

UHI Research Database pdf download summary

Can the common fisheries policy achieve good environmental status in exploited ecosystems:

Baudron, Alan R.; Serpetti, Natalia; Fallon, Niall G.; Heymans, Johanna J.; Fernandes, Paul G.

Published in:
Fisheries Research

Publication date:
2019

The re-use license for this item is:
CC BY-NC-ND

The Document Version you have downloaded here is:
Peer reviewed version

The final published version is available direct from the publisher website at:
[10.1016/j.fishres.2018.10.024](https://doi.org/10.1016/j.fishres.2018.10.024)

[Link to author version on UHI Research Database](#)

Citation for published version (APA):

Baudron, A. R., Serpetti, N., Fallon, N. G., Heymans, J. J., & Fernandes, P. G. (2019). Can the common fisheries policy achieve good environmental status in exploited ecosystems: The west of Scotland demersal fisheries example. *Fisheries Research*, 211, 217-230. <https://doi.org/10.1016/j.fishres.2018.10.024>

General rights

Copyright and moral rights for the publications made accessible in the UHI Research Database are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights:

- 1) Users may download and print one copy of any publication from the UHI Research Database for the purpose of private study or research.
- 2) You may not further distribute the material or use it for any profit-making activity or commercial gain
- 3) You may freely distribute the URL identifying the publication in the UHI Research Database

Take down policy

If you believe that this document breaches copyright please contact us at RO@uhi.ac.uk providing details; we will remove access to the work immediately and investigate your claim.

1 **Can the Common Fisheries Policy achieve Good Environmental Status in exploited**
2 **ecosystems: the west of Scotland demersal fisheries example**

3

4 Alan R. Baudron¹, Natalia Serpetti², Niall G. Fallon¹, Johanna J. Heymans^{2,3}, Paul G.
5 Fernandes¹

6

7 ¹Institute of Biological and Environmental Sciences, University of Aberdeen, Tillydrone
8 Avenue, Aberdeen, AB24 2TZ, Scotland UK

9

10 ²Scottish Association for Marine Science, Scottish Marine Institute, Oban, PA37 1QA,
11 Scotland UK

12

13 ³European Marine Board, Wandelaarkaai 7, Oostende 8400, Belgium

14

15 Corresponding author: Alan R. Baudron

16 Institute of Biological and Environmental Sciences, University of Aberdeen, Aberdeen AB24
17 2TZ, Scotland UK

18 +44 (0) 1224272648

19 alan.baudron@abdn.ac.uk

20

21 **Abstract**

22

23 The latest reform of the Common Fisheries Policy (CFP) which regulates the exploitation of
24 fish stocks in European waters entails a move from the traditional single stock management
25 towards Ecosystem Based Fisheries Management (EBFM). Meanwhile the Marine Strategy
26 Framework Directive dictates that Good Environmental Status (GES) should be achieved in
27 European waters by 2020. Here we apply an EBFM approach to the west of Scotland
28 demersal fisheries which are currently facing several management issues: depleted stocks of
29 cod (*Gadus morhua*) and whiting (*Merlangius merlangus*), increased predation from grey
30 seals (*Halichoerus grypus*), and large bycatch of juvenile whiting by crustacean fisheries. A
31 food web ecosystem model was employed to simulate the outcomes of applying the
32 traditional single stock fishing mortalities (F), and management scenarios which explored F
33 ranges in accord with the CFP recommendation. Ecosystem indicators were calculated to
34 assess the performance of these scenarios towards achieving GES. Our results highlight the
35 importance of considering prey-predator interactions, in particular the impact of the top
36 predators, cod and saithe (*Pollachius virens*), on juvenile cod and whiting. The traditional
37 single stock approach would likely recover cod, but not whiting. Exploring the F ranges
38 revealed that a drastic reduction of juvenile whiting bycatch is necessary for the whiting stock
39 to recover. Predation from grey seals had little impact overall, but did affect the timing of cod
40 and whiting recovery. With the exception of whiting, little difference was observed between
41 the single stock scenario, and the best scenario identified towards achieving GES. The
42 findings advocate for the use of ecosystem modelling alongside the traditional, single stock
43 assessment model used for tactical decision making in order to inform management.

44

45 **Keywords:** Common Fisheries Policy; Ecosystem Based Fisheries Management; ecosystem
46 modelling; Ecopath with Ecosim; Good Environmental Status

47

48 **1. Introduction**

49

50 The exploitation of fish stocks in European waters is regulated by the Common Fisheries
51 Policy (CFP). Since its creation in the 1970s this long-standing policy has been through
52 several reforms, the latest of which took effect on January 1st 2014 (EC, 2013). This latest
53 reform proposes a new framework to manage European fisheries, and amongst several new
54 initiatives, it highlights a need to move from traditional single-stock management towards an
55 ecosystem approach to fisheries (EAF) (Prellezo and Curtin, 2015). EAF originated from the
56 principle of sustainable development and aims at both human and ecosystem well-being
57 (Garcia et al., 2003). The implementation of EAF can vary between an Ecosystem Approach
58 to Fisheries Management (EAFM) in which ecosystem aspects are given consideration when
59 taking management decisions, to Ecosystem-Based Fisheries Management (EBFM) in which
60 ecosystem health becomes a management goal included in trade-offs when pursuing
61 competing management objectives (Patrick and Link, 2015). Most importantly, EBFM
62 prioritises the wellbeing of ecosystems over economic and social objectives since wellbeing
63 is considered a prerequisite for the last two objectives (Murawski et al., 2008).

64

65 While the new CFP advocates for the implementation of EBFM, it remains largely unclear
66 how to include conservation objectives within management measures in practice (Prellezo
67 and Curtin, 2015). The CFP currently aims to fish at levels consistent with achieving
68 Maximum Sustainable Yield (MSY) for all exploited stocks (EC, 2011). In northern
69 European waters, these fishing levels are proposed by the International Council for the
70 Exploration of the Sea (ICES) which delivers annual scientific advice for the management of
71 northern European fish stocks. This advice provides biological reference points for each
72 stock, including the level of fishing mortality (F) needed to achieve MSY (F_{MSY}). F_{MSY} is

73 defined on a single-stock approach, meaning that it is calculated individually for a stock
74 based on its own status only, regardless of the status of other stocks. However, this
75 contradicts EBFM (Prellezo and Curtin, 2015), where the interactions between species should
76 be taken into account when defining safe harvest levels for fish stocks. In fact, while F_{MSY}
77 has long been considered a desirable exploitation level for single stocks (Schaefer, 1954), its
78 performance in mixed fisheries, where several stocks are caught simultaneously by the same
79 fleet, has been challenged (Walters et al., 2005), largely due to the fact that it is virtually
80 impossible to apply F_{MSY} simultaneously to all stocks in mixed fisheries (Kumar et al., 2017;
81 Larkin, 1977). Nevertheless, despite this criticism recent empirical studies have shown that
82 the current MSY approach has succeeded in leading European fish stocks towards recovery
83 (Cardinale et al., 2013; Fernandes and Cook, 2013). This suggests that the traditional single
84 stock F_{MSY} values for European stocks may not be too far off the harvest levels needed to
85 achieve sustainable mixed fisheries, potentially facilitating the transition towards EBFM. For
86 example, Froese et al. (2008) have shown that EBFM can be achieved by improving existing
87 single-stock management.

88

89 In addition to the traditional advice and corresponding single stock F_{MSY} values, ICES now
90 also provides F_{MSY} ranges for most stocks in European waters, which consist of upper (F_{MSY}
91 _{upper}) and lower (F_{MSY} _{lower}) F boundaries around F_{MSY} within which fishing mortality is
92 deemed sustainable (ICES, 2016a, 2015). These ranges are a recent addition to the ICES
93 advice and were requested by the European Commission in order to develop long-term
94 management plans with quantifiable targets. F_{MSY} ranges should be precautionary and also
95 ensure that they deliver no more than a 5% reduction in long-term yield. Whilst they do not
96 originate from a proper multispecies approach such as the one used by the mixed fisheries
97 advice (ICES, 2017), the F_{MSY} ranges do provide some leeway around the single stock F_{MSY}

98 values which are usually difficult to apply simultaneously to all stocks. In mixed fisheries, the
99 Total Allowable Catch (TAC) derived from F_{MSY} for the least abundant stock is most likely
100 to be reached before the TACs of more abundant stocks are exhausted. Such a situation
101 typically leads to over-quota discarding, a practice no longer allowed as the landings
102 obligation is phased in for European fisheries (EC, 2015a). As a result, it has been proposed
103 that in mixed fisheries the most vulnerable stock with the lowest F_{MSY} should determine the
104 limit of exploitation for all other stocks caught in the same fishery (EC, 2011). However,
105 such an approach is likely to result in a ‘choke species’ scenario leading to the under-
106 exploitation of other stocks and ultimately jeopardising the fishery (Baudron and Fernandes,
107 2015).

108

109 Another regulation of European waters is the Marine Strategy Framework Directive adopted
110 in 2008 (EC, 2008) which states that all member states should reach Good Environmental
111 Status (GES) by 2020 (EC, 2009). Although achieving GES differs from achieving EBFM,
112 GES measures the performance towards most of the biological and environmental attributes
113 of EBFM (Ramírez-Monsalve et al., 2016). GES is defined by 11 descriptors. Descriptors 1
114 (biodiversity), 3 (commercial species), and 4 (food webs) directly relate to fisheries and are
115 therefore particularly relevant for EBFM. In order to integrate these GES descriptors into an
116 EBFM framework, indicators are needed to inform whether GES criteria are met for each
117 descriptor. Developing meaningful ecosystem indicators can be challenging due to a lack of
118 relevant data. However, ecosystem indicators for descriptors 1, 3 and 4 can be derived from
119 biomass and/or catch data which are available for most species in ecosystems found in EU
120 waters (Coll et al., 2016; Gascuel et al., 2016; Kleisner et al., 2015; Reed et al., 2017). In
121 addition, the information a single ecosystem indicator can provide is limited: it is therefore
122 preferable to use a portfolio of indicators to fully assess each descriptor (Samhuri et al.,

123 2009). Lastly, GES indicators also need to be informative. Ideally, what constitutes GES
124 should be defined for each indicator in order to assess whether an ecosystem has reached
125 GES or not based on indicator values. For example, Link (2005) proposed reference points
126 for some ecosystem indicators, in which case the examination of indicators' trends relative to
127 the reference point values can then be used as a basis for management recommendations
128 (Jennings and Rice, 2011). However, not all ecosystem indicators have clearly defined
129 reference points, and these reference points are not transferable across ecosystems with
130 different characteristics (Heymans et al., 2014).

131

132 EBFM can benefit from ecosystem modelling in order to explore policy options where
133 management objectives (e.g. diversity, abundance of non-target species, etc.) involve
134 multiple species and their trophic interactions which cannot be assessed with single-species
135 models (Christensen and Walters, 2005). Plagányi (2007) reviewed available ecosystem
136 models spanning a wide range of complexity levels from minimum realistic models to whole
137 ecosystem ones. This latter category includes Ecopath with Ecosim (EwE), a food web
138 ecosystem model (Christensen and Walters, 2004). EwE is the most applied tool for
139 modelling marine ecosystems (Colléter et al., 2015) and can be used to investigate marine
140 policy issues such as GES (Piroddi et al., 2015). However, it is crucial to demonstrate that a
141 model can replicate historical trends in ecosystems in order to make plausible predictions in
142 response to novel situations before any management decision can be based upon it
143 (Christensen and Walters, 2005). Of the vast number of EwE models that have been
144 published, only a few have been calibrated using historical time series of data and even fewer
145 have been employed for management purposes (Heymans et al., 2016). One EwE model
146 fulfilling these two criteria was recently published for the west of Scotland ecosystem
147 (Alexander et al., 2015; Serpetti et al., 2017).

148

149 The west of Scotland ecosystem (WoS) located in ICES Division VIa is home to numerous
150 valuable species of finfish and shellfish that support four fisheries: an inshore crustacean
151 fishery targeting the valuable Norway lobster (*Nephrops norvegicus*); a mixed demersal
152 fishery targeting cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and whiting
153 (*Merlangius merlangus*) on the continental shelf; a fishery for monkfish (*Lophius*
154 *piscatorius*), hake (*Merluccius merluccius*) and saithe (*Pollachius virens*) in the deeper
155 waters of the shelf edge; and a pelagic fishery targeting mainly mackerel (*Scomber scombrus*)
156 and herring (*Clupea harengus*) (ICES, 2016b, 2016c, 2016d, 2016e, 2016f, 2016g). In 2014,
157 these fisheries contributed to 35% of the total value of all commercial species caught in
158 Scotland, totalling £182.5 million (The Scottish Government, 2015) and are, therefore,
159 important for the Scottish fishing industry. However the WoS fisheries are currently facing
160 several management issues. First, the stocks of cod and whiting are depleted and their Total
161 Allowable Catches (TACs) have been set to zero since 2012 and 2006 respectively (ICES,
162 2016c). Secondly, the extensive bycatch of juvenile gadoids by the crustacean fishery is
163 thought to jeopardise gadoid stocks, whiting in particular (ICES, 2016c). Thirdly, the
164 population of grey seals (*Halichoerus grypus*), a top predator in the WoS, has been increasing
165 steadily over the last two decades (SCOS, 2015). While Alexander et al. (2015) suggest that
166 excessive exploitation rates rather than an increase in predators were to blame for the collapse
167 of cod and whiting, increased predation from seals seems to have offset the reduction of
168 fishing pressure on VIa cod (Cook et al., 2015) and is likely to hamper the recovery from low
169 stock sizes (Cook and Trijoulet, 2016). The complexity of the WoS food web and the mixed
170 fisheries it supports, coupled with management challenges and the availability of an
171 ecosystem model, makes the WoS an ideal case study to assess the performance of EBFM in
172 achieving specific management goals such as GES.

173

174 Here, we reviewed and updated the EwE model for WoS with the latest data available and
175 repeated the calibration procedure to extend the hindcasting period from 1985 to 2013. We
176 used this model to explore the F_{MSY} ranges of the demersal stocks by performing forward
177 simulations of every possible combination of fishing mortalities within these ranges.
178 Additional exploitation scenarios were performed to investigate the impact of juvenile
179 whiting bycatch by the crustacean fishery and grey seals predation. For each scenario,
180 ecosystem indicators related to GES descriptors 1, 3 and 4 were calculated. Outputs from the
181 models were analysed to assess whether the single stock F_{MSY} and/or F_{MSY} ranges
182 implemented by the CFP could achieve GES in WoS the demersal fishery. Management
183 measures required to recover the cod and whiting stocks were also identified.

184

185

186 **2. Material and methods**

187

188 ***2.1. The model***

189

190 The model was built using EwE software version 6.5 released in July 2016
191 (www.ecopath.org). EwE consists of two components: (i) Ecopath, a mass-balance model
192 accounting for energy transfers in the ecosystem which depicts a ‘snapshot’ of the ecosystem
193 in a given year; and (ii) Ecosim, the dynamic component which allows for temporal
194 simulations based on Ecopath. Ecosim is based on the foraging arena theory (Ahrens et al.,
195 2012), and each prey-predator interaction is defined by a vulnerability parameter that
196 describes whether the interaction is bottom-up (vulnerability < 2), top-down (vulnerability >
197 2), or neither bottom-up nor top-down (vulnerability = 2) controlled. Both Ecopath

198 (Christensen and Pauly, 1992; Polovina, 1984; Walters et al., 1997) and Ecosim (Christensen
199 and Walters, 2004; Walters and Christensen, 2007) have been documented extensively, and
200 further details can be found in the publications above.

201

202 The EwE model for WoS used in this study was first built by Haggan and Pitcher (2005),
203 then updated by Bailey et al. (2011) and Alexander et al. (2015). It was recently updated and
204 extended by Serpetti et al. (2017) who introduced species-specific thermal preference
205 functions in order to drive the model with ocean temperature. The impact of temperature is
206 beyond the scope of this study (see Serpetti et al. (2017) for more details). Here, we built on
207 the model published by Alexander et al. (2015) by applying the same update as done by
208 Serpetti et al. (2017), minus the inclusion of temperature as a driver. The area modelled
209 corresponds to the continental shelf of ICES Division VIa within the 200 m depth contour
210 and covers ~110,000 km² (Fig.1). The model comprises 41 functional groups (Table S1)
211 spanning ~ five trophic levels consisting of three marine mammals, seabirds (as a single
212 group), 23 fish, five invertebrate groups, one cephalopod group, two zooplankton, three
213 benthos, two primary producers, and one detritus group. The model has five fishing fleets:
214 demersal trawl, *Nephrops* trawl, other trawl, potting and diving, and pelagic trawl. The cod,
215 haddock and whiting groups are split between juvenile (age 0 and 1) and adult (age 2 and
216 above). The model start year in Ecopath is 1985 (see Bailey et al. (2011), Alexander et al.
217 (2015) and Serpetti et al. (2017) for more details about Ecopath parameters). Ecopath
218 parameter values employed are given in Tables S1-4.

219

220 ***2.2. Update***

221

222 The update of Ecopath consisted of two steps. Firstly, the 1985 biomass starting values of
223 groups for which data were available were updated using the latest stock assessments (Table
224 S1) while the total catch of each functional group was updated with the latest landings (Table
225 S2) and discards (Table S3) data (where available). In addition, the growth parameter (i.e. K
226 from the von Bertalanffy growth function) used to model the growth of the three multi-stanza
227 groups (cod, haddock and whiting) was updated by fitting a von Bertalanffy growth function
228 to age-length keys obtained from the ICES DATRAS database
229 (https://datras.ices.dk/Data_products/Download/Download_Data_public.aspx) for those three
230 groups. Secondly, the diet matrix used by Ecopath was updated. Adjusting the diet matrix is a
231 powerful and surprisingly underused way to improve EwE models (Ainsworth and Walters,
232 2015). To improve the model goodness of fit, the diet matrix was updated following these
233 consecutive steps: (i) the data and proxies used by Bailey et al. (2011) and Alexander et al.
234 (2015) to build the diet matrix were reviewed; (ii) the diet composition of each group was
235 checked individually against existing literature for unusual prey; (iii) when unusual
236 prey/predator links were found these were removed and/or amended based on (in the
237 following order): available literature; the DAPSTOM database (Pinnegar, 2014); the diet
238 matrices of the EwE models from two neighbouring and closely related ecosystems, North
239 Sea (Mackinson and Daskalov, 2007) and Irish Sea (Lees and Mackinson, 2007). The
240 updated diet matrix obtained through these three consecutive revisions is given in Table S4.
241 To ensure a coherent and ecologically sound mass-balance, the pre-balance (PREBAL)
242 analysis depicted by Link (2010) was applied to the updated Ecopath model.

243

244 To update Ecosim, the time series of biomass, catch, and fishing mortalities driving the
245 model were updated (from 1985 onwards) and extended (up to 2013) for as many groups as
246 possible using the latest data available. While catch time series were handled on an absolute

247 scale in the calibration process, biomass time series are handled on relative scale: having the
248 correct biomass trend is, therefore, more important than having the correct range of values.
249 To this end it was deemed preferable to estimate the biomass time series directly from
250 scientific survey data rather than from assessment model estimates, whenever possible. For
251 demersal and benthic groups, biomass time series were calculated using bottom trawl surveys
252 data obtained from the ICES DATRAS database following the method from Baudron and
253 Fernandes (2015) with the exception of cod, haddock and whiting for which stock assessment
254 estimates (ICES, 2014a) were necessary to obtain separate biomass time series for both
255 stanzas. For Norway lobster, abundance estimates from underwater TV surveys (ICES,
256 2014a) were summed across the three functional units within the model area (FU 11, 12 and
257 13) and used as biomass time series. Since pelagic species are not effectively captured by
258 bottom trawl surveys, whenever possible other data sources were preferred to get reliable
259 biomass trends. For herring, total stock biomass estimates from acoustic surveys available for
260 the subarea VIa north which comprises the bulk of the VIa stock (ICES, 2014b) were used.
261 For mackerel, horse mackerel *Trachurus trachurus* and blue whiting *Micromesistius*
262 *poutassou*, total stock biomass estimates for the western shelf (ICES, 2014c) were scaled
263 down to VIa using the average proportion of landings realised in this area. For grey seals,
264 estimates of pup production from Inner and Outer Hebrides (SCOS, 2015) were summed and
265 used as biomass trend. For harbour seals, pup count values were only available every five
266 years (SCOS, 2015) but were preferred to model estimates as the biomass trend indicator.
267 Abundances values of small (< 2 mm) and large (> 2 mm) zooplankton, and phytoplankton
268 Colour Index (PCI) were obtained from the Sir Alister Hardy Foundation for Ocean Science
269 (SAHFOS). The PCI constitutes a semi-quantitative representation of the total phytoplankton
270 biomass (Batten and Walne, 2011).

271

272 Catch time series for both stanzas of cod, haddock and whiting were obtained from stock
273 assessment reports as these include discards and are corrected for misreporting. Contrary to
274 cod and whiting assessed in VIa, haddock is now assessed for both areas IV and VIa (ICES,
275 2014d). As a result, it was assumed that 9.5 % of northern shelf haddock catches are realised
276 in VIa as this is the threshold managers agreed upon when splitting the TAC between areas
277 IV and VIa (EC, 2015b). For all other groups, 1985-2013 time series of VIa landings were
278 obtained from STATLANT (STATLANT, [http://ices.dk/marine-data/dataset-](http://ices.dk/marine-data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx)
279 [collections/Pages/Fish-catch-and-stock-assessment.aspx](http://ices.dk/marine-data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx)) and 2003-2013 discard rates were
280 obtained from STECF (<https://stecf.jrc.ec.europa.eu/reports>) to estimate the 2003-2013 catch
281 time series. The catch time series for 1985-2002 were estimated by inversely applying 2003-
282 2013 average discard rates to 1985-2002 landings time series. In EwE, F corresponds to the
283 exploitation rate which is the catch to biomass ratio (C/B). To get F time series, biomass time
284 series were adjusted so that the 1985 starting values correspond to the 1985 biomass
285 estimates from Ecopath before calculating C/B to ensure sensible F values: since biomass
286 values resulting from standardised survey sampling are often much smaller than those
287 estimated from stock assessments, the initial value derived from Ecopath was used. Lastly,
288 the “feeding time adjustment rate” was set to 0.5 for mammal groups as suggested by
289 Christensen *et al.* (2008) and to 0.2 for juvenile stanzas which still feed on egg content in
290 early life stages while the default value of 0 was used for all other groups. The time series of
291 biomass, catch, F, and forced catches (i.e. catches used to drive the model for groups for
292 which F could not be calculated due to lack of either C or B) inputs used to fit Ecosim are
293 given in Tables S5-8.

294

295 **2.3. Parameterisation**

296

297 For the model to be reliable enough for EBFM it is essential that Ecosim captures the food
298 web processes. This is shown by the ability to reproduce historical trends in biomass and
299 catches when historical fishing mortalities are applied. Ecosim includes a ‘fit to time series’
300 module which identifies the prey-predator interactions most sensitive to changes in
301 vulnerability (Tomczak et al., 2012). The calibration then consists of adjusting these
302 vulnerabilities until the best ‘fit’ of the model outputs to historical time series is achieved.
303 Goodness-of-fit is assessed by the sum of squared differences between the predicted and
304 observed values on a \log_{10} scale (Christensen et al., 2008). The fitting procedure described in
305 Alexander *et al.* (2015) was applied and the following model scenarios were tested (see
306 Mackinson et al. (2009) for more details):

307

- 308 (i) Baseline: no fishing or environmental forcing and vulnerabilities set at 2
- 309 (ii) Baseline + trophic effects: same as (i) except vulnerabilities are adjusted to fit the
310 data
- 311 (iii) Baseline + environmental forcing: same as (i) except the ‘fit to time series’
312 identifies a time series of values (forcing function) that improves the fit by
313 impacting the predicted biomasses through primary production (subsequent
314 analyses can be performed to link the forcing function to existing environmental
315 drivers). This forcing function is a spline curve, and the maximum number of
316 spline points tested was limited to five so as to not over-parameterise the model
317 (Tomczak et al., 2012), as done by Alexander et al. (2015).
- 318 (iv) Baseline + trophic effects + environmental forcing: combination of (ii) and (iii)
- 319 (v) Fishing: fishing mortalities are included to drive the model, no environmental
320 forcing and vulnerabilities set at 2

- 321 (vi) Fishing + trophic effects: fishing mortalities are included to drive the model and
322 vulnerabilities are adjusted to fit the data
- 323 (vii) Fishing + environmental forcing: combination of (iii) and (v)
- 324 (viii) Fishing + trophic effects + environmental forcing: combination of (vi) and (vii)

325

326 The best candidate was selected with Akaike's Information Criterion (AIC) which identifies
327 the best trade-off between goodness-of-fit and number of parameters (Mackinson et al.,
328 2009). Instead of manually selecting the number of vulnerabilities to adjust prior to running
329 the 'fit to time series' module (Alexander et al., 2015; Tomczak et al., 2012), an automated
330 stepwise fitting procedure (Scott et al., 2016) was used. This 'stepwise fitting' module has
331 been included in the latest release of the EwE software (version 6.5) and allows for testing
332 every possible combination of parameters by automatically running the 'fit to time series'
333 with successive increments of the number of vulnerabilities and/or spline points of the
334 forcing function for each candidate model (ii) to (viii). The stepwise fitting procedure tested
335 1,990 model interactions based on 28 time-series of relative biomasses, 22 time-series of
336 catches, 22 time-series of F and 9 time-series of forced catches with a total of 1,355
337 observations (observed data points) estimating a maximum number of 49 parameters (based
338 only on independent time-series). The fitting procedure searched for vulnerability parameters
339 "by predator" for all iterations assuming the same top-down or bottom up control of the
340 predator on all its prey (Scott et al., 2016).

341

342 ***2.4. Management scenario simulations***

343

344 Once parameterised, the best candidate model was used to explore the possible management
345 scenarios for the WoS demersal fishery which adhere to the current CFP recommendations.

346 The six demersal species considered here for the demersal fishery are cod, haddock, whiting,
347 saithe, hake, monkfish. Saithe and hake are part of larger groups, pollock and large demersals
348 respectively, composed of more than one species (Table S9). According to Bailey et al.
349 (2011), the pollock group is largely dominated by the saithe (97%) and the large demersals
350 group by hake (ca. 60%, although given recent estimates from Baudron and Fernandes
351 (2015), this proportion is likely to be much higher). The groups pollock and large demersals
352 were therefore considered here as being representative of these two single species, and are
353 hereafter referred to as saithe and hake. Forward simulations were performed for a period of
354 20 years (i.e. 2014-2033) for each scenario. Firstly, a status quo scenario ($F_{\text{status quo}}$) was
355 performed by keeping F equal to the last historical value (F_{2013}) for all species in the model
356 (Table 1) and used as a reference level. Secondly, a F_{MSY} scenario was performed by
357 applying the single stock F_{MSY} values from ICES (Table 1). Only cod and whiting have
358 stocks with a corresponding F_{MSY} defined for area VIa, in which the model area is located.
359 For other species, the F_{MSY} defined for stock areas which encompass area VIa were used as
360 best available proxies (Table 1). Lastly, the F_{MSY} ranges were explored for demersal species,
361 whilst single stock F_{MSY} values were applied to Norway lobster and pelagic species. Akin to
362 single stock F_{MSY} values, the best available proxies were used when needed (Table 1). The
363 F_{MSY} ranges were explored by simulating, for each species, the $F_{\text{MSY upper}}$ and $F_{\text{MSY lower}}$
364 boundaries and F values in between these two boundaries with a 0.05 increment (Fig. 2a). In
365 order to investigate management strategies likely to recover cod and whiting, the $F_{\text{MSY lower}}$
366 boundaries simulated were lowered to $F=0.05$, this value corresponding to the observed
367 residual F experienced by species not targeted by fisheries (e.g., juvenile cod, see Table S7).
368 Since haddock is also located on the shelf and likely to be caught together with these two
369 species, the cod F_{MSY} range was also applied to haddock (Fig. 2a). The F_{MSY} ranges simulated
370 therefore differed slightly from the ones given by ICES, but did however encompass them

371 (Table 1). To investigate the impact of reducing juvenile whiting bycatch by the crustacean
372 fishery, the F_{MSY} range applied to adult whiting was also applied to juvenile whiting in order
373 to simulate a reduction from $F_{status\ quo}$ of 0.17 (Table S7) down to $F=0.05$ (Fig. 2a). To
374 investigate the impact of a reduction in predation by grey seals, 5% and 10% culls were
375 simulated by applying F_s of 0.05 and 0.10 to grey seals, in addition of the current no cull
376 ($F=0$) situation (Fig. 2a). Simulations were carried out for all possible combinations of F_s
377 within the F_{MSY} ranges tested, resulting in 180,000 scenarios being explored in addition to the
378 $F_{status\ quo}$ and F_{MSY} scenarios. These simulations were performed using the Multisim plugin
379 from the EwE software (Steenbeek et al., 2016).

380

381 **2.5. GES indicators**

382

383 To assess whether the management scenarios tested achieve GES, and further identify which
384 scenario is most likely to achieve GES, the following ecosystem indicators (hereafter referred
385 to as GES indicators) were calculated using the model outputs for all scenarios.

386

387 *2.5.1. Biomass*

388

389 GES implies that all fish stocks are harvested sustainably and therefore within safe biological
390 limits: the spawning stock biomass (SSB, i.e. of adults) should be above biological reference
391 points. The stocks of cod and whiting which are currently depleted are the only two stocks
392 with the biological reference points biomass limit (B_{lim}) and precautionary biomass (B_{pa})
393 defined for area VIa (cod: $B_{lim} = 14,000$ t, $B_{pa} = 22,000$ t; whiting: $B_{lim} = 31,900$ t, $B_{pa} =$
394 $44,600$ t) in which the model area is located (ICES, 2016c). The biomass outputs from the
395 model were therefore used as indicators, in conjunction with the biological reference points,

396 to assess whether each scenario led to the cod and whiting stocks remaining depleted
397 (biomass < B_{lim}), being at risk (B_{lim} < biomass < B_{pa}), or recovering (biomass > B_{pa}). This
398 indicator relates to the GES descriptor 3: commercial species.

399

400 2.5.2. Shannon's diversity index

401

402 Shannon's diversity index (SI) is an indicator of biodiversity commonly used to assess the
403 impact of fishing on food webs (Gascuel et al., 2016). This indicator was calculated
404 following the formula from Shannon (1948):

405

$$406 SI = \sum_G (P_G \cdot \log_2(P_G)) \quad (1)$$

407

408 where P_G is the proportion in weight of the functional group G in the biomass. This indicator
409 relates to the GES descriptor 1: biodiversity.

410

411 2.5.3. Marine trophic index

412

413 The marine trophic index (MTI) is an indicator of the trophic structure of the upper (trophic
414 level 3.25 and above) part of the food web which includes most commercial fish species and
415 therefore is expected to be impacted the most by fishing (Pauly and Watson, 2005). This
416 indicator was calculated as follows:

417

$$418 MTI = \sum(TL_G \cdot W_G) / \sum W_G \quad (2)$$

419

420 where TL_G is the trophic level of the functional group G (for groups with a trophic level \geq
421 3.25), W_G is the weight of the functional group G in the biomass. This indicator relates to the
422 GES descriptor 4: food webs.

423

424 *2.5.4. Mean maximum length*

425

426 The mean maximum length (MML) is an indicator of the species composition of the food
427 web where fishing is expected to lead to a decline in the proportion of large species (Shin et
428 al., 2005). This indicator was calculated as follows:

429

$$430 \quad MML = \frac{\sum(W_G \cdot L_{\infty G})}{\sum W_G} \quad (3)$$

431

432 where W_G is the weight of the functional group G present and $L_{\infty G}$ is the asymptotic length of
433 the functional group G obtained by averaging L_{∞} values obtained from Fishbase (Froese and
434 Pauly, 2017; www.fishbase.org) across species in each functional group (Table S9). This
435 indicator relates to the GES descriptor 4: food webs.

436

437 *2.5.5. Food web evenness index*

438

439 The Food Web Evenness index (FWE) is an indicator of biodiversity which, unlike
440 Shannon's diversity index, not only considers the overall diversity of species but also a
441 balanced biomass distribution across trophic levels and evenness of species within each
442 trophic level. This indicator is obtained by inverting either the Canberra or the Bray-Curtis
443 dissimilarity index, BC , calculated based on the dissimilarity of the expected and observed
444 biomass of a functional group G , as follows:

445

$$446 \quad BC = (\sum_G |B_{Ge} - B_{Go}|) / \sum_G (B_{Ge} + B_{Go}) \quad (4)$$

447

448 where B_{Ge} and B_{Go} are the expected and observed biomass of the functional group G within
449 its trophic level, respectively. The expected biomass is calculated by defining a reference
450 state of ‘food web evenness’ in which group biomasses are decreasing with increasing trophic
451 levels, and all groups within a trophic level have equal biomasses (for more details please
452 refer to Appendix A). An advantage of FWE is that it is independent of the total biomass in
453 the system. Therefore FWE only tracks relative changes in species biomasses, i.e. in the
454 compositional diversity of the community. This indicator relates to the GES descriptor 1:
455 biodiversity.

456

457 **2.6. Identify the best GES scenario**

458

459 Apart from the biomass indicator for which thresholds (i.e. B_{lim} and B_{pa}) are defined for the
460 depleted stocks of cod and whiting, none of the four GES indicators used to assess descriptors
461 1 and 4 have clear thresholds defined above which GES is considered reached. Instead, for
462 these four indicators (H, MTI, MML, FWE) it was simply considered that the higher the
463 value the better, and that a scenario achieving high values across these four indicators is more
464 likely to achieve GES than a scenarios achieving lower values (Coll et al., 2016; Kleisner et
465 al., 2015; Reed et al., 2017). Therefore, in order to identify the scenario most likely to
466 achieve GES (hereafter referred to as best GES scenario) the following framework was
467 applied:

- 468 (i) To achieve GES, a scenario should recover the depleted stocks of cod and whiting
469 within safe biological limits (i.e. above B_{pa})

- 470 (ii) The recovery of depleted stocks should be achieved as early as possible
- 471 (iii) Among scenario(s) that satisfy conditions (i) and (ii), the best GES scenario is the
472 one achieving the highest values overall across the four GES indicators H, MTI,
473 MML, and FWE. The best GES scenario was identified through the following
474 three steps:
- 475 a. firstly, the amplitude of the time series of all four GES indicators was
476 standardised by subtracting the mean and dividing by the standard deviation;
 - 477 b. secondly, for each indicator, the difference between each scenario's value
478 reached in 2033 and the maximum across all scenarios was calculated;
 - 479 c. thirdly, the best GES scenario is the one with the smallest sum of differences
480 across the four GES indicators.

481

482 ***2.7. Model uncertainty***

483

484 In order to investigate the impact of parameter uncertainty on the reliability of the model
485 outputs, Monte-Carlo simulations were performed to assess the sensitivity of Ecosim to
486 uncertainty in the following Ecopath inputs: biomass, production to biomass ratio,
487 consumption to biomass ratio, and ecotrophic efficiency (Heymans et al., 2016). The model
488 identified as the best GES scenario was run with the parameter value for each of these inputs
489 randomly selected from within 10% of the original value, as done by Serpetti et al. (2017).
490 100 runs were performed, and the confidence interval around the time series of biomass
491 outputs were determined by calculating the 5% and 95% quantiles.

492

493

494 **3. Results**

495

496 **3.1. Hindcast**

497

498 Once the updated Ecopath model was successfully balanced, PREBAL (Link, 2010)
499 diagnostics were carried out and confirmed that: the biomass slope on a log scale declines by
500 ca. 5 – 10% with increasing trophic levels; predator/biomass ratios are <1; and vital rates
501 decline with increasing trophic levels (Appendix B). These diagnostics suggest that the
502 Ecopath model is ecologically sound (Link, 2010). The structure of the updated Ecopath food
503 web is depicted in Figure 3, and the final balanced model parameters can be found in Table
504 S1.

505

506 The best fitted model with the lowest AIC was achieved when fishing, trophic effects and
507 environmental forcing were applied (Model 8, see Table 2). This model improved the fit by
508 62% compared to the baseline model. Adding fishing alone improved the fit by 25%, while
509 the combination of fishing and trophic effects reduced the sum of squares by 61%. Adding a
510 forcing function further reduced the sum of squares by 1%, resulting in the lowest AIC. The
511 environmental forcing function on primary producers identified by the fitting procedure is a
512 spline curve with three spline points. Correlations between this forcing function and
513 environmental indices North Atlantic Oscillation (NAO) and Atlantic Multidecadal
514 Oscillation (AMO), as well as the Sea Surface Temperature (SST) were explored with
515 Pearson product moment correlation tests. SST data was obtained from the Hadley Centre
516 HadISST dataset (<http://www.metoffice.gov.uk/hadobs/hadisst/>), while NAO and AMO data
517 were obtained from NOAA (<https://www.esrl.noaa.gov/psd/data/timeseries/>). While
518 correlations with SST and NAO were marginally (cor. = 0.107, p = 0.046) and not significant
519 (cor. = -0.099, p = 0.066) respectively, AMO was the index most correlated with the forcing

520 function with a highly significant correlation ($\text{cor.} = 0.583, p < 0.001$, Fig. S1). As a result, a
521 smoothed AMO index obtained by fitting a Loess (local regression) smoother with a span of
522 0.5 (Fig. S1c) was substituted with the three spline point curve in the model and used as the
523 environmental forcing function on producers.

524

525 The best model (model 8, see Table 2) performed fairly well in reproducing the historical
526 biomass trends of most functional groups over the hindcast period (1985-2013), particularly
527 for demersal species such as cod, whiting, saithe and monkfish (Fig. 4). Biomass trends were
528 also fairly well captured for *Nephrops* and pelagic species except in early years (1985-1990)
529 for mackerel and horse mackerel. The historical biomass trends of grey seals was not
530 captured as well, although the model did produce an increasing trend as observed from the
531 historical data. The confidence intervals calculated from the Monte-Carlo simulations were
532 reasonably narrow for a majority of groups, but did reveal large uncertainties around the
533 estimates of cod, haddock and whiting due to the top-down and bottom-up interactions
534 between the adult and juvenile stages of these multi-stanza groups as previously noted by
535 Serpetti et al. (2017). The model also reproduced the observed catch trends for most groups
536 apart from monkfish over the 1990-2000 period (Fig. S2). Catches of hake, mackerel and
537 *Nephrops* were slightly overestimated, while blue whiting catches were slightly
538 underestimated over the 1995-2000 period. The model showed mixed results regarding the
539 ability to reproduce historical trends of GES indicators (Fig. 5). Historical values for the two
540 food web indicators, MML and MTI, were well matched apart from a peak in the mid-2000s
541 largely driven by the large increase in hake biomass (Fig. 4). The two diversity indicators SI
542 and FWE, however, were overestimated by the model, especially SI. Nevertheless, the model
543 outputs did reproduce the shape of the historical trends to some extent, indicating that the

544 GES indicators returned by the model can be used to compare management scenarios to one
545 another.

546

547 **3.2. Forecast**

548

549 No forward projections of the AMO index are available. However, this index has been
550 increasing over the model hindcast period (1985-2013), is known to follow a cyclical pattern,
551 and is now approaching a cooling phase (Kotenev et al., 2011). Thus, the mirror values of the
552 smoothed AMO index over 1985-2013 (Fig. S1c) were used as best available proxy and
553 applied as the environmental forcing function of primary producers over the simulation
554 period (2014-2033) when simulating the management scenarios, as done by Serpetti et al.
555 (2017).

556

557 The $F_{\text{status quo}}$ scenario revealed little to no change for most species biomass (Fig. 4) and catch
558 (Fig. S2) levels compared to the last historical year: cod and whiting remained depleted,
559 while other species either remained on par with 2013 levels or quickly reached a plateau,
560 except herring and horse mackerel which kept declining over the simulation period. The F_{MSY}
561 scenario entailed an increase in F for all species except cod, herring and horse mackerel
562 (Table 1). This led to a recovery of cod SSB above B_{pa} and an increase in horse mackerel
563 biomass but did not stop herring biomass from decreasing despite temporarily curbing the
564 decline. Single stock F_{MSY} values did not recover whiting SSB which remained well below
565 B_{lim} . However, despite experiencing a F three times greater, whiting achieved a higher SSB
566 with F_{MSY} ($F=0.18$) than with $F_{\text{status quo}}$ ($F=0.06$). Similar observations were made for haddock
567 which experienced an increase from $F_{\text{status quo}} = 0.17$ to $F_{\text{MSY}} = 0.19$. This is most likely due to
568 a reduction in the predation pressure from the piscivorous top predators saithe, monkfish and

569 hake which all experienced substantial biomass reductions under F_{MSY} . Grey seals also
570 suffered from a reduction in biomass despite experiencing no cull under F_{MSY} , likely due to a
571 reduction in food supply caused by the lower biomass overall across fish species, in particular
572 the important preys saithe and hake (Fig. S3). Catches realised under F_{MSY} were greater than
573 under $F_{status\ quo}$ across all species except *Nephrops*, suggesting that F_{MSY} would lead to higher
574 yield even for species experiencing a reduction in F .

575

576 Out of the 180,000 scenarios tested to explore the F_{MSY} ranges, only 260 recovered both the
577 stocks of cod and whiting above B_{pa} by 2033 (Table S10). Out of these 260 scenarios, the
578 earliest date at which recovery above B_{pa} was achieved for both depleted stocks differed
579 among the levels of seal cull considered: 10 scenarios achieved recovery in 2027 with no seal
580 cull, 20 scenarios achieved recovery in 2028 with a 5% seal cull, and 5 scenarios achieved
581 recovery in 2029 with a 10% seal cull. These 35 scenarios are hereafter referred to as
582 recovery scenarios. Culling grey seals had no effect on how quickly the depleted stocks
583 recovered above B_{lim} : cod and whiting reached the threshold in 2021 and 2024 at the earliest,
584 respectively, regardless of the level of culling applied here. However, culling grey seals had
585 an effect on how quickly the depleted stocks recovered above B_{pa} . Cod reached the threshold
586 in 2022 with a 10% cull, a year earlier than with a 5% cull or no cull. In contrast, the
587 recovery of whiting above B_{pa} appeared slower with higher levels of culling, with the
588 threshold reached in 2027 without cull while a 5% and 10% cull led to the threshold being
589 reached in 2028 and 2029 respectively.

590

591 The fishing mortalities applied in the 35 recovery scenarios are displayed in grey in Figure 2b
592 and the corresponding biomass trajectories in Figure 4. The recovery of the cod and whiting
593 stocks was achieved with F values within the F_{MSY} ranges from ICES, with the exception of

594 whiting which required a much lower F (Fig. 2b). Although these 35 recovery scenarios did
595 achieve the recovery of both cod and whiting above B_{pa} , for both species the increase in
596 biomass plateaued around 2030 after which it started decreasing again, with the whiting SSB
597 dipping below B_{pa} by 2033 in all recovery scenarios (Fig. 4). Extending the simulation until
598 2100 as done by Serpetti et al. (2017) revealed that, while the cod SSB remained above B_{pa}
599 after the ecosystem reached equilibrium, the whiting SSB fluctuated around B_{pa} before
600 stabilising between B_{lim} and B_{pa} by 2060 (Fig. S4). This suggests that the scenarios identified
601 as achieving the fastest recovery of cod and whiting above B_{pa} may not maintain whiting
602 within sustainable limits in the long term. The large uncertainty around whiting biomass
603 estimates prevents any firm conclusions, with ca. half of the confidence interval being above
604 B_{pa} (and ca. two thirds above B_{lim}) by 2100. Out of the 35 recovery scenarios, the recovery of
605 both cod and whiting was only achieved when the highest F of the ranges explored was
606 applied to cod ($F=0.25$) and saithe ($F=0.42$), and the lowest possible F (0.05) applied to both
607 adult and juvenile whiting. In contrast, recovery was achieved with all possible F values of
608 the range explored for monkfish and grey seals which indicate that these two top predators
609 did not hinder the cod and whiting stocks recovery, although the predation from grey seals
610 had a slight impact on the date when B_{pa} was reached for these two stocks, as detailed above.

611

612 The 35 recovery scenarios all resulted in similar values of GES indicators across the
613 simulation period, with the exception of the FWE index which showed more variability
614 across scenarios (Fig. 5). As a result, the scenario identified as the best GES scenario was
615 also the one returning the highest FWE values. Both the best GES scenario and the F_{MSY}
616 scenario produced similar trajectories for all GES indicators over the simulation period,
617 except for the FWE index between 2014 and 2025. However, for all GES indicators the best
618 GES scenario either slightly outperformed the F_{MSY} scenario (e.g. SI), or caught up with it by

619 2033 (e.g. MML). Both the best GES and F_{MSY} scenarios resulted in lower values than the
620 $F_{status\ quo}$ scenario for the two food web indicators, MML and MTI, although for MTI all three
621 scenario ended up with similar values in 2033. This is likely due to the high biomasses of
622 saithe and hake observed under the $F_{status\ quo}$ scenario, with the abundance of these two large
623 top predator species resulting in high MML and MTI values despite the low biomasses of
624 other large top predators such as cod and whiting. In contrast, the best GES and F_{MSY}
625 scenarios both resulted in higher values than the $F_{status\ quo}$ scenario for the two biodiversity
626 indicators SI and FWE, indicating that these two scenarios led to a more diverse and even
627 species composition of the WoS ecosystem.

628

629 The best GES scenario identified via the GES indicators was achieved when the highest F of
630 the ranges explored for haddock ($F=0.25$) and monkfish ($F=0.41$) were applied, while an F
631 slightly above the middle of the range explored ($F=0.35$) was applied to hake (Fig. 2c). While
632 the non-culled biomass of grey seals did not prevent the recovery of cod and whiting, despite
633 slightly impacting the date when this recovery was achieved as explained above, the best
634 GES scenario was achieved when a 5% cull was applied to grey seals. This indicates that,
635 while the predation from grey seals does not prevent stock recovery, it does have an impact,
636 however small, on the food web structure and biodiversity of the WoS ecosystem. Apart from
637 grey seals which experience a 5% cull under the best GES scenario, the best GES and F_{MSY}
638 scenarios produced similar biomass trajectories which were actually closely aligned for most
639 species with one major exception, whiting, which did not recover under the F_{MSY} scenario
640 (Fig. 4). Likewise, apart from cod and haddock which experienced higher F values under the
641 best GES scenario, the catch trajectories produced by the best GES and F_{MSY} scenarios were
642 also similar, even for whiting which experienced a much lower F (0.05) under the best GES
643 scenario the F_{MSY} (0.18) scenario (Fig. S2).

644

645

646 **4. Discussion**

647

648 The results from the model simulations suggest that the single stock F_{MSY} values currently
649 advised by ICES, if applied to all stocks in WoS, would likely recover cod whilst achieving
650 catches on par with historical levels for most species. This management scenario would also
651 lead to an increase in whiting SSB, but would fail to recover this stock to within safe
652 biological limits, suggesting that the current F_{MSY} value for whiting in ICES area VIa is
653 incompatible with this stock's recovery. In contrast, the results from the simulations
654 exploring the F ranges used in this study suggest that it would be possible to recover both cod
655 and whiting stocks by applying F within these ranges. However, two crucial conditions were
656 necessary for the recovery of both these depleted stocks to happen. Firstly, the recovery of
657 whiting required that the lowest possible F ($F = 0.05$) of the ranges explored was applied to
658 both juvenile and adult whiting. Due to the depleted status of the VIa whiting stock, adult
659 whiting is no longer actively targeted in WoS and is currently experiencing an $F_{status\ quo}$ of ca.
660 0.06 due to bycatch. Juvenile whiting, on the other hand, is caught as bycatch by the small
661 meshed crustacean fishery targeting the highly valuable *Nephrops* (the crustacean fishery
662 account for 77% of the discards of age 0 and age 1 (i.e., juvenile) groups), and is currently
663 experiencing an $F_{status\ quo}$ of ca. 0.17 as a result (ICES, 2016c). Our results strongly suggest
664 that a substantial reduction in the bycatch of juvenile whiting by the crustacean fishery is
665 essential to the recovery of the VIa whiting stock. This contradicts the previous findings from
666 Alexander et al. (2015) who concluded that there is insufficient bycatch from the crustacean
667 fishery to prevent the recovery of whiting. While measures to prevent bycatch of juvenile
668 whiting by the crustacean fishery could potentially jeopardise one of the most profitable

669 fisheries in WoS, they will soon become a CFP requirement as the landings obligation is
670 being phased in for demersal stocks (EC, 2015a), with whiting already identified to become a
671 choke species for the crustacean fishery in WoS (ICES, 2016c).

672

673 The second requirement for the recovery of cod and whiting we identified is that the
674 simultaneous recovery of cod and whiting was achieved only when the highest possible F
675 from the ranges explored were applied to cod ($F = 0.25$) and saithe ($F = 0.42$). Both cod and
676 saithe are piscivorous top predators (trophic level ca. 4) of the WoS ecosystem. Saithe, along
677 with mackerel, is one of the main predators of both juvenile cod (Fig. 6a) and juvenile
678 whiting (Fig. 6b), and the increasing saithe biomass over the historical period has led to an
679 increase in predation pressure on these two juvenile stanzas. Scenarios with the highest F s on
680 saithe therefore resulted in a decrease in predation mortality on juvenile cod and whiting, thus
681 enabling these two species to recover. Likewise, cod is the main predator of whiting (Fig. 6c)
682 and the third most prevalent predator of juvenile cod after saithe and mackerel (Fig. 6a).
683 Applying the highest possible F on cod therefore limited the increase in predation mortality
684 on whiting, thus enabling the recovery of whiting, whilst also limiting cannibalism on
685 juvenile cod and facilitating the recovery of cod. These results suggest that reducing the
686 biomass of saithe, the main predator of juvenile cod and whiting, together with limiting the
687 increase of cod, the main predator of whiting, are necessary to recover both VIa cod and
688 whiting stocks. The fact that the recovery of cod and whiting, two piscivorous top predators,
689 seems unattainable without curbing the increase of another piscivorous top predator, saithe,
690 indicates that it may not be possible to simultaneously maximise the biomass of all demersal
691 piscivorous top predators of the WoS ecosystem (which also include hake and monkfish).
692 Therefore, it may be necessary to identify the optimum balance between these species to
693 achieve sustainable stocks statuses and a healthy food web.

694

695 The concept of ‘balanced fishing’ was first introduced by Garcia et al. (2012) and has gained
696 momentum in recent years as EBFM garnered more attention, although it remains a hotly
697 debated topic (ICES, 2014e). The intricacies and consequences of prey-predator interactions
698 in exploited ecosystems, and the importance of considering them in the management of
699 mixed fisheries are particularly relevant at a time when improved stewardship in the
700 management of European fisheries is leading to the recovery of most commercial stocks
701 (Fernandes and Cook, 2013) resulting in the increase in the biomass of many top predator as
702 they approach their MSY status, with knock-on implications for prey-predator interactions
703 (ICES, 2016h, 2014e). For example, the recovery of the northern hake stock has led to a large
704 increase in the biomass of this top predator across most of northern Europe, including WoS
705 (Baudron and Fernandes, 2015), with repercussions on prey-predator interactions such as the
706 increased competition with saithe for access to their common prey, as documented in the
707 North Sea (Cormon et al., 2016). Although a similar increase has yet to be reported for saithe,
708 the biomass trend from survey data presented here suggest that this species has been
709 increasing continuously from 1985 to 2013 in WoS, whilst fish stock recoveries have been
710 linked to a decline in fishing exploitation and associated harvest rates in ICES area VI
711 overall, and the neighbouring ICES area V for saithe specifically (Jayasinghe et al., 2015).
712 The possible application of ‘balanced fishing’ in European fisheries and its consequences for
713 ecosystems are currently being investigated by the ICES Working Group on the Ecosystem
714 Effects of Fishing Activities who concluded that, as fish stock recoveries are expected to
715 have significant trophic effects, ecosystem models such as the one employed here could be
716 used to predict the ecological consequences of stock rebuilding (ICES, 2016h).

717

718 Implementing a cull of grey seals, the main predator of cod and one of the main predators of
719 gadoid fish species in WoS, had little impact overall on the recovery of cod and whiting. Both
720 species were able to recover when no cull was applied, an observation consistent with the
721 previous findings from Alexander et al. (2015) who concluded that the rise in grey seals
722 biomass had not led to the collapse of these species. This observation contradicts, however,
723 the findings from a recent modelling study which suggests that the sustained high mortality
724 due to increased predation from grey seals is preventing the recovery of the VIa cod stock
725 (Cook et al., 2015). Reducing the grey seals population by 5% every year had no impact of
726 the recovery of cod, however a 10% reduction led to cod recovering within safe biological
727 limits a year earlier. While the difference is small, this observation is consistent with another
728 recent modelling study showing that the VIa cod stock recovery under current levels of grey
729 seals predation is possible although it would remain precarious (Cook and Trijoulet, 2016).
730 Our results showed that a yearly 10% decrease in grey seals biomass led to a slightly earlier
731 cod recovery, suggesting that an increase in grey seals biomass would potentially delay the
732 recovery, a finding consistent with Serpetti et al. (2017) who identified grey seals as exerting
733 a top-down control on their prey. We also showed that a decrease in grey seals biomass could
734 be detrimental for the whiting recovery: the increase in cod biomass associated with a
735 decrease in grey seals biomass would increase predation mortality on whiting, thus delaying
736 its recovery. This potential impact has not yet been reported for whiting in WoS and
737 highlights the need for considering prey-predator interactions in the management of exploited
738 ecosystems, as previously mentioned. Lastly, the best GES scenario identified here included a
739 5% cull of grey seals, further demonstrating the impact of the abundance of top predators on
740 the food web structure and diversity. However, the small differences observed between
741 scenarios with and without grey seals cull, coupled with the fact that the absence of cull did

742 not prevent the recovery of cod and whiting, do not provide enough support for culling grey
743 seals as a management measure.

744

745 The performance of the exploitation scenarios simulated here towards achieving GES was
746 assessed based on five indicators which only related to three out of the eleven GES
747 descriptors: biodiversity (two indicators), commercial species (one indicator) and food webs
748 (two indicators). GES was therefore not comprehensively assessed in this study as many
749 descriptors were omitted from the analyses since it was not possible to model them due to
750 lack of data (e.g., descriptor 10: Marine litter) or lack of processes included in the model
751 (e.g., descriptor 5: Eutrophication). In addition, apart from the biomass indicator for which
752 reference points are defined for the two depleted stocks, the biodiversity and food web
753 indicators employed here have no clearly established thresholds to enable assessing whether
754 GES is reached (i.e., indicator > threshold). This is further complicated by the fact that there
755 is currently no stringent framework that uses indicators in assessing GES criteria (Queirós et
756 al., 2016). Lastly, one of the two food web indicators employed, MTI, was calculated using
757 fixed trophic levels per species, a practice not as efficient as the use of variable trophic levels
758 which better detects the impact of fishing pressure (Reed et al., 2017). These drawbacks were
759 mitigated through the use of two indicators (i.e., diversity and food web) and the use of an ad-
760 hoc approach to identify the best scenario. Notwithstanding these caveats, the use of a food
761 web ecosystem model combined with biomass thresholds enabled the identification of the
762 management measures necessary to recover the depleted stocks of cod and whiting, thus
763 addressing the most pressing environmental issue in WoS fisheries. Whether or not these
764 management measures would also lead to GES for the WoS ecosystem is ambiguous. This is
765 due to the caveats listed above, but also to the fact that, although the two biodiversity
766 indicators increased under the best management scenario identified here compared to status

767 quo, the two food web indicators decreased. This suggests that it might not be possible to
768 simultaneously maximise both the biodiversity and the food web trophic structure (as
769 measured by MML and MTI). With both biodiversity and trophic structure potentially
770 impacting the WoS ecosystem resilience to fishing and other pressures, GES may only be
771 achieved through appropriate trade-offs between these two descriptors. Nonetheless, the
772 approach employed here (i.e., using biodiversity and food web indicators derived from food
773 web ecosystem model simulations) has been successfully used in previous studies
774 investigating the performance of fishing management scenarios towards the contrasting
775 objectives of MSY and GES (Lynam and Mackinson, 2015; Stäbler et al., 2016). Here, the
776 chosen indicators replicated historical trends, suggesting that perhaps they could be used to
777 explore future trends and compare candidate scenarios to one another in order to inform
778 management decisions. Such an approach is employed, for example, when using surveillance
779 indicators for which there is insufficient information to establish a clear target (Shephard et
780 al., 2015). Future work using greater model complexity could achieve comprehensive
781 assessments of GES. For instance, Alexander et al. (2016) have developed a EwE model for
782 WoS built on their previous work (Alexander et al., 2015) which includes a spatial
783 component. Such a model could allow, for example, mapping trawl fishing activities in WoS
784 and investigating descriptor 6 (Sea-floor integrity), thus improving on the GES assessment
785 presented here.

786

787 The Ecopath model presented here entailed an update of the mass balance model from
788 Alexander et al. (2015), as well as extensive changes to the diet matrix. This updated model
789 was recently employed by Serpetti et al. (2017) to assess the long-term impacts of rising sea
790 temperatures on WoS fisheries. In addition, the data time series used to update the Ecosim
791 hindcast period from 1985-2008 to 1985-2013 included biomass trends derived from survey

792 data for saithe and monkfish, where previously proxies derived from stock assessment model
793 estimates were used (Bailey et al., 2011). This improves the credibility of the model since
794 using raw data avoids the uncertainty and possible errors associated with estimates produced
795 by statistical models (Dickey-Collas et al., 2014), especially when these statistical models
796 were designed for different areas than the model area considered here. Another update was
797 the inclusion of biomass time series of zooplankton and phytoplankton used to fit the model.
798 This addition contributes to further improving the credibility of the model by constraining the
799 model calibration at multiple trophic levels, a practice shown to lead to a better and more
800 credible parameterisation especially when both fishing and environmental effects are
801 considered (Mackinson, 2014). Overall, the updated model showed an improvement of the fit,
802 with the hindcast better reproducing the historical biomass trends of most species compared
803 to the hindcast shown in Alexander et al. (2015) whilst being similar to the hindcast shown
804 by Serpetti et al. (2017). Most importantly, the updated model seems to behave more
805 realistically when performing forward simulations. When reducing F , the biomass estimates
806 produced by the updated model showed a gradual increase, as expected in complex
807 ecosystems where trophic interactions may buffer the impact of a decrease in F . In contrast,
808 the results shown in Alexander et al. (2015) showed a sudden increase in the annual biomass
809 of cod and whiting of several thousands of tonnes within a couple of years when a reduction
810 in F was applied. Whilst not disputing the magnitude of the biomass increase observed by
811 Alexander et al. (2015), such an increase within such a short time seems rather unrealistic.
812 The time scale within which the updated model recovers seems more realistic which is a
813 necessary component when testing fishing management strategies and their impact (Lynam
814 and Mackinson, 2015) such as the date when depleted stocks recover, as investigated here.
815

816 Ecosystem modelling is a valuable tool for the implementation of EBFM. The inclusion of
817 multiple species spanning several trophic levels and their trophic interactions is necessary to
818 investigate the impact of management strategies on environmental and conservation
819 objectives such as GES (Christensen and Walters, 2005). Yet, as these conservation
820 objectives become a requirement while the latest CFP reform steers European fisheries
821 management away from the traditional approach and towards EBFM, ecosystem modelling
822 tools are still scarcely used in tactical fisheries management which remains very much single
823 stock orientated (Skern-Mauritzen et al., 2015). EwE has benefited from a continuous
824 development spanning over 30 years (Villasante et al., 2016) and has been successfully
825 employed on numerous occasions to investigate marine policy issues (Christensen and
826 Walters, 2004; Colléter et al., 2015), with recent examples including the investigation of the
827 impact of fisheries management strategies on GES (Lynam and Mackinson, 2015; Stäbler et
828 al., 2016), as implemented in this study. However, the use of EwE as a fisheries management
829 tool has been heavily criticised (Plagányi and Butterworth, 2004), since major pitfalls in the
830 application of EwE can produce misleading predictions about the direction of change caused
831 by management strategies simulated, let alone their magnitude (Christensen and Walters,
832 2004). In addition, it has been shown that EwE models can produce significantly different
833 results from the same analyses depending on how the model has been calibrated (Mackinson,
834 2014), indicating that such models should be employed with care, particularly when
835 investigating policy issues. The model employed here has been improved four times since its
836 development (Alexander et al., 2015; Bailey et al., 2011; Haggan and Pitcher, 2005; Serpetti
837 et al., 2017). While the model is able to reproduce historical biomass and catch, suggesting
838 that it successfully captures the dynamics of the WoS food web, many assumptions were
839 made during the parameterisation process. Therefore, the model presented here cannot, in its
840 present state, be employed to make tactical management decisions (e.g., setting a Total

841 Allowable Catch) due to the number of uncertainties (e.g., parameter uncertainty) linked to
842 the various processes it describes. Indeed, the sensitivity of the model to parameter
843 uncertainty led to large uncertainties being observed around the biomass estimates of cod and
844 whiting, the two species on which scenario selection was based. In addition, extending the
845 simulation beyond the period of interest until the ecosystem reached equilibrium revealed that
846 the scenarios identified as achieving the fastest recovery of cod and whiting may not maintain
847 whiting within sustainable limits in the long term although no firm conclusions could be
848 drawn owing to the aforementioned large uncertainties around biomass estimates. However,
849 the model could be used to evaluate trade-offs between species, fisheries, and human uses'
850 impacts which is central to the ecosystem approach (Kaplan and Marshall, 2016). We suggest
851 that it is useful in an EBFM context, possibly alongside the use of traditional tactical models
852 (e.g. stock assessment), to explore various 'what if' scenarios, as done here, to inform
853 managers on the likely future trends of biomass and ecosystem indicators.

854

855

856 **5. Conclusion**

857

858 Using a food web ecosystem model to simulate management scenarios accounted for prey-
859 predator interactions whilst investigating biodiversity and food web indicators related to GES
860 descriptors. Our results suggest that the single stock F_{MSY} values currently advised by ICES
861 would recover the VIa cod stock, providing that F_{MSY} is applied to all stocks in VIa, but
862 would fail to recover the VIa whiting stock. The exploration of alternative management
863 scenarios led to the identification of the exploitation levels required to recover both the cod
864 and whiting stocks, and revealed that two conditions are necessary for these recoveries to
865 happen. Firstly, a reduction in the F experienced for juvenile whiting was necessary to

866 recover whiting, indicating that a reduction in the bycatch of juvenile whiting by the
867 crustacean fishery is needed for the VIa whiting stock to recover. Secondly, the simultaneous
868 recovery of cod and whiting was achieved only when the highest possible F_s were applied to
869 both cod, the main predator of whiting, and saithe, the main predator of juvenile cod and
870 whiting, highlighting the need to consider the impact of prey-predator interactions when
871 managing fish stocks. The best GES scenario identified here resulted in biomass trajectories
872 similar to the ones achieved with the single stock F_{MSY} scenario, with the exception of
873 whiting which did not recover under this latter scenario. Likewise, the GES indicators
874 trajectories achieved by the best GES scenario were broadly similar to the ones achieved by
875 the single stock F_{MSY} scenario. Most importantly, the recovery of the cod and whiting stocks
876 were achieved with F values within the F_{MSY} ranges identified by ICES for the six demersal
877 stock considered here, with the exception of whiting. This suggests that the current
878 management measures enforced in European fisheries by the CFP could achieve GES in the
879 WoS ecosystem, provided that existing management issues such as the bycatch of whiting by
880 the crustacean fishery are resolved, and that prey-predator interactions are accounted for, a
881 component which will increasingly be taken into consideration as European fisheries
882 management is evolving towards EBFM.

883

884

885 **6. Acknowledgements**

886

887 Alan R. Baudron, Niall G. Fallon and Paul G. Fernandes were funded by the Horizon 2020
888 European research project MareFrame (grant No. 613571). Natalia Serpetti and Johanna J.
889 Heymans were funded by the Natural Environment Research Council and Department for
890 Environment, Food and Rural Affairs under the Marine Ecosystems Research Programme

891 (MERP) (grant No. NE/L003279/1). We thank two anonymous reviewers for their insightful
892 comments.

893

894

895 **7. References**

896

897 Ainsworth, C.H., Walters, C.J., 2015. Ten common mistakes made in ecopath with ecosim
898 modelling. *Ecol. Modell.* 308, 14–17. <https://doi.org/10.1016/j.ecolmodel.2015.03.019>

899 Alexander, K.A., Heymans, J.J., Magill, S., Tomczak, M.T., Holmes, S.J., Wilding, T.A.,
900 2015. Investigating the recent decline in gadoid stocks in the west of Scotland shelf
901 ecosystem using a foodweb model 72, 436–449.

902 Alexander, K.A., Meyjes, S.A., Heymans, J.J., 2016. Spatial ecosystem modelling of marine
903 renewable energy installations: Gauging the utility of Ecospace. *Ecol. Modell.* 1–14.
904 <https://doi.org/10.1016/j.ecolmodel.2016.01.016>

905 Bailey, N., Bailey, D., Bellini, L., Fernandes, P., Fox, C., Heymans, S., Holmes, S., Howe, J.,
906 Hughes, S., Magill, S., McIntyre, F., McKee, D., Ryan, M., Smith, I., Tyldsley, G.,
907 Watret, R., Turrell, W., 2011. The West of Scotland Marine Ecosystem : A Review of
908 Scientific Knowledge. *Mar. Scotl. Sci. Rep.* 292.

909 Batten, S.D., Walne, A.W., 2011. Variability in northwards extension of warm water
910 copepods in the NE Pacific. *J. Plankton Res.* 33, 1643–1653.
911 <https://doi.org/10.1093/plankt/fbr065>

912 Baudron, A.R., Fernandes, P.G., 2015. Adverse consequences of stock recovery: European
913 hake, a new “choke” species under a discard ban? *Fish Fish.* 16, 563–575.
914 <https://doi.org/10.1111/faf.12079>

915 Cardinale, M., Dörner, H., Abella, A., Andersen, J.L., Casey, J., Döring, R., Kirkegaard, E.,

916 Motova, A., Anderson, J., Simmonds, E.J., Stransky, C., 2013. Rebuilding EU fish
917 stocks and fisheries, a process under way? *Mar. Policy* 39, 43–52.
918 <https://doi.org/10.1016/j.marpol.2012.10.002>

919 Christensen, V., Pauly, D., 1992. ECOPATH II—a software for balancing steady-state
920 ecosystem models and calculating network characteristics. *Ecol. Modell.* 61, 169–185.

921 Christensen, V., Walters, C., 2005. Using ecosystem modeling for fisheries management:
922 Where are we. *ICES J. Mar. Sci.* 19, 20–24.

923 Christensen, V., Walters, C.J., 2004. Ecopath with Ecosim: Methods, capabilities and
924 limitations. *Ecol. Modell.* 172, 109–139.
925 <https://doi.org/10.1016/j.ecolmodel.2003.09.003>

926 Christensen, V., Walters, C.J., 2004. Trade-offs in ecosystem-scale optimization of fisheries
927 management policies. *Bull. Mar. Sci.* 74, 549–562.

928 Christensen, V., Walters, C.J., Pauly, D., Forrest, R., 2008. Ecopath with Ecosim, version 6.
929 User Guide., Fisheries Bethesda. University of British Columbia, Vancouver, B.C.,
930 Canada. [https://doi.org/10.1016/0304-3800\(92\)90016-8](https://doi.org/10.1016/0304-3800(92)90016-8)

931 Coll, M., Shannon, L.J., Kleisner, K.M., Juan-Jordá, M.J., Bundy, A., Akoglu, A.G., Banaru,
932 D., Boldt, J.L., Borges, M.F., Cook, A., Diallo, I., Fu, C., Fox, C., Gascuel, D., Gurney,
933 L.J., Hattab, T., Heymans, J.J., Jouffre, D., Knight, B.R., Kucukavsar, S., Large, S.I.,
934 Lynam, C., MacHias, A., Marshall, K.N., Masski, H., Ojaveer, H., Piroddi, C., Tam, J.,
935 Thiao, D., Thiaw, M., Torres, M.A., Travers-Trolet, M., Tsagarakis, K., Tuck, I., Van
936 Der Meeren, G.I., Yemane, D., Zador, S.G., Shin, Y.J., 2016. Ecological indicators to
937 capture the effects of fishing on biodiversity and conservation status of marine
938 ecosystems. *Ecol. Indic.* 60, 947–962. <https://doi.org/10.1016/j.ecolind.2015.08.048>

939 Colléter, M., Valls, A., Guitton, J., Gascuel, D., Pauly, D., Christensen, V., 2015. Global
940 overview of the applications of the Ecopath with Ecosim modeling approach using the

941 EcoBase models repository. *Ecol. Modell.* 302, 42–53.
942 <https://doi.org/10.1016/j.ecolmodel.2015.01.025>

943 Cook, R.M., Holmes, S.J., Fryer, R.J., 2015. Grey seal predation impairs recovery of an over-
944 exploited fish stock. *J. Appl. Ecol.* 52, 969–979. [https://doi.org/10.1111/1365-](https://doi.org/10.1111/1365-2664.12439)
945 [2664.12439](https://doi.org/10.1111/1365-2664.12439)

946 Cook, R.M., Trijoulet, V., 2016. The effects of grey seal predation and commercial fishing on
947 the recovery of a depleted cod stock. *Can. J. Fish. Aquat. Sci.* 73, 1–11.
948 <https://doi.org/10.1139/cjfas-2015-0423>

949 Cormon, X., Kempf, A., Vermard, Y., Vinther, M., Marchal, P., 2016. Emergence of a new
950 predator in the North Sea: evaluation of potential trophic impacts focused on hake,
951 saithe, and Norway pout. *ICES J. Mar. Sci.* 73, 1370–1381.

952 Dickey-Collas, M., Payne, M.R., Trenkel, V.M., Nash, R.D.M., 2014. Hazard warning:
953 Model misuse ahead. *ICES J. Mar. Sci.* 71, 2300–2306.
954 <https://doi.org/10.1093/icesjms/fst215>

955 EC, 2015a. COMMISSION DELEGATED REGULATION (EU) 2015/2438 of 12 October
956 2015 establishing a discard plan for certain demersal fisheries in north-western waters.
957 *Off. J. Eur. Union L* 336/29.

958 EC, 2015b. Agreed record of fisheries consultations between the European Union and
959 Norway for 2015.

960 EC, 2013. REGULATION (EU) No 1380/2013 OF THE EUROPEAN PARLIAMENT AND
961 OF THE COUNCIL of 11 December 2013 on the Common Fisheries Policy, amending
962 Council Regulations (EC) No 1954/2003 and (EC) No 1224/2009 and repealing Council
963 Regulations (EC) No 2371/2002 and (EC. *Off. J. Eur. Union L*354/22.

964 EC, 2011. COMMUNICATION FROM THE COMMISSION TO THE EUROPEAN
965 PARLIAMENT, THE COUNCIL, THE EUROPEAN ECONOMIC AND SOCIAL

966 COMMITTEE AND THE COMMITTEE OF THE REGIONS. Reform of the Common
967 Fisheries Policy COM (2011).

968 EC, 2009. Reform of the Common Fisheries Policy. Brussels, 22.4.2009 COM(2009)163
969 final.

970 EC, 2008. Directive 2008/56/EC of the European Parliament and of the Council. Off. J. Eur.
971 Union 164, 19–40. <https://doi.org/10.1016/j.biocon.2008.10.006>

972 Fernandes, P.G., Cook, R.M., 2013. Reversal of fish stock decline in the northeast atlantic.
973 *Curr. Biol.* 23, 1432–1437. <https://doi.org/10.1016/j.cub.2013.06.016>

974 Froese, R., Pauly, D., 2017. FishBase. World Wide Web electronic publication.

975 Froese, R., Stern-Pirlot, A., Winker, H., Gascuel, D., 2008. Size matters: How single-species
976 management can contribute to ecosystem-based fisheries management. *Fish. Res.* 92,
977 231–241. <https://doi.org/10.1016/j.fishres.2008.01.005>

978 Garcia, S., Kolding, J., Rice, J., Rochet, M., Zhou, S., 2012. Reconsidering the Consequences
979 of Selective Fisheries. *Science* (80-.). 335, 1045–1048.

980 Garcia, S.M., Zerbi, A., Aliaume, C., Do Chi, T., Lasserre, G., 2003. The ecosystem
981 approach to fisheries. *FAO Fish. Tech. Pap.* 443, 71. [https://doi.org/10.1111/j.1467-](https://doi.org/10.1111/j.1467-2979.2010.00358.x)
982 [2979.2010.00358.x](https://doi.org/10.1111/j.1467-2979.2010.00358.x)

983 Gascuel, D., Coll, M., Fox, C., Guénette, S., Guitton, J., Kenny, A., Knittweis, L., Nielsen,
984 J.R., Piet, G., Raid, T., Travers-Trolet, M., Shephard, S., 2016. Fishing impact and
985 environmental status in European seas: A diagnosis from stock assessments and
986 ecosystem indicators. *Fish Fish.* 17, 31–55. <https://doi.org/10.1111/faf.12090>

987 Haggan, N., Pitcher, T.J., 2005. Fisheries Centre Research Reports Ecosystem Simulation
988 Models of Scotland ' s West Coast and Sea Lochs. *Fish. Cent. Res. Reports* 13.

989 Heymans, J.J., Coll, M., Libralato, S., Morissette, L., Christensen, V., 2014. Global Patterns
990 in Ecological Indicators of Marine Food Webs: A Modelling Approach. *PLoS One* 9,

991 e95845. <https://doi.org/10.1371/journal.pone.0095845>

992 Heymans, J.J., Coll, M., Link, J.S., Mackinson, S., Steenbeek, J., Walters, C., Christensen,
993 V., 2016. Best practice in Ecopath with Ecosim food-web models for ecosystem-based
994 management. *Ecol. Modell.* <https://doi.org/10.1016/j.ecolmodel.2015.12.007>

995 ICES, 2017. WGMIXFISH - Report of the Working Group on Mixed Fisheries Advice for
996 the North Sea 1–24.

997 ICES, 2016a. EU request to provide a framework for the classification of stock status relative
998 to MSY proxies for selected category 3 and category 4 stocks in ICES subareas 5 to 10.
999 V2 9, 1–7.

1000 ICES, 2016b. Celtic Seas Ecoregion – Ecosystem overview Version 2, 1–16.

1001 ICES, 2016c. Report of the Working Group on Celtic Seas Ecoregion (WGCSE) ICES CM
1002 20.

1003 ICES, 2016d. Report of the Working Group on the Assessment of Demersal Stocks in the
1004 North Sea and Skagerrak (WGNSSK). ICES C. 2016/ ACOM14.

1005 ICES, 2016e. Report of the Working Group on Widely Distributed Stocks (WGWIDE). ICES
1006 C. 2016/ACOM16 588. <https://doi.org/ICES CM 2011/ACOM:15>

1007 ICES, 2016f. Report of the Herring Assessment Working Group for the Area South of 62°N
1008 (HAWG). ICES C. 2016/ACOM07. <https://doi.org/ICES CM 2016/ACOM:07>

1009 ICES, 2016g. Report of the Working Group for the Bay of Biscay and the Iberian waters
1010 Ecoregion (WGBIE). ICES C.

1011 ICES, 2016h. Report of the Working Group on Ecosystem Effects of Fishing Activities (
1012 WGECO). ICES C. 2016/ACOM25.

1013 ICES, 2015. EU request to ICES to provide FMSY ranges for selected North Sea and Baltic
1014 Sea stocks. ICES Advice 2015, B. 6 11 pp.

1015 ICES, 2014a. Report of the Working Group for the Celtic Seas Ecoregion (WGCSE) ICES

1016 CM 20.

1017 ICES, 2014b. Report of the Herring Assessment Working Group for the Area South of 62°N
1018 (HAWG). *Ices C. 2014 ACOM:06*, 1257 pp. <https://doi.org/2015/ACOM:06>

1019 ICES, 2014c. Report of the Report of the Working Group on Widely Distributed Stocks
1020 (WGWIDE). *ICES C. 2014/ACOM15*.

1021 ICES, 2014d. Report of the Working Group for the Assessment of Demersal Stocks in the
1022 North Sea and Skagerrak (WGNSSK). *ICES C. 2014/ACOM13*.

1023 ICES, 2014e. Report of the Working Group on Ecosystem Effects of Fishing Activities (
1024 WGECO). *ICES C. 2014/ACOM26*.

1025 Jayasinghe, R.P.P.K., Amarasinghe, U.S., Newton, A., 2015. Evaluation of status of
1026 commercial fish stocks in European marine subareas using mean trophic levels of fish
1027 landings and spawning stock biomass. *Ocean Coast. Manag.* 1–10.
1028 <https://doi.org/10.1016/j.ocecoaman.2016.07.002>

1029 Jennings, S., Rice, J., 2011. Towards an ecosystem approach to fisheries in Europe: A
1030 perspective on existing progress and future directions. *Fish Fish.* 12, 125–137.
1031 <https://doi.org/10.1111/j.1467-2979.2011.00409.x>

1032 Kaplan, I.C., Marshall, K.N., 2016. A guinea pig’s tale: learning to review end-to-end marine
1033 ecosystem models for management applications. *ICES J. Mar. Sci.* 73, 1715–1724.

1034 Kleisner, K.M., Coll, M., Lynam, C.P., Bundy, A., Shannon, L., Shin, Y.J., Boldt, J.L., Maria
1035 F., B., Diallo, I., Fox, C., Gascuel, D., Heymans, J.J., Juan Jordá, M.J., Jouffre, D.,
1036 Large, S.I., Marshall, K.N., Ojaveer, H., Piroddi, C., Tam, J., Torres, M.A., Travers-
1037 Trolet, M., Tsagarakis, K., Van Der Meeren, G.I., Zador, S., 2015. Evaluating changes
1038 in marine communities that provide ecosystem services through comparative
1039 assessments of community indicators. *Ecosyst. Serv.* 16, 413–429.
1040 <https://doi.org/10.1016/j.ecoser.2015.02.002>

1041 Kotenev, B.N., Krovnin, A.S., Rodionov, S.N., 2011. Climate trend forecast for the
1042 Norwegian and Barents Seas in 2012–2025. *Inst. Mar. Res. - IMR, Bergen, Norw.*

1043 Kumar, R., Pitcher, T.J., Varkey, D.A., 2017. Ecosystem approach to fisheries: Exploring
1044 environmental and trophic effects on Maximum Sustainable Yield (MSY) reference
1045 point estimates. *PLoS One* 12, e0185575. <https://doi.org/10.1371/journal.pone.0185575>

1046 Larkin, P.A., 1977. An epitaph for the concept of maximum sustained yield. *Trans. Am. Fish.*
1047 *Soc.* 106, 1–11.

1048 Lees, K. and M., Mackinson, S., 2007. An Ecopath model of the Irish Sea : ecosystems
1049 properties and sensitivity. *Sci. Ser. Tech Rep., Cefas Lowestoft* 138, 49.

1050 Link, J.S., 2010. Adding rigor to ecological network models by evaluating a set of pre-
1051 balance diagnostics: A plea for PREBAL. *Ecol. Modell.* 221, 1580–1591.
1052 <https://doi.org/10.1016/j.ecolmodel.2010.03.012>

1053 Link, J.S., 2005. Translating ecosystem indicators into decision criteria. *ICES J. Mar. Sci.* 62,
1054 569–576. <https://doi.org/10.1016/j.icesjms.2004.12.015>

1055 Lynam, C.P., Mackinson, S., 2015. How will fisheries management measures contribute
1056 towards the attainment of Good Environmental Status for the North Sea ecosystem?
1057 *Glob. Ecol. Conserv.* 4, 160–175. <https://doi.org/10.1016/j.gecco.2015.06.005>

1058 Mackinson, S., 2014. Combined analyses reveal environmentally driven changes in the North
1059 Sea ecosystem and raise questions regarding what makes an ecosystem model 's
1060 performance credible? *Can. J. Fish. Aquat. Sci.* 71, 31–46. [https://doi.org/10.1139/cjfas-](https://doi.org/10.1139/cjfas-2013-0173)
1061 [2013-0173](https://doi.org/10.1139/cjfas-2013-0173)

1062 Mackinson, S., Daskalov, G., 2007. An ecosystem model of the North Sea to support an
1063 ecosystem approach to fisheries management: description and parameterisation. *Sci. Ser.*
1064 *Tech Rep., Cefas Lowestoft* 196pp.

1065 Mackinson, S., Daskalov, G., Heymans, J.J., Neira, S., Arancibia, H., Zetina-Rejón, M.,

1066 Jiang, H., Cheng, H.Q., Coll, M., Arreguin-Sanchez, F., Keeble, K., Shannon, L., 2009.
1067 Which forcing factors fit? Using ecosystem models to investigate the relative influence
1068 of fishing and changes in primary productivity on the dynamics of marine ecosystems.
1069 *Ecol. Modell.* 220, 2972–2987. <https://doi.org/10.1016/j.ecolmodel.2008.10.021>

1070 Murawski, S.A., Davidson, C.N., Hart, Z., NOAA, Balgos, M., Wowk, K., Cicin-Sain, B.,
1071 2008. Ecosystem-based Management and Integrated Coastal and Ocean Management
1072 and Indicators for Progress. *Glob. Forum Ocean. Coasts, Islands Work. Gr. Ecosyst.*
1073 *Manag. Integr. Coast. Ocean Manag. Indic. Progress.*

1074 Patrick, W.S., Link, J.S., 2015. Myths that Continue to Impede Progress in Ecosystem-Based
1075 Fisheries Management. *Fisheries* 40, 155–160.
1076 <https://doi.org/10.1080/03632415.2015.1024308>

1077 Pauly, D., Watson, R., 2005. Background and interpretation of the “Marine Trophic Index” as
1078 a measure of biodiversity. *Philos. Trans. R. Soc. B Biol. Sci.* 360, 415–423.
1079 <https://doi.org/10.1098/rstb.2004.1597>

1080 Pinnegar, J.K., 2014. DAPSTOM - An Integrated Database & Portal for Fish Stomach
1081 Records. *Cefas Contract Rep. DP332, C3746, ME1228* 1–35.

1082 Piroddi, C., Teixeira, H., Lynam, C.P., Smith, C., Alvarez, M.C., Mazik, K., Andonegi, E.,
1083 Churilova, T., Tedesco, L., Chifflet, M., Chust, G., Galparsoro, I., Garcia, A.C., Kämäri,
1084 M., Kryvenko, O., Lassalle, G., Neville, S., Niquil, N., Papadopoulou, N., Rossberg,
1085 A.G., Suslin, V., Uyarra, M.C., 2015. Using ecological models to assess ecosystem
1086 status in support of the European Marine Strategy Framework Directive. *Ecol. Indic.* 58,
1087 175–191. <https://doi.org/10.1016/J.ECOLIND.2015.05.037>

1088 Plagányi, E., 2007. Models for an ecosystem approach to fisheries.

1089 Plagányi, É.E., Butterworth, D.S., 2004. A critical look at the potential of Ecopath with
1090 ecosim to assist in practical fisheries management. *African J. Mar. Sci.* 26, 261–287.

1091 <https://doi.org/10.2989/18142320409504061>

1092 Polovina, J.J., 1984. Model of a coral reef ecosystem. The ECOPATH model and its
1093 application to French Frigate Shoals. *Coral Reefs* 3, 1–11.

1094 Prellezo, R., Curtin, R., 2015. Confronting the implementation of marine ecosystem-based
1095 management within the Common Fisheries Policy reform. *Ocean Coast. Manag.* 117,
1096 43–51. <https://doi.org/10.1016/j.ocecoaman.2015.03.005>

1097 Queirós, A.M., Strong, J.A., Mazik, K., Carstensen, J., Bruun, J., Somerfield, P.J., Bruhn, A.,
1098 Ciavatta, S., Flo, E., Bizsel, N., Özaydinli, M., Chuševè, R., Muxika, I., Nygård, H.,
1099 Papadopoulou, N., Pantazi, M., Krause-Jensen, D., 2016. An Objective Framework to
1100 Test the Quality of Candidate Indicators of Good Environmental Status. *Front. Mar. Sci.*
1101 3. <https://doi.org/10.3389/fmars.2016.00073>

1102 Ramírez-Monsalve, P., Raakjær, J., Nielsen, K.N., Santiago, J.L., Ballesteros, M., Laksá, U.,
1103 Degnbol, P., 2016. Ecosystem Approach to Fisheries Management (EAFM) in the EU -
1104 Current science-policy-society interfaces and emerging requirements. *Mar. Policy* 66,
1105 83–92. <https://doi.org/10.1016/j.marpol.2015.12.030>

1106 Reed, J., Shannon, L., Velez, L., Akoglu, E., Bundy, A., Coll, M., Fu, C., Fulton, E.A.,
1107 Grüss, A., Halouani, G., Heymans, J.J., Houle, J.E., John, E., Le Loc'h, F., Salihoglu,
1108 B., Verley, P., Shin, Y.J., 2017. Ecosystem indicators - Accounting for variability in
1109 species' trophic levels. *ICES J. Mar. Sci.* 74, 158–169.
1110 <https://doi.org/10.1093/icesjms/fsw150>

1111 Samhuri, J.F., Levin, P.S., Harvey, C.J., 2009. Quantitative evaluation of marine ecosystem
1112 indicator performance using food web models. *Ecosystems* 12, 1283–1298.
1113 <https://doi.org/10.1007/s10021-009-9286-9>

1114 Schaefer, M.B., 1954. Some Aspect of The Dynamics of Populations Important to The
1115 Management of The Commercial Merine Fisheries. *Bull. Math. Biol.*

1116 <https://doi.org/10.1017/CBO9781107415324.004>

1117 SCOS, 2015. Scientific advice on matters related to the management of seal populations:
1118 2015. Sci. Advice Matters Relat. to Manag. Seal Popul. 2015 SCOS-BP 15/02.

1119 Scott, E., Serpetti, N., Steenbeek, J., Heymans, J.J., 2016. A Stepwise Fitting Procedure for
1120 automated fitting of Ecopath with Ecosim models. *SoftwareX* 5, 25–30.
1121 <https://doi.org/10.1016/J.SOFTX.2016.02.002>

1122 Serpetti, N., Baudron, A.R., Burrows, M.T., Payne, B.L., Helaouët, P., Fernandes, P.G.,
1123 Heymans, J.J., 2017. Impact of ocean warming on sustainable fisheries management
1124 informs the Ecosystem Approach to Fisheries. *Sci. Rep.* 7, 1–15.
1125 <https://doi.org/10.1038/s41598-017-13220-7>

1126 Shannon, C.E., 1948. A mathematical theory of communication. *Bell Syst. Tech. J.* 27, 379–
1127 423. <https://doi.org/10.1145/584091.584093>

1128 Shephard, S., Greenstreet, S.P.R., Piet, G.J., Rindorf, A., Dickey-Collas, M., 2015.
1129 Surveillance indicators and their use in implementation of the Marine Strategy
1130 Framework Directive. *ICES J. Mar. Sci.* 72, 2269–2277.

1131 Shin, Y.J., Rochet, M.J., Jennings, S., Field, J.G., Gislason, H., 2005. Using size-based
1132 indicators to evaluate the ecosystem effects of fishing. *ICES J. Mar. Sci.* 62, 384–396.
1133 <https://doi.org/10.1016/j.icesjms.2005.01.004>

1134 Skern-Mauritzen, M., Ottersen, G., Handegard, N.O., Huse, G., Dingsør, G.E., Stenseth,
1135 N.C., Kjesbu, O.S., 2015. Ecosystem processes are rarely included in tactical fisheries
1136 management. *Fish Fish.* 165–175. <https://doi.org/10.1111/faf.12111>

1137 Stäbler, M., Kempf, A., Mackinson, S., Poos, J.J., Garcia, C., Temming, A., 2016.
1138 Combining efforts to make maximum sustainable yields and good environmental status
1139 match in a food-web model of the southern North Sea. *Ecol. Modell.* 331, 17–30.
1140 <https://doi.org/10.1016/j.ecolmodel.2016.01.020>

1141 Steenbeek, J., Buszowski, J., Christensen, V., Akoglu, E., Aydin, K., Ellis, N., Felinto, D.,
1142 Guitton, J., Lucey, S., Kearney, K., Mackinson, S., Pan, M., Platts, M., Walters, C.,
1143 2016. Ecopath with Ecosim as a model-building toolbox: Source code capabilities,
1144 extensions, and variations. *Ecol. Modell.* 319, 178–189.
1145 <https://doi.org/10.1016/j.ecolmodel.2015.06.031>

1146 The Scottish Government, 2015. Scottish Sea Fisheries Statistics 2014.

1147 Tomczak, M.T., Niiranen, S., Hjerne, O., Blenckner, T., 2012. Ecosystem flow dynamics in
1148 the Baltic Proper-Using a multi-trophic dataset as a basis for food-web modelling. *Ecol.*
1149 *Modell.* 230, 123–147. <https://doi.org/10.1016/j.ecolmodel.2011.12.014>

1150 Villasante, S., Arreguín-Sánchez, F., Heymans, J.J., Libralato, S., Piroddi, C., Christensen,
1151 V., Coll, M., 2016. Modelling marine ecosystems using the Ecopath with Ecosim food
1152 web approach: New insights to address complex dynamics after 30 years of
1153 developments. *Ecol. Modell.* 331, 1–4. <https://doi.org/10.1016/j.ecolmodel.2016.04.017>

1154 Walters, C., Christensen, V., 2007. Adding realism to foraging arena predictions of trophic
1155 flow rates in Ecosim ecosystem models: Shared foraging arenas and bout feeding. *Ecol.*
1156 *Modell.* 209, 342–350. <https://doi.org/10.1016/j.ecolmodel.2007.06.025>

1157 Walters, C., Christensen, V., Pauly, D., 1997. Structuring dynamic models of exploited
1158 ecosystems from trophic mass-balance assessments. *Rev. Fish Biol. Fish.* 7, 139–172.

1159 Walters, C.J., Christensen, V., Martell, S.J., Kitchell, J.F., 2005. Possible ecosystem impacts
1160 of applying MSY policies from single-species assessment. *ICES J. Mar. Sci.* 62, 558–
1161 568. <https://doi.org/10.1016/j.icesjms.2004.12.005>

1162

1163

1164 **8. Tables**

1165

1166 **Table 1.** Fishing mortalities for the main west of Scotland commercial species used in the
 1167 model simulations with corresponding references. $F_{\text{status quo}}$ corresponds to the last historical F
 1168 value observed (i.e. F_{2013}). F_{MSY} corresponds to the single stock F value from ICES supposed
 1169 to achieve MSY. For demersal species, the $F_{\text{MSY lower}}$ and $F_{\text{MSY upper}}$ values from ICES
 1170 defining the $F_{\text{MSY range}}$ are also given with their corresponding references (* for monkfish,
 1171 since no $F_{\text{MSY range}}$ values are defined for the stock comprising ICES area VIa the $F_{\text{MSY range}}$
 1172 values for ICES areas IIXc and IXa were used instead as best available proxy).

1173

Fishery	Species	$F_{\text{status quo}}$	F_{MSY}	Reference	$F_{\text{MSY lower}}$	$F_{\text{MSY upper}}$	Reference
Demersal	Cod	0.60	0.17	ICES, 2016c	0.11	0.25	ICES, 2016a
	Whiting	0.06	0.18	ICES, 2016c	0.15	0.18	ICES, 2016a
	Haddock	0.17	0.19	ICES, 2016d	0.18	0.19	ICES, 2016d
	Saithe	0.07	0.36	ICES, 2016d	0.20	0.42	ICES, 2015
	Hake	0.04	0.28	ICES, 2016g	0.18	0.45	ICES, 2016a
	Monkfish	0.14	0.31	ICES, 2016g	0.18*	0.41*	ICES, 2016a
Pelagic	Herring	0.21	0.16	ICES, 2016f			
	Mackerel	0.13	0.22	ICES, 2016e			
	Horse mackerel	0.30	0.09	ICES, 2016e			
	Blue whiting	0.11	0.30	ICES, 2016e			
Crustaceans	Nephrops	0.08	0.109	ICES, 2016c			

1174

1175

1176 **Table 2.** Comparison of the eight candidate models fitted with the stepwise fitting procedure showing the total number parameters estimated
 1177 (equal to the sum of the number of vulnerabilities and the number of spline points of the forcing function estimated), the model sum of squares
 1178 (SS), the percentage of reduction of SS compared to the baseline model, and the Akaike Information Criterion (AIC). The best fitted model is
 1179 highlighted in bold.

1180

Model	Description	Number of vulnerabilities	Number of spline points	Total number of parameters estimated	SS	AIC	Fitting: % improvement SS
1	Baseline	0	0	0	1620.04	242.07	-
2	Baseline + trophic effects	0	0	0	1620.04	242.07	0
3	Baseline + environmental forcing	0	5	5	1550.87	192.99	4
4	Baseline + trophic effects + environmental forcing	34	5	39	1177.68	-109.68	27
5	Fishing	0	0	0	1219.31	-142.97	25
6	Fishing + trophic effects	29	0	29	626.61	-985.70	61
7	Fishing + environmental forcing	0	5	5	1113.15	-256.37	31
8	Fishing + trophic effects + environmental forcing	24	3	27	614.30	-1016.76	62

1181 **9. Figure legends**

1182

1183 **Figure 1.** Shelf area of the west of Scotland (blue) included in the model.

1184

1185 **Figure 2. a:** Fishing mortalities used to perform forward simulations, together with the F_{MSY}
1186 $_{range}$ from ICES and the F_{MSY} $_{range}$ explored with the model. **b:** Fishing mortalities achieving
1187 the earliest recovery of cod and whiting above B_{pa} across all levels of seal cull (no cull, 5%
1188 cull and 10% cull) together with the F_{MSY} $_{range}$ values from ICES. **c:** Fishing mortalities
1189 identified for the scenario achieving the best GES indicator values overall together with the
1190 F_{MSY} $_{range}$ values from ICES.

1191

1192 **Figure 3.** Food web structure of the model. Nodes represent functional groups within the
1193 ecosystem; the size of the node is proportional to the biomass it represents. Biomass flows
1194 enter a node from the bottom and exit a node from the top and are scaled to flow proportion.
1195 The y-axis indicates the trophic level of the functional groups.

1196

1197 **Figure 4.** Biomass outputs from the model plotted with the observed biomass data time series
1198 used to fit the model (black dots). From 1985 to 2013, the black line shows the outputs from
1199 the model hindcast. From 2014 to 2033, outputs from the forward simulation are shown for
1200 the status quo scenario (in black), F_{MSY} scenario (in red), scenarios achieving the earliest
1201 recovery of cod and whiting above B_{pa} (in grey) across all levels of seal cull (no cull, 5% cull
1202 and 10% cull), and the scenario achieving the best GES indicator values overall (in green).
1203 Scenarios with the earliest cod and whiting recovery were achieved with only one F for some
1204 groups (e.g., whiting), but several possible F values for others (e.g., monkfish, see Fig. 2)
1205 resulting in several grey lines over the simulation period. The grey shaded area shows the

1206 confidence interval around the model hindcast from 1985 to 2013, and around the best GES
1207 scenario (in green) from 2014 to 2033.

1208

1209 **Figure 5.** GES indicators calculated from the model outputs plotted with the values
1210 calculated from observed data (black dots). From 1985-2013, the black line shows the GES
1211 indicators calculated from the model hindcast. From 2014 to 2033, GES indicators calculated
1212 from the forward simulations outputs are shown for the status quo scenario (in black), F_{MSY}
1213 scenario (in red), scenarios achieving the earliest recovery of cod and whiting above B_{pa} (in
1214 grey) across all levels of seal cull (no cull, 5% cull and 10% cull), and the scenario achieving
1215 the best GES indicator values overall (in green).

1216

1217 **Figure 6.** Predation mortality (year^{-1}) under the single stock F_{MSY} scenario experienced by
1218 juvenile cod (a), juvenile whiting (b) and whiting (c).

1219

1220 **Supplementary figure S1.** The three spline points forcing function (in grey) from the best
1221 model identified by the fitting procedure plotted together with the environmental indices **a:**
1222 Sea Surface Temperature (SST), **b:** North Atlantic Oscillation (NAO) and **c:** Atlantic
1223 Multidecadal Oscillation (AMO). On each panel, the index smoothed values and the obtained
1224 by fitting a Loess (local regression) smoothing curve with a span of 0.5 (thick black line) are
1225 shown alongside the raw values (thin black line) for easier visual comparison with the trend
1226 of the forcing function.

1227

1228 **Supplementary Figure S2.** Catch outputs from the model plotted with the observed biomass
1229 data time series used to fit the model (black dots). From 1985-2013, the black line shows the
1230 outputs from the model hindcast. From 2014 to 2033, outputs from the forward simulation are

1231 shown for the status quo scenario (in black), F_{MSY} scenario (in red), scenarios achieving the
1232 fastest recovery of cod and whiting above B_{pa} (in grey) across all levels of seal cull (no cull,
1233 5% cull and 10% cull), and the scenario achieving the best GES indicator values overall (in
1234 green). Scenarios with the earliest cod and whiting recovery were achieved with only one F
1235 for some groups (e.g., whiting), but several possible F values for others (e.g., monkfish)
1236 resulting in several grey lines over the simulation period.

1237

1238 **Supplementary Figure S3.** Comparison of the temporal changes in the diet composition (in
1239 % of prey consumed) of grey seals between the status quo scenario (top panel) and the F_{MSY}
1240 scenario (bottom panel).

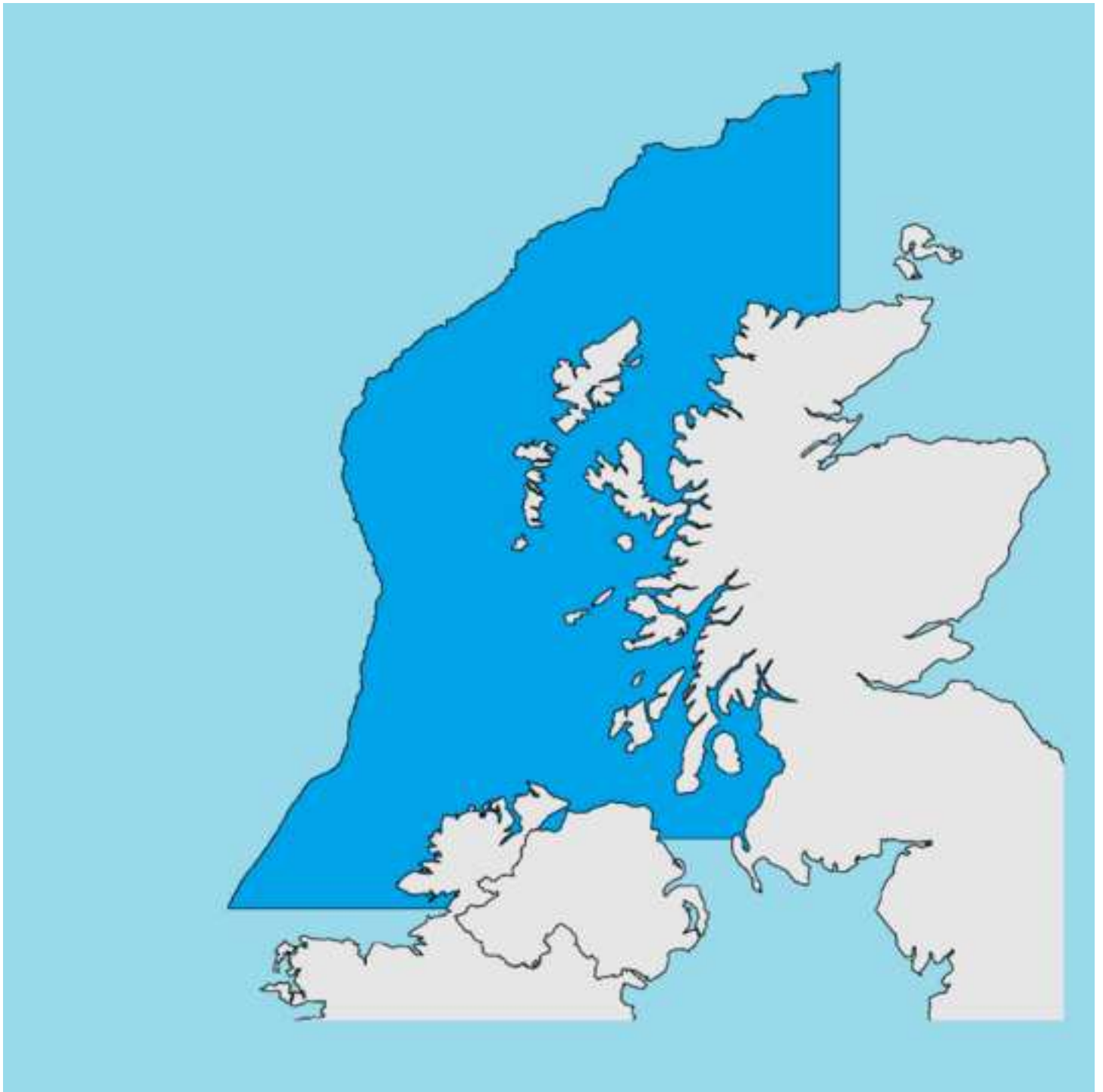
1241

1242 **Supplementary Figure S4.** Biomass outputs from model simulations extended to 2100 to
1243 allow for the ecosystem to reach equilibrium. The observed biomass data time series used to
1244 fit the model are shown with black dots. From 1985 to 2013, the black line shows the outputs
1245 from the model hindcast. From 2014 to 2100, outputs from the forward simulation are shown
1246 for the status quo scenario (in black), F_{MSY} scenario (in red), scenarios achieving the earliest
1247 recovery of cod and whiting above B_{pa} (in grey) across all levels of seal cull (no cull, 5% cull
1248 and 10% cull), and the scenario achieving the best GES indicator values overall (in green).
1249 Scenarios with the earliest cod and whiting recovery were achieved with only one F for some
1250 groups (e.g., whiting), but several possible F values for others (e.g., monkfish) resulting in
1251 several grey lines over the simulation period. The grey shaded area shows the confidence
1252 interval around the model hindcast from 1985 to 2013, and around the best GES scenario (in
1253 green) from 2014 to 2100.

1254

Figure

[Click here to download high resolution image](#)



Figure

[Click here to download high resolution image](#)

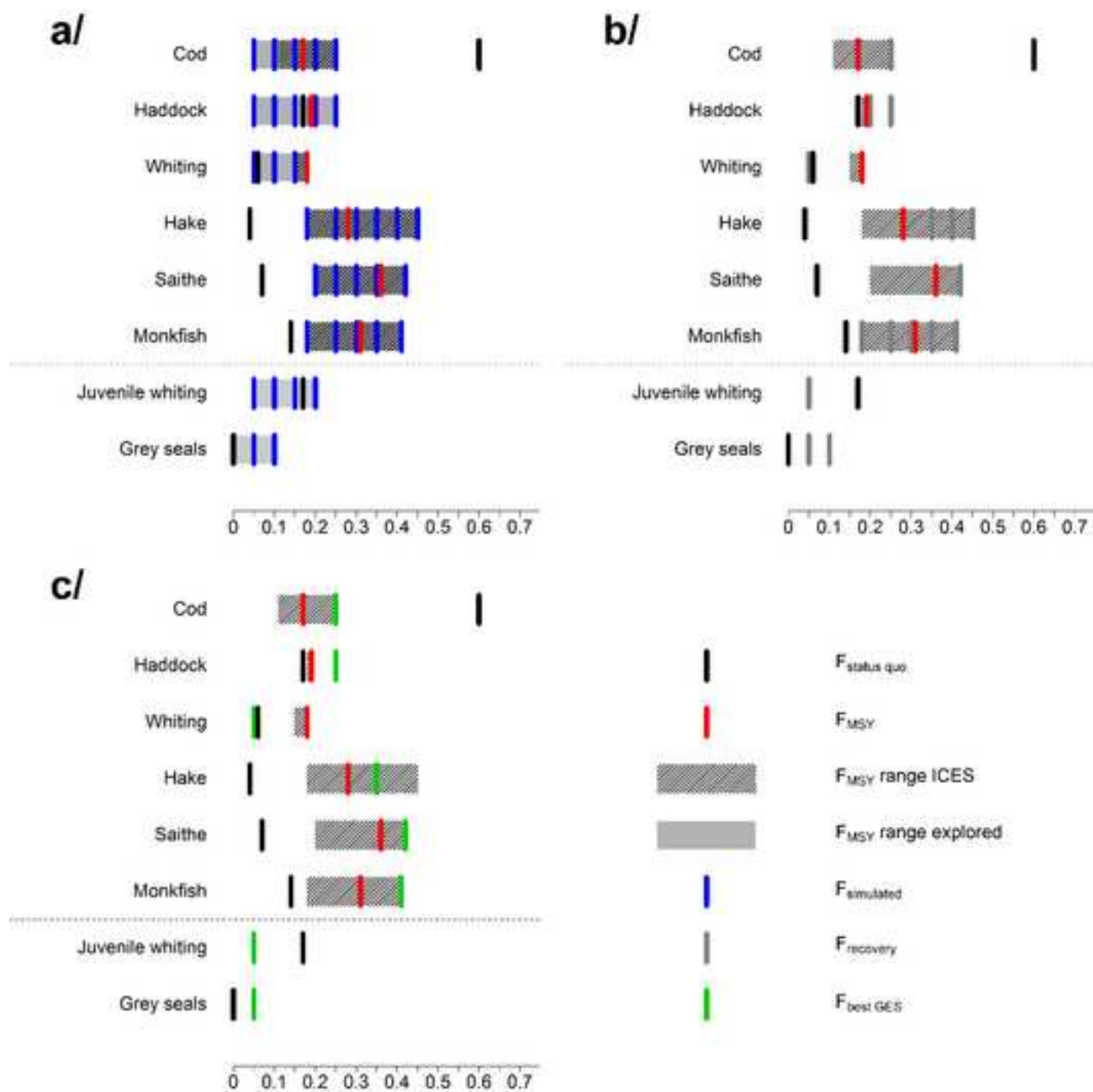
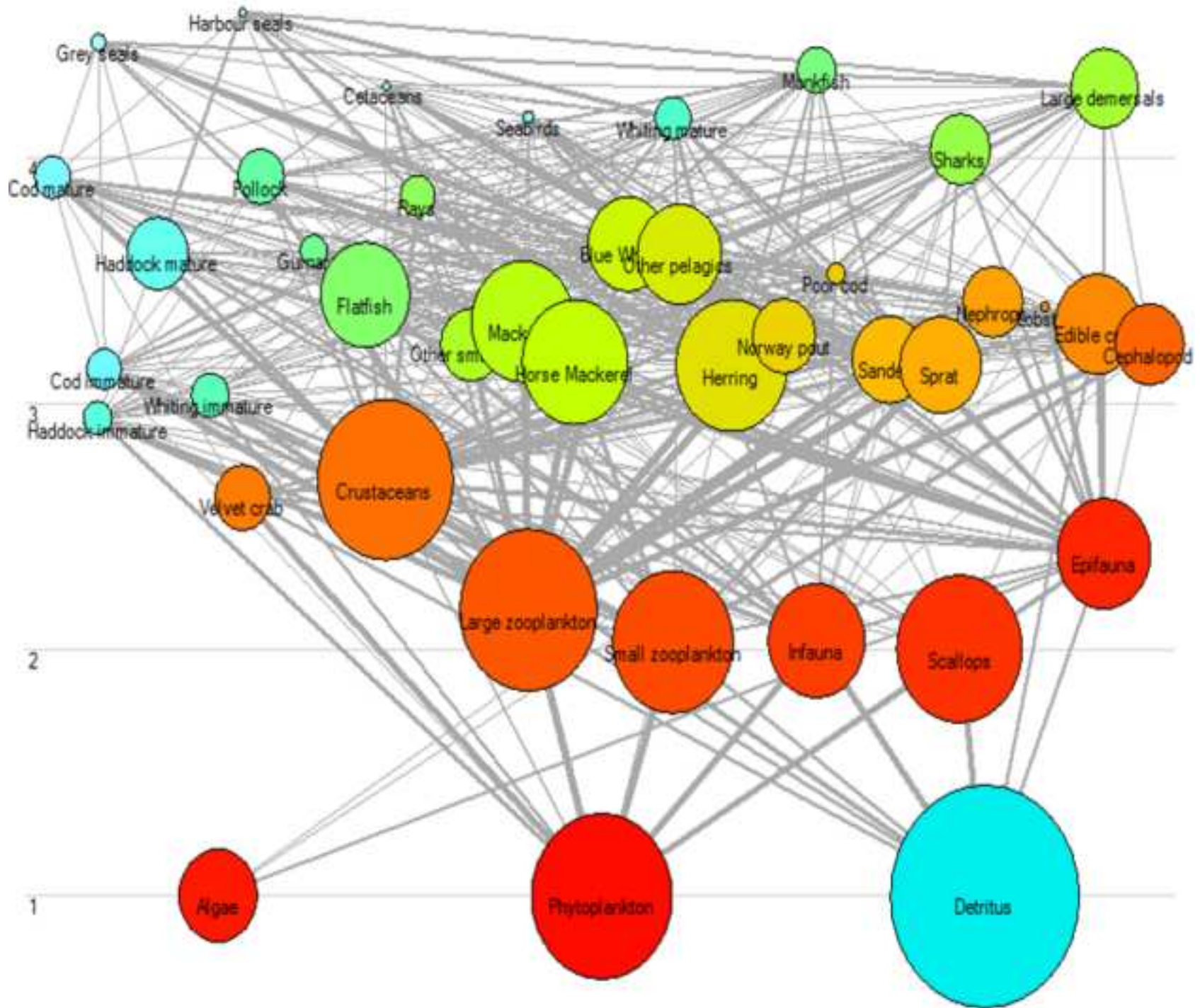


Figure
[Click here to download high resolution image](#)



Figure

[Click here to download high resolution image](#)

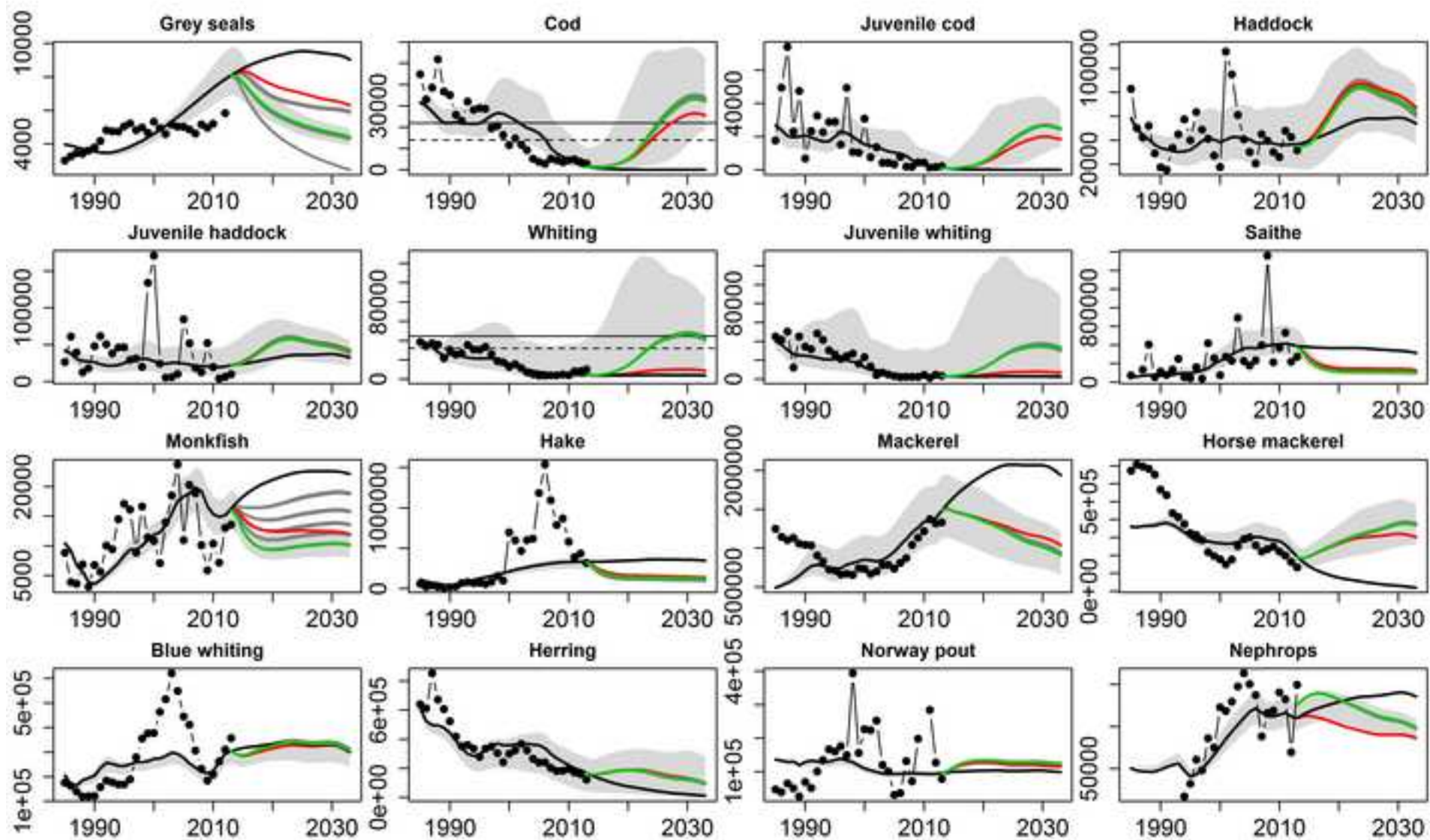
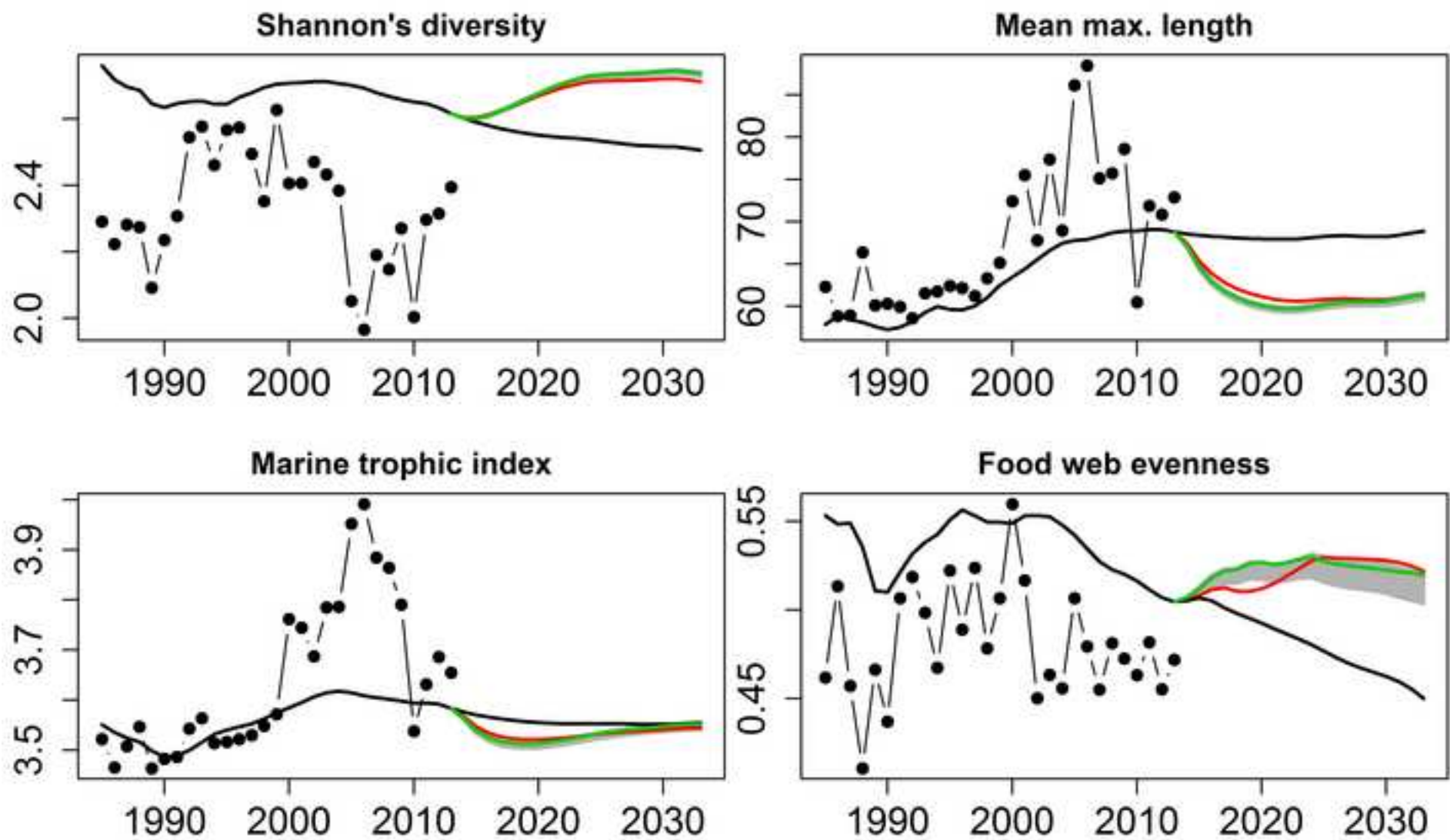
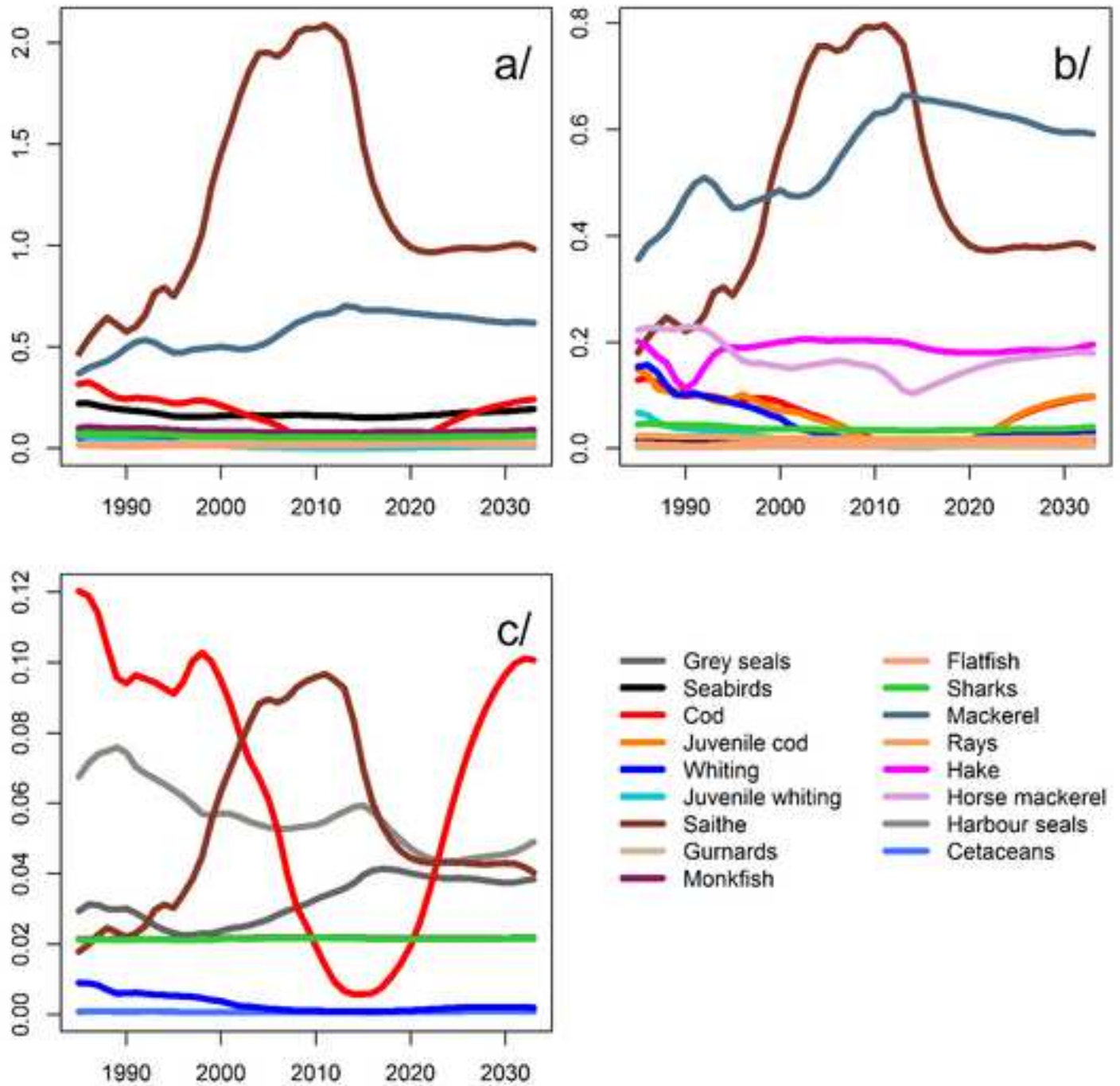


Figure
[Click here to download high resolution image](#)



Figure

[Click here to download high resolution image](#)



Figure

[Click here to download high resolution image](#)

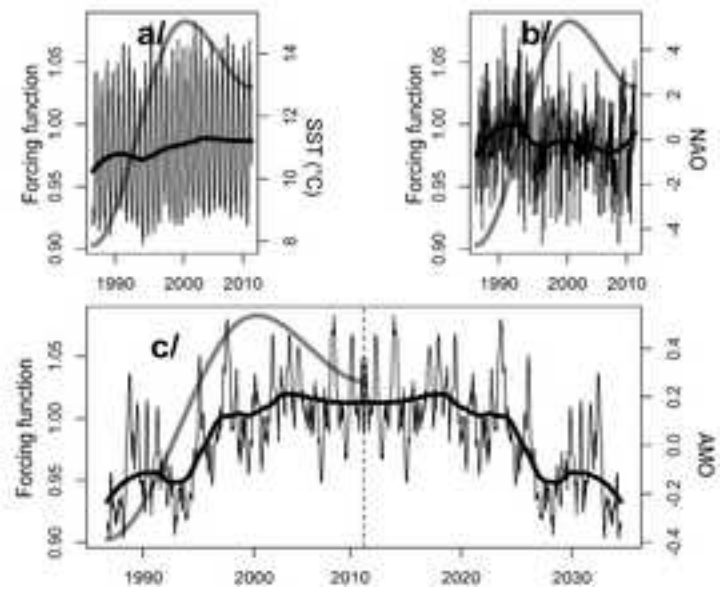
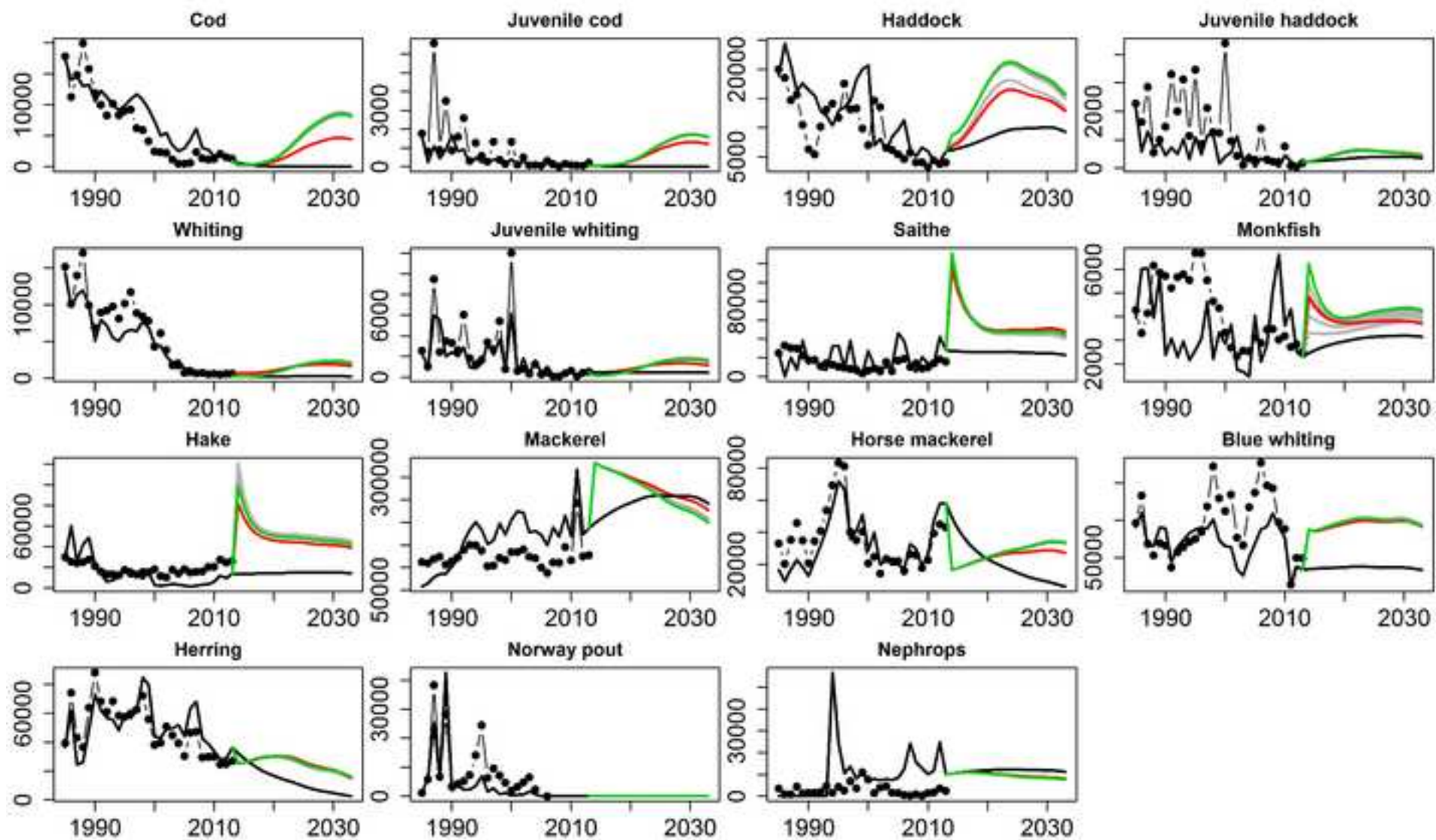
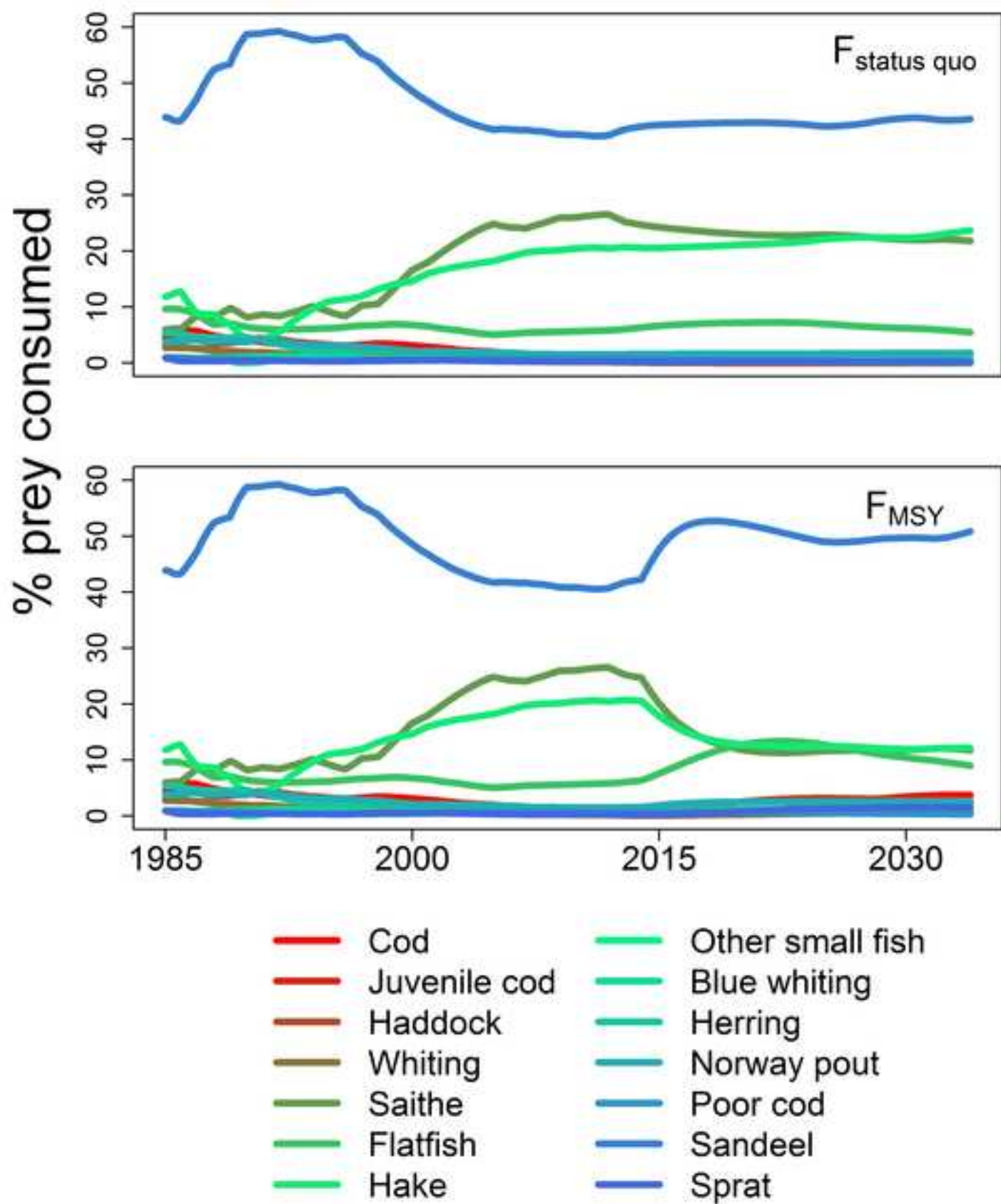


Figure
[Click here to download high resolution image](#)



Figure

[Click here to download high resolution image](#)



Figure

[Click here to download high resolution image](#)

