estimates of

311 abundance for each species by sizes (Sparholt 1990; Fraser et al., 2007). An average

312 catchability estimate was applied to similar species, where individual species values were

313 not available.

314

315 Corrected abundance = uncorrected abundance*(1/catchability)

316

317   Table 3. Table summarizing catchability correction values by species and sizes (based on

318   Simpson et al., 2011).

Species	Size (cm)	Catchability correction
Chelidonichthys lucerna	1-20, 21-22, 23-25, 26-30, 31-33, 34, 25-80	0.21, 0.18, 0.17, 0.16, 0.14, 0.13, 0.11
Clupea harengus	1-100	0.1
Gadus morhua	1-31, 32-36, 37-39, 40-42, 43-45, 46-47, 48-49, 50-51, 52-53, 54-55, 56, 57-58, 59, 60-61, 62, 63-64, 65, 66, 67, 68, 69-70, 71, 72, 73, 74, 75, 76, 77, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 93, 94, 95, 96, 97-200	0.16, 0.17, 0.18, 0.19, 0.2, 0.21, 0.22, 0.23, 0.24, 0.25, 0.26, 0.27, 0.28, 0.29, 0.3, 0.31, 0.32, 0.33, 0.34, 0.35, 0.36, 0.37, 0.38, 0.39, 0.4, 0.41, 0.42, 0.43, 0.44, 0.45, 0.46, 0.47, 0.48, 0.49, 0.5, 0.52, 0.53, 0.54, 0.55, 0.56, 0.58, 0.59, 0.6, 0.61, 0.63, 0.64, 0.65, 0.67
Glyptocephalus cynoglossus	1-20, 21, 22-23, 24, 25, 26-27, 28-31, 32-34, 35-38, 39-60	0.11, 0.09, 0.08, 0.07, 0.06, 0.05, 0.04, 0.03, 0.04, 0.05
Hippoglossoides platessoides	1-5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16-19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30-60	0.11, 0.16, 0.2, 0.23, 0.26, 0.29, 0.32, 0.34, 0.36, 0.37, 0.38, 0.39, 0.38, 0.37, 0.35, 0.33, 0.31, 0.29, 0.26, 0.22, 0.19, 0.15, 0.1
Lepidorhombus whiffiagonis	1-60	0.06
Melanogrammus aeglefinus	1-11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26-27, 28-33, 34-35, 36-37, 38, 39, 40, 41, 42, 43, 44, 45, 46-80	0.01, 0.04, 0.06, 0.09, 0.11, 0.13, 0.15, 0.17, 0.19, 0.2, 0.21, 0.23, 0.24, 0.25, 0.26, 0.27, 0.28. 0.27, 0.26, 0.25, 0.24, 0.22, 0.21, 0.2, 0.18, 0.16, 0.14, 0.12
Molva molva	1-11, 12-200	0.05, 0.1
Raja montagui	1-200	0.15
Sardina pilchardus	1-100	0.1
Scomber scombrus	1-100	0.19
Scophthalmus maximus	1-21, 22-24, 25-28, 29-31, 32-34, 35-38, 39-41, 42-200	0.05, 0.06, 0.07, 0.08, 0.09, 0.1, 0.11, 0.12
Scyliorhinus canicula	1-200	0.22
Solea solea	1-22, 23-60	0.04, 0.05
Sprattus sprattus	1-100	0.1
Trachurus trachurus	1-100	0.19
Trisopterus esmarkii	1-100	0.19
Trisopterus luscus	1-11, 12-60	0.05, 0.1

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320

Model validation

322 All survey data were aggregated into a 0.5º × 0.5º cell grid to match the SS-DBEM grid. To

323 compare simulated changes with observations from surveys, time-series at different

324 aggregation scales (e.g. aggregating all the cells, or all the species in a cell) were extracted

325 and projected biomass was scaled to lie between 0 and 1. Since multiple species at

326 multiple cells are considered, we ensured that results were comparable by omitting time-

327 series of survey data with more than 3 years of missing data. Then, time-series output

328 from the SS-DBEM models were extracted for the remaining years, species and cells

329 where there were data from the surveys at the 0.5º × 0.5º grid and yearly resolution. This

330 restricted the data that could be analysed to the time period 1982 to 2007 (26 years) and

331 to 18 species, including 5 pelagic species: Atlantic herring (*Clupea harengus*), Atlantic

332 mackerel (*Scomber scombrus*), Atlantic horse mackerel (*Trachurus trachurus*), European

333 pilchard/sardine (*Sardina pilchardus*), sprat (*Sprattus sprattus*); and 13 demersal

334 species: haddock (*Melanogrammus aeglefinus*), plaice (*Hippoglossoides platessoides*),

335 witch (*Glyptocephalus cynoglossus*), megrim (*Lepidorhombus whiffiagonis*), cod (*Gadus

336 morhua*), common sole (*Solea solea*), lesser spotted dogfish (*Scyliorhinus canicula*),

337 Norway pout (*Trisopterus esmarkii*), turbot (*Scophthalmus maximus*), tub gurnard

338 (*Chelidonichthys lucerna*), pouting/bib (*Trisopterus luscus*), ling (*Molva molva*) and

339 spotted/cuckoo ray (*Raja montagui*). We chose these species as they are both

340 commercially important for local fisheries and include some species with distributions

341 centred on the North Sea, Celtic Sea and Irish Sea alongside those with more northerly

342 (high latitude) and southerly (low latitude) centres of distribution.

343

344 We compared model projections with data at different scales, spanning those used in

345 previously published projections of climate-driven changes in fish distribution and/or

346 abundance (e.g. Fernandes et al., 2016; Fernandes et al., 2017; Jones et al., 2013; Mullon

347 et al., 2016; Queiros et al., 2015; Queiros et al., 2016; Coccoli et al., 2018). We consider

348 the following (Fig. 1): (1) all the cells are considered for all the species (325 cells and 18

349 species) named "Species by cells" in a first spatial validation; (2) time series for individual

350 species aggregated over all cells ("All species" or individual species) in a first temporal

351 validation; and, (3) time series for each of the 325 cells where all the species are

352 aggregated ("All cells" or individual cells) in a spatial and temporal validation, and, (4) a

353 time series for each species aggregating all the cells for which survey information was

available (species cells sum). A species could be present in between 75 (turbot) and 325 (Herring) cells.
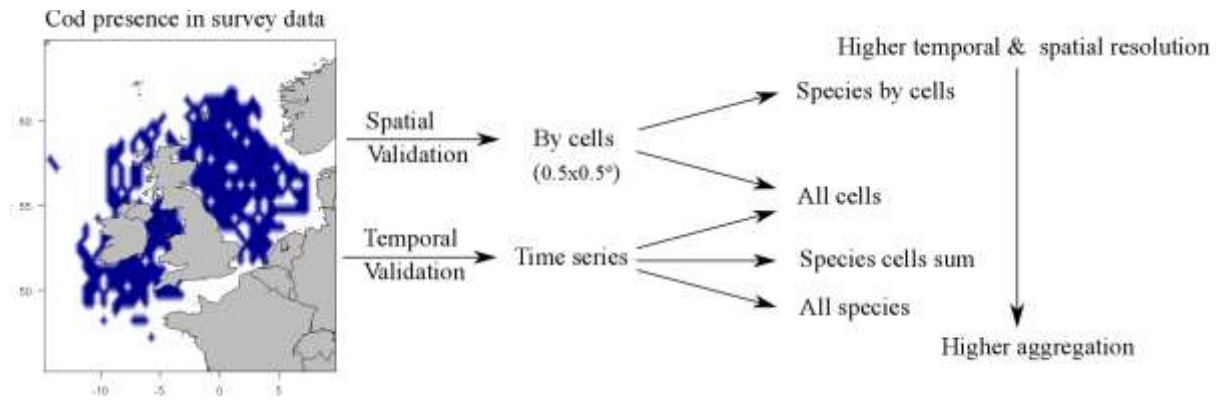

Figure 1. Example of survey data for cod (one of the species with more coverage) in Celtic Sea, Irish Sea and North Sea (left side). Scheme of spatial and temporal validation resolutions in the right side.

The time-series 1-3 were generated for both the survey data and the model projections and comparisons between data and projections were reported as absolute error (AE):

$$AE_j = |p_j - x_j| \qquad\qquad (1)$$

where, p is the scaled biomass predicted in a SS-DBEM model in a particular year for a species, and x is the scaled biomass from the survey. The use of scaled values enables direct comparison of data and SS-DBEM projections across species and levels of aggregation.

Results

The main environmental drivers of SS-DBEM and other fisheries models are temperature and net primary production, which are obtained from the ocean biogeochemical models. Most forcing models show an increasing trend in temperature over the 1982-2007 period for which we have fish survey data (Fig 2). There is spread in the absolute temperature with some models simulating temperatures of 10.5 to 11.5 °C in cells included in the fish surveys, while others projecting temperatures of 9.5 to 10.5°C (Fig. 1). Trends in primary production are more uncertain than those in temperature, with some models showing no trends, while others project decreases of 10-15% over the 1982-2007 period.
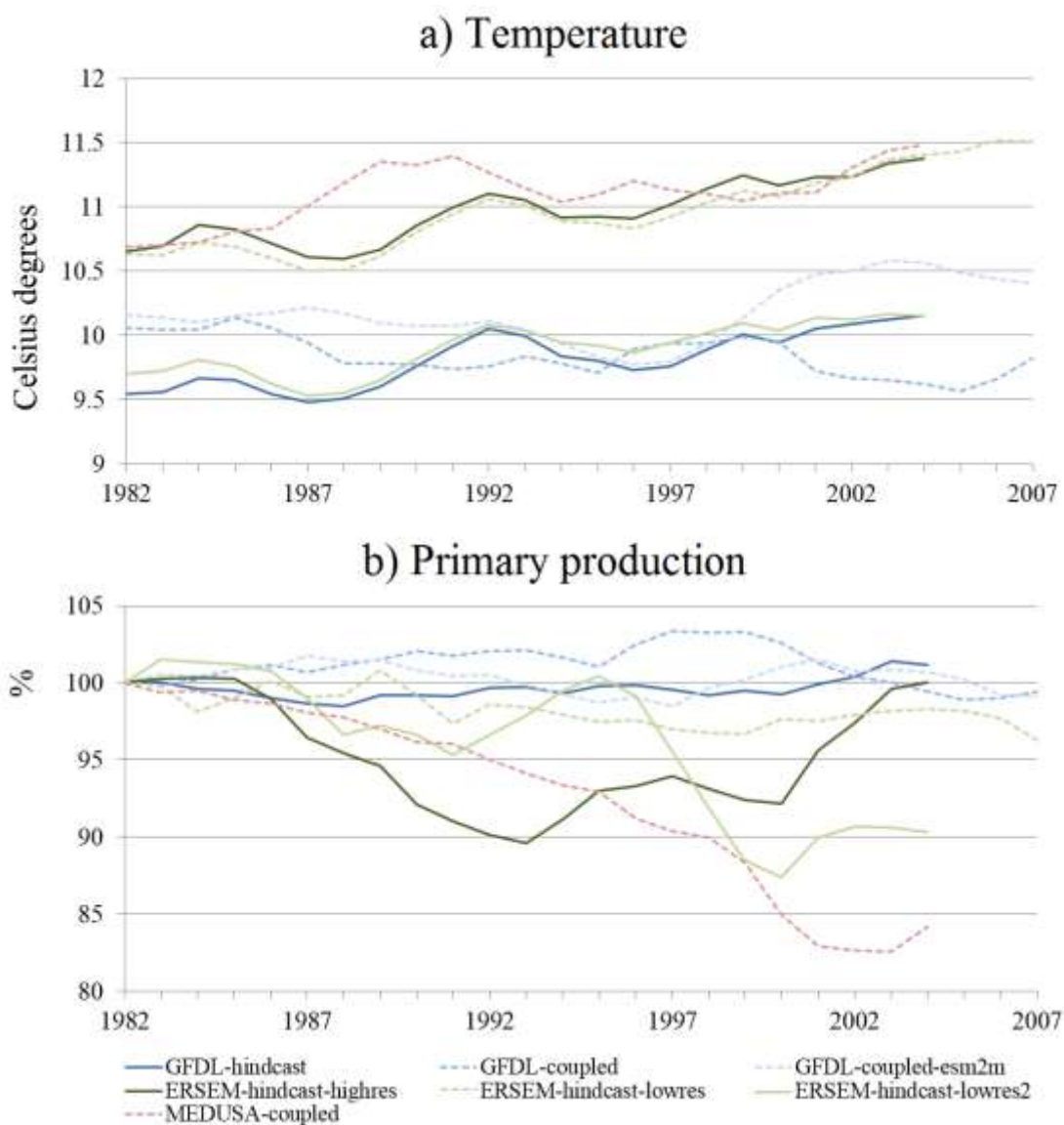
Figure 2. Simulated annual sea surface temperature and net primary production changes from 1982 to 2007 of different biogeochemical models. The reported values are the average across cells where fish survey data is considered. The time-series has been smoothed with a five-year moving average. Solid lines indicate reanalysis projections and dashed lines fully coupled projections.

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There are multiple examples where there is a good fit between SS-DBEM projections and survey data with high correlation (Pearson) among projections and survey data (Fig. 3): herring between 0.73 (GFDL-hindcast) and 0.96 (GFDL-coupled), Cod 0.76 (MEDUSA-coupled-forced), haddock between 0.92 (ERSEM-hindcast-lowres2) and 0.95 (GFDL-coupled), sprat between 0.88 (GFDL-hindcast) and 0.96 (ERSEM-hindcast-lowres), sole between 0.81 (ERSEM-hindcast-highres) and 0.91 (GFDL-coupled),
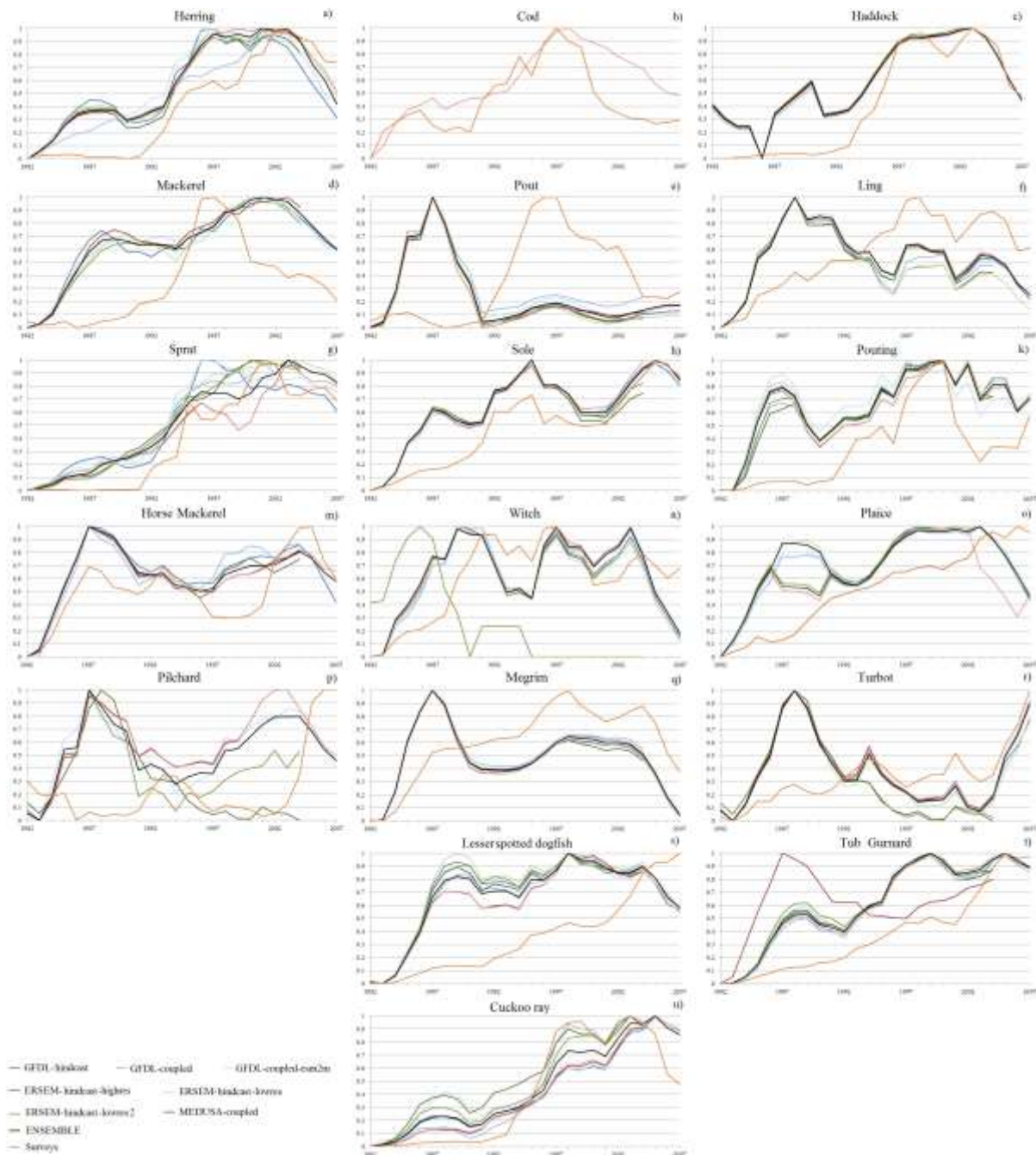

Figure 3. Scaled biomass projections (5 years moving average) for 5 pelagic and 13 demersal species with different biogeochemical model forcings in cells where fish survey abundance data were also available. Note that Cod projections failed with several inputs from biogeochemical models.

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pouting between 0.65 (GFDL-coupled-esm2m) and 0.78 (ERSEM-hindcast-highres), horse mackerel between 0.69 (ERSEM-hindcast-lowres) and 0.76 (MEDUSA-coupled-forced), plaice between 0.49 (MEDUSA-coupled-forced) and 0.87 (ERSEM-hindcast-highres), or cuckoo ray between 0.79 (GFDL-coupled-esm2m) and 0.99 (GFDL-coupled). Witch is another species where most models seem to perform well with correlations between 0.59 (ERSEM-hindcast-lowres2) and 0.75 (GFDL-coupled), but where one model performs very bad showing high negative correlation of -0.74 (ERSEM-hindcast-lowres). Model runs for mackerel and megrim do not perform so well, but still show competitive correlations between 0.58 (GFDL-hindcast) and 0.66 (ERSEM-hindcast-lowres) for mackerel, and between 0.45 (ERSEM-hindcast-highres) and 0.54 (GFDL-coupled) for Megrim. Model runs for dogfish and tub can achieve high correlations of 0.74 (GFDL-coupled) and 0.87 (GFDL-coupled) respectively, however some of the models show also very low performances of 0.36 (ERSEM-hindcast-lowres2) and 0.3 (MEDUSA-coupled-forced) respectively. Finally, a few species show very low correlations for all model runs (Ling between 0.01 and 0.28) or even negative correlations: turbot between -0.17 and 0.44, pout -0.41 and -0.47, and pilchard between -0.14 and -0.54.

These results suggest that an increase in spatial resolution does not necessarily mean a higher performance in species biomass trends. The highest resolution model (ERSEM-hindcast-highres) sometimes shows higher correlation with survey data for some demersal species (pouting and plaice) than the lowest resolution models. However, for other pelagic and demersal species often the lowest resolution model runs (GFDL) are the ones showing the highest correlations (e.g. herring, haddock, sprat, sole). In other cases, although the higher resolution model runs may show superior correlations these may be very close to lower resolution model correlations and not be statistically significant different from them (paired t-test).

Fits tend to improve in later years in the time series for several species, perhaps reflecting the reduction in fishing mortality (Simpson et al., 2011) and its effect on survey data distributions in later years (Fig. 3). However, this could also be the result of a more representative area being covered by the surveys since their geographical extend has increased over time (Baudron et al., 2020).

429   The different biogeochemical models generate rather similar error, with more variation
430   between models for the pelagic fish species and for sharks and rays (Fig. 4). In "Species
431   by cells" comparisons (1) median error is 0.42-0.44, with similar results between runs.
432   At the "All species" or individual species level (2), the median of the error is 0.27-0.31.
433   This means that when looking at the species aggregated biomass, the SS-DBEM is more
434   reliable and that there is rather little impact of the biogeochemical chosen for
435   environmental conditions projection. The lowest error values correspond to the
436   reanalysis run (GFDL) and the latest runs (ascending order in Table 1) showing that
437   improvements in the forcing models (e.g. new data or reparameterization) are translating
438   into more reliable projections from the SS-DBEM. However, the performance differences
439   are small in most species and levels of aggregations which highlight the higher role of the
440   model uncertainty in the fisheries model. With "All cells" (3) the error range is 0.16-0.18
441   which shows the ability of the forcing and SS-DBEM model to forecast variations in total
442   biomass at 0.5° resolution. Ensemble model results are within those error ranges and do
443   not improve performance when working with "All cells" (Fig. 2i).

444   In general, errors are smaller for "All species" (2) than for the species in each cell
445   ("Species by cells", 1). The mean and standard deviation for the former are 0.25±0.11 and
446   0.40±0.14 for the latter (Fig. 4). This confirms higher model performance for total
447   biomass than for species biomass in each cell. The results by species can help to identify
448   where the SS-DBEM needs improvement. In general, widely distributed pelagic species
449   (e.g. Herring, Horse mackerel, mackerel, sprat) have among the highest errors at the
450   "Species by cells" (1) level, but a better performance when the total species biomass in
451   each cell is considered ("All species", 2). This indicates that there is something
452   systematically wrong with the way that the SS-DBEM handles those species, even though
453   the general allocation of biomass to pelagics is reasonable. Note, however, that the
454   bottom trawl surveys are not designed to sample pelagic species (ICES, 2016) and
455   relatively short tows with limited time in the water column can provide a misleading
456   picture of abundance and distribution for predominantly shoaling species (Battaglia et al.
457   2006). At the "Species by cells" (1) level the species for which the models perform best
458   are pout, haddock, plaice and lesser-spotted dogfish, all bottom-dwelling species that are
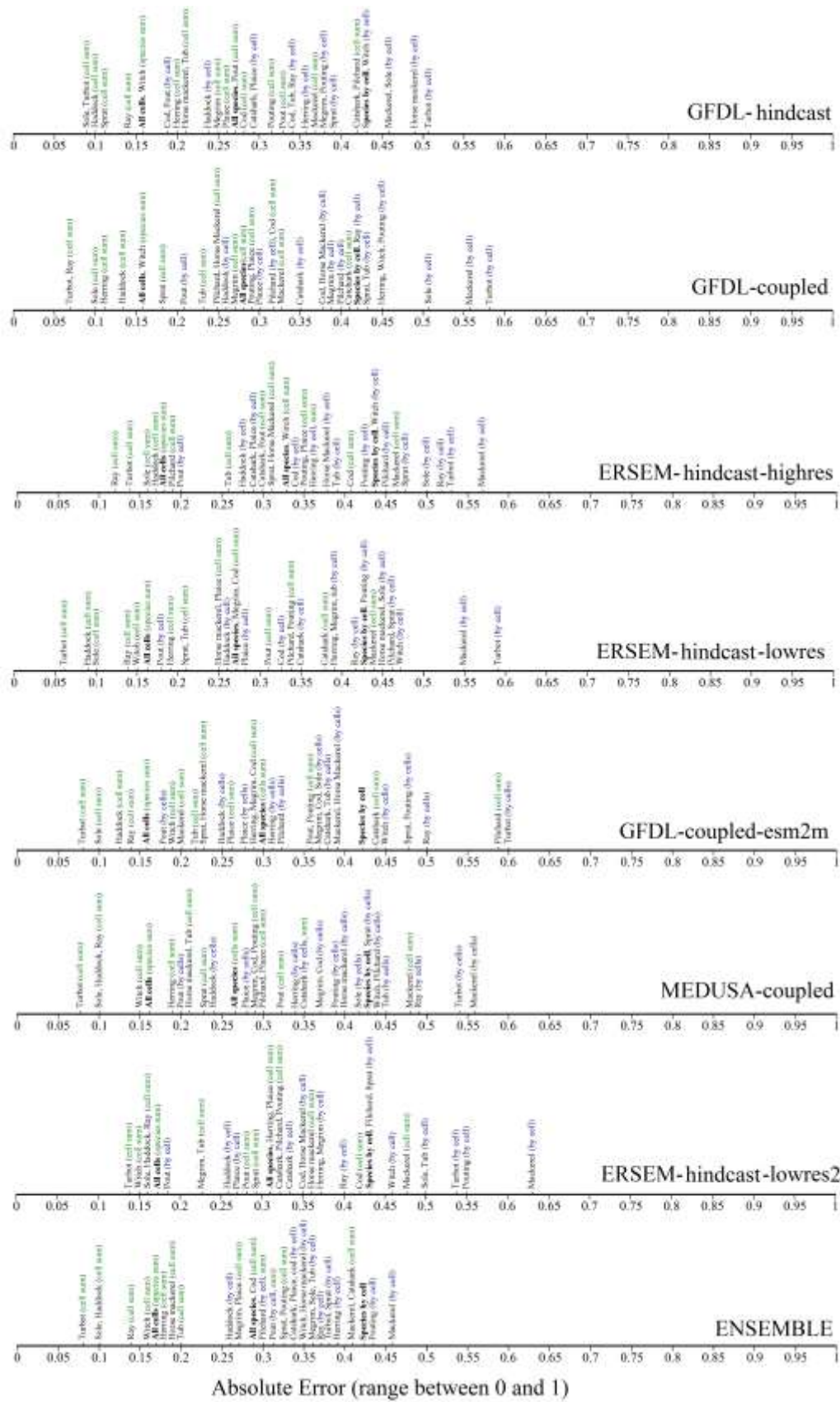459   effectively sampled by the survey gear (Fraser et al 2007; Walker et al. 2017).

Figure 4. Median of the absolute error at different scales of analysis for species and overall (bold) where (1) all the cells are considered for all species (325 cells and 18 species) named "Species by cells"; (2) time series for each species where all the cells are considered aggregated ("All species"); (3) time series for each of the 325 cells where all the species are aggregated ("All cells" (species sums)); and, (4) a time series is produced for each species aggregating all the cells with survey information (species cells sum). See text for additional explanation.

Discussion

While there was generally good agreement among biogeochemical models on the sign and extent of the temperature increase, the trends in primary production were less consistent. These differences can be attributed to a variety of factors such as model uncertainty and internal model variability (Hawkins and Sutton, 2009; Naujokaitis-Lewis et al., 2013; Payne et al., 2015, Cheung et al. 2016, Frölicher et al. 2016). Especially on local-to-regional scale (i.e. North-East Atlantic), model uncertainty and internal variability may play a dominant role in differences across model runs (Hawkins and Sutton, 2009; Chust et al. 2014; Frölicher et al. 2016). Here it seems that model uncertainty/resolution may play a bigger role than internal variability given that uncertainty in NPP trends is as large or larger for models forced in the same way (reanalysis) than for models that are forced differently (i.e. coupled or forced), but share the same biogeochemical model. For example, Laufkötter et al. (2015) have identified how uncertainty in the representation of underlying physiological processes influences the trends in net primary production. Here, we can observe in the multiple runs of historical and forced GFDL the uncertainty due to internal variability seems to be smaller than model uncertainty in marine biogeochemical models. Detailed comparisons of six different biogeochemical models (including MEDUSA and ERSEM used here) in physically-identical model simulations have shown the importance of the underlying modelled biogeochemistry on biogeochemical indicators including primary production (Kwiatkowski et al., 2014). However, the main characteristics of the trends of the two sets of environmental variables from the biogeochemical models used in this study to drive the fisheries simulations are in line with the results from global model data sets (Steinacher et al. 2010, Laufkötter et al. 2015, Frölicher et al. 2016).

Existing studies have made projections of fish distribution and abundance at scales ranging from higher resolution (Cheung et al., 2011; Burrows et al., 2014; Molinos et al., 2015) to higher level of aggregation (Mullom et al., 2016; Fernandes et al., 2016). Many studies, including those for fisheries management, only need information at relatively low level of aggregation such as LMEs, FAO areas, seas, ICES areas, EEZs or subregions (Blanchard et al., 2012; Fernandes et al., 2016; Mullon et al., 2016; Queiros et al., 2015; Queiros et al., 2018). Applications not dependent on high resolution data are often used

499 for management and economic research, linked with long term scenarios (Mullon et al.
500 2016; Queiros et al., 2018) or ecological studies looking at overall impacts on specific
501 species or habitats (Queiros et al., 2015). However, other studies and management
502 research aims for or requires a higher level of detail such as cells of 0.5° x 0.5° or smaller
503 as in the case of ICES rectangles or even 1x1 km² for local marine spatial planning or
504 studies of shifts of species abundance centroids (Jones et al., 2013; Queiros et al., 2016;
505 Fernandes et al., 2017; Coccoli et al., 2018). Some applications requiring higher resolution
506 are marine spatial planning (Queiros et al., 2016, Coccoli et al., 2018) or studies about
507 shifts of species abundance centroid (Jones et al., 2013).

508

509 The widely reported regime shift in the late 1980's in the North Sea (Reid and Edwards
510 2001, Beaugrand 2004, Weijerman, Lindeboom et al. 2005) suggested to have affected
511 several species in this analysis (Fig. 4) providing evidence of biogeochemical drivers for
512 the shifts. The reported shifts are sparse such as the increase in horse mackerel, sprat and
513 reduction of cod in abundance (Reid, Borges et al. 2001, Alheit, Mollmann et al. 2005)
514 despite other species shifts might have occur. However, a recent publication shows
515 species distribution shifts for 17 main widely distributed species in the North East
516 Atlantic (Baudron et al., 2020). The comparison of the performance of the models at
517 different resolutions shows, in general, that outputs are more reliable when aggregated
518 at larger time- and space- scales. As such, these would be favoured for reporting.
519 However, users of projections will often seek projections for individual species of
520 conservation or fisheries significance and small areas that reflect those accessible to, or
521 used by, a defined fishing fleet. For example projections at small space and time scales
522 may be requested to assess the abundance of "choke" species under climate change, given
523 their potential effects on the capacity of a fishery to access available quota (Baudron and
524 Fernandes, 2015).

525

526 Predicted latitudinal shifts of species are difficult to compare with empirical data since
527 data collection is often focused in areas where species have been distributed in the past
528 (ICES, 2016). This is the case of our survey data (Simpson et al., 2011) where sampling
529 centres on the Celtic Sea, Irish Sea and North Sea (up to ICES area IVa) or sprat surveys
530 that are focused in the Baltic Sea. Sparse data are available for ICES area IVa (ICES, 2016)

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531   and North of the Faroe Islands. However, species latitudinal shifts have been observed in
532   the global catch data (Cheung et al., 2013). There is limited knowledge North of ICES area
533   IVa due to limited international cooperation to share survey data and even South of ICES
534   area IVa the surveys mostly target higher value demersal species (ICES, 2016). However,
535   the aim of models such as SS-DBEM is not to predict accurately (Planque et al., 2016;
536   Dickey-Collas et al., 2014) where the species are present or will be present, but to
537   highlight the species and areas where changes are more likely to happen, and generate
538   uncertainty estimates (Planque et al., 2016; Payne et al., 2016). There is a trade-off
539   between goodness-of-fit and generalization power (Fernandes et al., 2015). Models that
540   very precisely represent the present have a performance that deteriorates faster as
541   projections are made further into the future (Rutterford et al., 2015).

542

543   At the highest output resolution we considered (0.5 × 0.5 degrees by year and species)
544   error was relatively high. Rutterford et al. (2015) also compared observed data with
545   predicted values using a GAM to project changes in distribution and abundance of
546   demersal species, obtaining correlations >0.5 for a 10 year forecast, but decreasing to
547   ≤0.5 at 10 year or longer-term forecasts. Statistical methods based on observations may
548   have limited value in long-term forecasting of systems that are expected to depart
549   markedly from their past state due to the long-term impacts of climate change (Barnsley
550   et al., 2007; Queiros et al., 2015; Payne et al., 2016). In addition, statistical models that
551   consider interactions between species are rare (Fernandes et al., 2013b), whereas this is
552   more common in mechanistic models (Blanchard et al. 2012; Fernandes et al., 2013a;
553   Thorpe et al., 2015). The survey data used in statistical models are relatively costly to
554   obtain and in many regions such observations are sparse or non-existent (e.g.
555   Bangladesh; Fernandes et al., 2016).

556

557   Variation between biogeochemical models is limiting predictions for several pelagic
558   species, whereas for most of the remaining species the choice of the biogeochemical
559   model makes little difference. Therefore, for most of the species the validation performed
560   here can guide improvement in fisheries models. Another alternative is the use of model
561   ensembles as a means of increase the reliability of projections (Araújo & New, 2007; Jones
562   et al., 2012; McKenna et al., 2013; Scales et al., 2015). In this study, the ensemble of
563   forcing-model runs did not affect performance of the SS-DBEM on average, but reduced

564 the probability of extreme errors, which would be an important consideration for some

565 applications. Outcomes from any given ensemble are highly dependent on the diversity

566 of constituent models, so it is unlikely our result can be generalised. Recent research is

567 moving towards ensembles of biological models which could benefit from similar

568 validation exercises (Lotze et al., 2019; Hermann et al., 2019) and collaborative protocols

569 for integration and comparison of multiple fisheries models (Tittensor, et al. 2018).

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