

Highlights

- i. GAMM derivative changes used to assess the effect of a fisheries prohibition.
- ii. An increase in endangered and sympatric skates observed during the fisheries ban.
- iii. Population recovery tailed off after the lifting of the ban.
- iv. Recovery only observed when juvenile survival increased.
- v. Evaluation of fisheries bans should take place once a steady state is observed.

Evaluating the effectiveness of management measures on skates in a changing world

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1 **Evaluating the effectiveness of management measures on skates in a**
2 **changing world**

ABSTRACT

3 Global declines in elasmobranchs have been observed. Conservation
4 measures such as area closures and fisheries prohibitions have been put in place to
5 support the recovery of vulnerable species. However, the effectiveness of such
6 measures is rarely evaluated in the context of other factors that may affect
7 population abundance. This study investigates the effectiveness of management
8 measures using 1) General additive mixed model derivative changes, taking into
9 account environmental factors that may affect population stochasticity and 2) an
10 age-structured density dependent population dynamic model. The *Raja undulata*
11 (undulate ray) 2009 targeted fisheries prohibition was used as a case study.
12 Potential beneficial responses on sympatric species *Raja clavata* (thornback ray)
13 were modelled.

14 A significant increase in abundance was observed in both IUCN red list
15 species during the ban. Surface seawater temperature had a marginal effect on the
16 abundance of both species. The prohibition was in place for an insufficient length
17 of time for long lasting effects to be detected on skate length. The population
18 dynamic model indicated that the increase in abundance was only possible when
19 combining the fisheries ban with increased juvenile discard survival. Our results
20 indicate that species conservation measures may not only have positive effects on
21 the species in question, but also on species with a niche overlap. Nonetheless, due
22 to ongoing fishing for other species, the full potential of fisheries prohibitions may
23 not be realised. For real benefits to be assessed, evaluation of bans should take
24 place once a steady state is observed.

25

26 **Keywords:** climate change, elasmobranchs, IUCN red list species, management
27 measures, population dynamic model, species conservation.

28

29 1. Introduction

30 The rise in demand for fish and fish products has led to increased fishing
31 pressure, declines and collapses in both targeted and non-targeted species.
32 Pressures from fishing, alongside climate change effects, have been attributed as
33 the most important reasons for declines in populations and changes in species
34 distribution (Halpern et al., 2007; Heath et al., 2012; Perry et al., 2010). Pressures
35 from fishing activity not only have an impact on the size and structure of fish
36 populations and their habitats, but also their life-history traits. Fisheries induced
37 pressures have been observed to modify size and age at maturation, reproductive
38 effort and growth rates, among other effects (Enberg et al., 2009; Heino and Godø,
39 2002; Stevens et al., 2000). Effects from climate change on fish, can include
40 modifications to their distribution, loss of coastal habitats, changes in productivity,
41 etc. (Dulvy et al., 2003; Perry, 2010; Perry et al., 2010).

42 Larger, slower maturing and less fecund species, such as elasmobranchs, are
43 more vulnerable to anthropogenic pressures than most teleost fish (Dulvy et al.
44 2000, Stevens et al. 2000, Ellis et al. 2011). Their life history traits lead to low
45 rates of reproduction, and therefore low rates for population recovery (Dulvy et
46 al., 2000; Stevens et al., 2000; Walker and Hislop, 1998). As a result of severe
47 global declines observed during the late twentieth century (Dulvy et al., 2017;
48 Stevens et al., 2000), conservation management measures were set up to protect
49 elasmobranch species (e.g. added to IUCN red list, prohibited from commercial

50 exploitation, country specific national action plans, etc.) (Dulvy et al., 2017).
51 However, few studies have evaluated the effectiveness of such measures (Dulvy et
52 al., 2017; Hutchings, 2000; Shiffman and Hammerschlag, 2016).

53 Before after control impact studies (Underwood, 1992, 1994) are widely
54 accepted as the most appropriate method to assess the effectiveness of spatial
55 management measures (Ahmadi et al., 2015; Clarke et al., 2015; Claudet and
56 Guidetti, 2010). Nonetheless, to evaluate spatial management measures using
57 before after control impact methods, control areas are required. Other possible
58 methods to assess population recovery following the implementation of
59 management measures include evaluating biomass time series trends, as
60 undertaken within demographic analysis and stock assessments (Dowling et al.,
61 2019; Hutchings, 2000). For data deficient species, as is the case for most
62 elasmobranchs, such assessments often lack reference points at which populations
63 trends should be compared against (ICES, 2018a-d; Dowling et al., 2019). The study
64 of surrogate species is also increasingly used in conservation when species of
65 conservation focus cannot be used, or to study the response of a given species from
66 a disturbance, to predict the response of another species to a similar disturbance
67 (Caro et al., 2005).

68 In this study, we used long-term fisheries dependent (2003 to 2018) and
69 independent (1995 to 2018) data on skate abundance (the mean number of skate
70 individuals observed per haul) and length. We analysed significant generalised
71 additive mixed model derivative changes according to the implementation of a
72 species-specific fisheries ban. We used the *Raja undulata* (undulate ray) fisheries
73 ban, set up in 2009, prohibiting targeted fishing and bycatch landing (EC 43/2009;
74 Ellis et al. 2012). Due to declines in *R. undulata* abundance, it was categorised

75 under the IUCN red list as ‘Endangered’ (IUCN, 2019). The imposition of this ban
76 was controversial with certain fishers due to high capture rates observed (ICES,
77 2018a & b). Consequently, *R. undulata* was removed from the prohibition list in
78 2015, and a small but annually increasing quota was permitted in the English
79 Channel (112 in 2016 to 180 tonnes in 2018) and the Bay of Biscay (25 in 2016 to 30
80 tonnes in 2018) (EC 2015/960; ICES 2018a & b).

81 As a result of missing control data on *R. undulata* to undertake a before
82 after control impact study, sympatric species *Raja clavata* (thornback ray;
83 classified as ‘Near threatened’) (IUCN, 2019; Ellis et al., 2004; Martin et al., 2012),
84 was analysed as a surrogate species which may benefit from the ban. To
85 understand whether changes in skate abundance were due to the fisheries ban
86 rather than climate change, the trend in abundance was modelled with seawater
87 temperature. French fishing effort changes (fished days at sea) were also
88 evaluated. To assess recovery of populations from potential fisheries induced
89 effects, length changes over time were modelled. Finally, a density dependent age-
90 structured Leslie matrix population dynamic model was developed to determine
91 historical trends in exploitation and assess the compensatory ability of such a k-
92 strategy species to a fisheries ban.

93 It was hypothesised that an increase in mean abundance would be observed
94 in both species some time after the fisheries ban, as a result of their sympatric
95 nature. It was also hypothesised that climate change would accentuate the
96 increase in mean abundance of both species, and, in particular *R. undulata* given
97 its warmer water preference (Sguotti et al., 2016). An immediate slight increase in
98 size of both species was expected due the removal of targeted fishing of larger
99 individuals. However, no overall long-term increase in mean size was expected due

100 to the reintroduction of the quotas. Given the fishing effort data analysed was
101 measured in days at sea for all species catch, by the gear types which caught
102 skates (partly as bycatch), it was expected that the overall fishing effort would
103 have remained more or less constant.

104

105 **2. Method**

106 *2.1. Survey data*

107 Fisheries independent Channel Ground Fish Survey (CGFS) data and French
108 fisheries dependent observer (ObsMer) data were analysed from North-Eastern
109 Atlantic waters (Fig. 1). CGFS surveys have been carried out annually within the
110 Eastern English Channel (International Council for the Exploration of the Sea (ICES)
111 division 7.d) between September and November since 1988 using a fixed sampling
112 design. Only data from 1995 were used due to standardisation in the survey
113 locations from this date. The sampling gear for CGFSs are Grande Ouverture
114 Verticale trawls with a 10 m horizontal by 3 m vertical opening and a codend of 20
115 mm (Bourdaud et al., 2017). Scientific bottom trawl survey data from the North
116 Sea (International Bottom Trawl Survey) and the west coast of Europe, were not
117 used for *R. undulata* due to excessively high zero counts (i.e. 99%).

118 ObsMer data provides targeted and bycatch, landed and discarded data from
119 fishing vessels throughout the year from the Greater North Sea, Celtic Sea, the Bay
120 of Biscay and the Mediterranean. Only data from ICES divisions which contained the
121 two species skates were considered (ICES divisions 4.c, 7.d, 7.e, 7.g and 7.h, 8.a
122 and 8.b). The ObsMer programme begun in 2003. The procedure for ObsMer data
123 collection is summarised in Fauconnet et al., (2015).

124 For both datasets, species caught were identified, the number of individuals
125 of each species per haul recorded, and their length to the nearest cm. Catch per
126 unit effort was not calculated due to a large number of unavailable information in
127 both datasets. In addition, for the ObsMer data, insufficient survey information was
128 available to calculate catch per unit effort for each gear type. Hauls that did not
129 contain skate landings were included to account for zeros.

130

131 2.2. Skate abundance variations

132 All statistical modelling and mapping were undertaken within R CRAN free
133 software (version 3.3, <http://cran.r-project.org>). The mean number of skates per
134 haul was modelled against year rather than the total number per haul per year to
135 reduce the stochasticity of population trends. Due to the large spatio-temporal
136 differences between the fisheries dependent and independent datasets, the
137 datasets were analysed independently. Potential outliers were identified with
138 boxplots and mapping aberrant values. Generalised additive mixed models were
139 implemented to observe non-linear trends over the years. Negative binomial
140 distributions were implemented to account for over dispersion. The abundances
141 were square root transformed to reduce right skewness and improve the model fit.

142 To reduce counting false zeros within the ObsMer dataset, only complete
143 observations from each haul were used, and both landed and discarded individuals
144 were considered. To reduce zero inflation, spatial and temporal bias, and presence
145 over estimations, a skate catch of more than one percent, and only gear types with
146 an even spatial-temporal coverage were used for analysis. For both skates, these
147 included trammel nets, otter beam and otter twin trawls. Data outside the known
148 ranges of the skates depth distribution (>100 m for *R. undulata* and >150 m for *R.*

149 *clavata*; accessed from ObsMer, CGFSs and published literature) (Ellis et al., 2012;
150 Serra-Pereira et al., 2010) were removed to reduce zero inflation. To account for
151 gear and area (ICES divisions) effects on skate abundance from the ObsMer data,
152 both variables were incorporated into the model as random effects. To account for
153 varying trawl durations using the CGFSs, swept surface area (km²) was included in
154 the model as an offset.

155 For both CGFS and ObsMer abundance models, violations assumptions of
156 homogeneity of variance were observed, and refitted with a varPower variance
157 structure (Zuur 2009). Backward stepwise model selection was implemented
158 (Bolker et al., 2009; Zuur et al., 2009) and a log likelihood ratio test was used to
159 test model significance against the null hypothesis in addition to checking residual
160 plots.

161 To interpret the fitted trends and identify whether there were any changes
162 in abundance over year, significant derivative changes from zero, along with the
163 95% confidence intervals were calculated. The model's fitted values were
164 calculated at 200 equally spaced points and were calculated again along the trend
165 line and the model refitted. The difference between the two sets of fitted values
166 was divided by the difference in year to give a predictor matrix of the slope of the
167 spline. The predictor matrix was then multiplied by the coefficients of 10,000
168 random simulations from the posterior distribution of the model. From this
169 method, 95% confidence intervals of the derivatives were calculated by taking the
170 two extreme quantiles of the distribution. When the 95% confidence intervals of
171 the derivative did not include zero, a significant increase or decrease in the
172 abundance was recorded (Clarke et al., 2015; Simpson, 2019).

173

174 *2.3. Climate change effects*

175 To explore whether climate change effects were responsible for the increase
176 in skate abundance, monthly mean sea surface temperature data were downloaded
177 from Copernicus (1995 to 2016; <http://marine.copernicus.eu/>) and Pathfinder
178 (2003 to 2018; <https://www.nodc.noaa.gov/SatelliteData/pathfinder4km/>)
179 websites. For the years that temperature data were accessible from both datasets
180 (2003 to 2016), the mean monthly temperature was used. Copernicus temperature
181 data are based on NEMO v3.6 ocean general circulation model and is run at 1/12
182 (+/-6-9 km) horizontal resolution. Pathfinder v5.2 is a satellite based temperature
183 estimate with a resolution of ~ 4 km.

184 To explore which variable was more important, generalised additive mixed
185 models with just ‘years’ as an explanatory variable, just ‘temperature’ (°C), and
186 ‘temperature’ and ‘years’ were implemented (Table 1). The Akaike information
187 criterion score with the lowest value was used as the factor discriminating the
188 variable of greatest influence (Table 1).

189

190 *2.4. Length variations*

191 Changes in length over time were explored using generalised additive mixed
192 models. The aforementioned derivative analysis was then applied to explore
193 potential changes in mean length per haul over time. Kernel smoothed probability
194 density length plots were also analysed to understand potential changes in length
195 distribution according to the different management regimes.

196 Other parameters to investigate potential fisheries induced evolution effects
197 were not taken into consideration, due to insufficient biological information on
198 maturity and age. Life history trait information is scarce in elasmobranchs and the

199 baseline information which exists for these species varies greatly between regions
200 (e.g. Ellis et al., 2005; Mccully et al., 2012).

201

202 *2.5. Fishing effort changes*

203 To infer fishing effort change over the years, aggregated fishing effort data
204 (days at sea per year by gear type per region) were provided by the Institut
205 Français de Recherche pour l'Exploitation de la MER (an oceanographic institution
206 in France -IFREMER). The aggregated fishing effort data was analysed between 2006
207 and 2018 using general and linear mixed effect models. Only gear types (trammel
208 nets, otter beam and otter twin trawls) and regions (Bay of Biscay and the English
209 Channel) used in the abundance models were taken into consideration for
210 comparative purposes.

211

212 *2.6. The Population Dynamic Model*

213 To understand the compensatory ability of *R. undulata* to a fishery ban and
214 identify parameters that most affected population dynamics, an age-structured
215 population dynamic model, with density dependent fecundity was developed from
216 the von Bertalanffy growth function calculation. The population dynamic model
217 was developed from similar fishing scenarios to those experienced by *R. undulata*
218 (a set fishing mortality prior to the ban, followed by zero fishing mortality during
219 the ban (2008 to 2015) and set fishing mortality after the relax in measures in
220 2015). A 'recovered' population was calculated from 1945, after the second world
221 war, when skate populations were supposed to have recovered from pre-war fishing
222 pressure (Walker and Hislop, 1998).

223

224 2.6.1. Length at age and maturity estimations

225 Length at age was calculated from Von Bertalanffy Growth Function (VBGF)
226 (Equation 1), using length information from the ObsMer dataset. ObsMer data were
227 used since it is collected throughout the year and can therefore provide
228 information on skate growth. The VBGF was performed using electronic length
229 frequency analysis with genetic algorithm used for estimating growth parameters in
230 the TropFish R package (Mildenberger et al., 2017).

231
$$TL_t = L_\infty(1 - \exp(-K(t - t_0))) \quad (1)$$

232 here TL_t (cm) is total length expected at age, t is time (year), L_∞ (cm) is the
233 theoretical asymptotic length, \exp is the exponential function, K is the growth rate
234 and t_0 is the theoretical age when length equals zero. The VBGF parameters were
235 $L_\infty = 108$ cm, $K = 0.25 - 0.27$, $t_{\text{anchor}} = 0.45$. t_{anchor} replaces t_0 in the VBGF, and refers
236 to the time of year where a new cohort is identified in each year.

237 Age at maturity was estimated from Coelho and Erzini, (2006), McCully et al,
238 (2012) and Moura et al, (2007). More emphasis was placed on calculations by
239 McCully et al, (2012), given she studied *R. undulata* populations around the British
240 Isles. Portuguese *R. undulata* populations have been observed to be smaller than
241 those found in the Channel and the Bay of Biscay.

242

243 2.6.2. Density dependent Leslie matrix model

244 A density dependent Leslie matrix model for *R. undulata* was developed
245 (equation 2).

246
$$n_{t+1} = Ln_t, \quad n_t = \begin{bmatrix} n_t^1 \\ \vdots \\ n_t^{12} \end{bmatrix}, \quad L = \begin{bmatrix} f_1 & \dots & f_{11} & f_{12} \\ s_1 h_1 & \dots & 0 & 0 \\ \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & s_{11} h_{11} & 0 \end{bmatrix} \quad (2)$$

247 Here n_t is a vector containing the abundance of individuals in each age class, i.e.
 248 n_t^i the abundance of individuals between age $(i - 1)$ and i , L is the Leslie matrix for
 249 the system, and f_i , s_i , , and h_i denote the fecundity, natural survival rate, and
 250 fishing (or discard) survival rate for each age class i respectively (Table 2 and 3).

251 As far as possible, we parameterised the model (natural survival, fecundity,
 252 maturity, fishing and discard survival) from existing literature (Frisk et al., 2001;
 253 Froese et al., 2019; Hordyk et al., 2019; Serra-Pereira et al., 2015) and by
 254 comparison to stock records (ICES, 2018a & b). However, the precise parameter
 255 values are uncertain so we performed a sensitivity analysis, centred on the chosen
 256 parameter set, to assess the effect of variation in these parameters (Fig. S1; Table
 257 2 and 3).

258 Originally fishing survival and discard survival were taken equal to 1 in an
 259 unfished scenario. In a fished scenario, fishing survival was fixed for all age-classes.
 260 However, it was observed that model predictions of population recovery after the
 261 ban did not match empirical data. Since the sensitivity analysis highlighted the
 262 importance of juvenile survival (age-1 to age-3) (Fig. S1), we introduced a survival
 263 rate for juveniles in the fished scenario. This represents the probability that a
 264 juvenile survived having been caught and discarded (juvenile discard survival
 265 (Table 3; Fig. S2).

266 Following Levin and Goodyear (1981), we assumed that fecundity varied with
 267 total population $P_t = \sum_{i=1}^{12} n_t^i$ according to a Ricker equation (equation 3).

$$268 \quad f_i = \begin{cases} 0, & i < a_m \\ f \exp(-\beta P_t), & i \geq a_m \end{cases} \quad (3)$$

269 where f is the maximum fecundity (taking into account sex ratio), a_m the age of
 270 maturity and β scales the density dependent effect.

271

272 3. Results

273 3.1. Skate abundance variations

274 Using both datasets, a significant increase in the number of *R. undulata* and
275 *R. clavata* was observed during the fisheries ban, which tailed off shortly after
276 quotes for *R. undulata* was reintroduced in 2015 (Fig. 2). From the CGFS data, the
277 significant increase in *R. undulata* occurred from 2010 (Fig. 2.a.i), whereas the
278 significant increase in *R. clavata* began just before 2009 (Fig. 2.b.i). Using the
279 ObsMer dataset, for both species, a decline in individuals was observed at the
280 beginning of data collection (Fig. 2.ii). *R. undulata* abundance increased as of 2008
281 (Fig. 2.a.ii), whereas the number of *R. clavata* increased between 2005 and 2007
282 and again as of 2011 (Fig. 2.b.ii).

283

284 3.2. Climate change effects

285 For both species the model of best fit was that of an interaction between
286 temperature and year (Table 1). Both species had a non-linear preference for
287 warmer water (Fig. 3). The increased abundance observed during in the later years
288 with increased temperature will most likely as a result of the ban and other
289 external factors. When comparing predictor variables independently, year was the
290 stronger predictor variable for both species (Table 1).

291

292 3.3. Length variations

293 For both species and both datasets, there was little if any mean length
294 variation from the derivative plots in relation to the different management
295 measures (Fig. S3). However, using both datasets a higher probability density

296 function of small *R. undulata* (~20-40 cm) was observed before the ban than during
297 or after, whereas the probability density function of larger individuals (~30-50 cm)
298 evened out after the ban (Fig. 4.a). Fig S2, also shows larger *R. undulata* discarded
299 during the ban than before, albeit landings still took place during the ban. For *R.*
300 *clavata*, the results between the different dataset was mixed (Fig. 4.b).

301

302 3.4. Fishing effort changes

303 A slight decrease in fishing effort (fishing days per gear type and region) was
304 observed from 2006 to 2018 (log likelihood ratio = -1594.81, degrees of freedom =
305 4, $p < 0.001$; Fig. 5).

306

307 3.5. The population dynamic model

308 The long-term behaviour of the population was predicted by analysis of the
309 Leslie matrix model. Population growth occurs when the leading Leslie matrix
310 eigenvalue (λ) is greater than one (Leslie, 1945). We found that, for an
311 unfished population, the best-case scenario, λ is 1.06; so, the population is
312 sustainable. When fishing was included in the model, reducing survival, λ
313 decreased. In particular, using this model, we identified that a fishing survival rate
314 of less than 88% would reduce λ below 1, resulting in the population declining to
315 extinction. Consequently, this model predicts that sustainable fishing is only
316 possible when fishing mortality is less than 12% (Fig. 6).

317 Fishing survival and juvenile discard survival were varied in order to match the
318 behaviour of the CGFS and ObsMer data (Fig. 2.a.i-ii; Fig 6). Similar recovery
319 dynamics to the real data were only observed for *R. undulata* when the fishing ban
320 increased juvenile discard survival (Table 3; Fig. 6iii.b-c). However, the rapid

321 decline after the end of the ban predicted by the population dynamic model (Fig.
322 6), was not observed within the real data. The sensitivity analysis demonstrated
323 that the recovery dynamics were highly sensitive to juvenile survival rates and
324 fishing survival, and somewhat sensitive to fecundity, while being relatively
325 insensitive to the other model parameters (Fig. S1).

326

327 4. Discussion

328 Given our increasing human population causing growing pressures on our
329 natural resources (Lotze, 2006), the implementation and monitoring of
330 management measures are of ever greater importance (Hutchings and Reynolds,
331 2004; Ward-Paige et al., 2012). However, the effectiveness of management
332 measures is rarely evaluated in the context of other factors that may affect
333 populations. In this study, we combined statistical and theoretical models to
334 distinguish the effect of a fisheries ban from other external factors that may affect
335 the two species of skate.

336

337 4.1. Abundance changes

338 Using the derivative model, we were able to detect a slight but significant
339 increase in the skate abundance in both the fisheries dependent and independent
340 data. The generalised additive mixed models suggest that the increase in
341 abundance was due to the implementation of the *R. undulata* fisheries ban. Similar
342 trends were observed within ICES stock assessment, albeit with stochastic variation
343 (ICES 2018a & b). The results from CGFS and ObsMer data indicate slightly different
344 patterns, most likely due to different geographical coverage (Eastern Channel and
345 North Sea, Channel and Bay of Biscay, respectively).

346 An increase in sympatric *R. clavata* was also observed. The increase in *R.*
347 *clavata* detected in both datasets may have been as a result of beneficial effect of
348 the fisheries ban on *R. clavata*, given the overlap in niche of these species (Elliott
349 et al., 2020; Ellis et al., 2004; Martin et al., 2012). The increase in the number of
350 *R. clavata* began slightly before the *R. undulata* ban was implemented. The latter
351 is most likely a result of a natural increase in abundance beginning prior to the
352 knock-on benefits of the ban, as observed within stock assessments (ICES, 2018c).
353 Once the *R. undulata* quota was reintroduced in 2015, the increase in abundance of
354 both species tailed off. Albeit, for *R. clavata*, this curtail was not so prominent.
355 From looking at ICES stock assessments for both species (ICES, 2018a & c) similar
356 trends can be observed.

357 The use of surrogate species is cautioned against since each species has its
358 own specific life history and ecological traits (Caro et al., 2005; Henry et al.,
359 2019). Nonetheless, the analysis of management measures on sympatric species has
360 benefits to better understand potential ecosystem effects of species-specific
361 conservation measures and anthropogenic pressures (Henry et al., 2019).

362

363 4.2. Climate change effects

364 Although statistically, the implementation of the fisheries ban, had the most
365 important effect on abundance variations in the skates studied, the increase in
366 mean seawater temperature was also of consequence. An increase in seawater
367 temperature may initially be of benefit to *R. undulata*. However, given *R.*
368 *undulata*'s patchy and shallow water habitat occupancy (Elliott et al., 2020; Ellis et
369 al., 2012), in future, temperatures may increase beyond its tolerance threshold.
370 The latter may lead to *R. undulata* becoming unable to undertake range shifts

371 (Heath et al., 2012; Perry et al., 2010), exposing it to greater ecological risk
372 (Musick, 1999; Simpfendorfer et al., 2011).

373 From the two datasets, different temperature ranges were observed for *R.*
374 *clavata*, possibly as a result of distinct populations between the Channel and the
375 Bay of Biscay (ICES, 2018d & e). Distinct species population temperature
376 preferences have previously been observed (Heath et al., 2012). These results
377 demonstrate the importance of taking into account potential effects of global
378 warming when studying long-term distribution and abundance changes in species
379 (Barausse et al., 2014), and in particular over their entire geographic extent. It
380 should be noted that the adjusted R^2 value for the models were relatively low.
381 Other factors will therefore have contributed to abundance changes over the years.

382

383 4.3. Length changes

384 Given our long history of fishing pressure on commercially important species,
385 fisheries-induced evolution effects have been recorded on a number of species
386 (e.g. Hunter et al., 2015; Walker and Hislop, 1998; Wright and Trippel, 2009).
387 Although a reverse in such effects have not been recorded, they have been
388 discussed (Sguotti et al., 2016). The lack of obvious mean length changes from the
389 derivative model was most likely due to the short period of time the ban was in
390 place relative to the life cycle of the skates. Time to maturation for *R. undulata* is
391 between five and seven years (Coelho and Erzini, 2006; Mccully et al., 2012; Moura
392 et al., 2007). The higher probability density function of larger *R. undulata* observed
393 within the density plots during and after the ban, and the larger discarded
394 individuals during the ban, will have likely been due to decreased fishing effort

395 during the ban. Such length variation changes according to the ban in *R. clavata*
396 were not so prominent.

397

398 *4.4. Use of fisheries dependent and independent data*

399 The coherent results, across both data sets strengthen the outcomes
400 observed. The slight differences detected will have been residual effects from
401 spatial and gear variations between the two datasets. Fisheries dependent data are
402 not often used to assess abundances due to their targeted nature. The comparable
403 results between the fisheries dependent and independent data highlight the
404 potential utility of such abundant and opportunistic data. Bourdaud et al., (2017)
405 similarly compared abundance trends of a range of commercially fished species
406 using fisheries dependent data with fisheries independent data, and found
407 coherence between datasets in a number of species.

408

409 *4.5. Fishing effort*

410 From the fishing effort data obtained, a slight decrease in days at sea was
411 observed for the gear types analysed. These results are in line with France AgriMer
412 information, where the number of small, medium and large fishing vessels fishing
413 across France Metropolitan have been recorded to decrease between 1995 and 2014
414 (<https://www.franceagrimer.fr/>). It should be noted that the cessation of targeted
415 fishing for demersal species rarely eliminates fishing mortality. The latter is
416 because of the low selectivity of fishing gear, the ongoing habitat destruction from
417 demersal fishing (Dulvy et al., 2003; Hutchings, 2000), and illegal fishing which
418 takes place (Davidson et al., 2016; Hutchings and Reynolds, 2004; Worm et al.,
419 2013).

420

421 4.6. *The population dynamics model*

422 The population dynamic model sensitivity analysis, indicate that the factors
423 most affecting *R. undulata*'s ability to recover from fishing are early years survival
424 rates and fishing survival. Developing a detailed understanding of the effect of
425 individual parameters can inform conservation measures. In particular, our results
426 suggest that protecting juveniles through measures such as minimum landing sizes
427 and nursery areas could have important benefits to species survival. Brander,
428 (1981) and Ward-Paige et al., (2012), came to similar conclusions regarding the
429 importance of juvenile survival to elasmobranch population recovery.

430 Little data regarding age specific natural survival rates for these
431 elasmobranchs exist. However, the sensitivity analysis suggests that most of these
432 parameters are relatively unimportant. Instead, it is more important to
433 characterise early years survival of *R. undulata* in both unfished and fished
434 regimes, and its fecundity. Further research on skate bycatch survival is essential
435 and gear specific mortality should be incorporated into future population dynamic
436 models. Furthermore, at present we are unsure of skate mortality within their
437 nursery habitats. For *R. undulata* this is particularly important, given juveniles
438 inhabit coastal and estuarian areas which are subject to a range of anthropogenic
439 pressures (Elliott et al., 2018).

440 4.7. **Implications for conservation and management**

441 To be able to manage our natural resources sustainably and minimise
442 impacts on industry, monitoring of management measures is key to the long-term
443 viability of populations (Hilborn, 2007; Parma et al., 2006; Pauly, 1995).

444 Surprisingly, very few case studies have been undertaken to explore the effect of
445 fisheries management measures beyond stock assessments (e.g. Clarke et al., 2015;
446 Fernandes and Cook, 2013; Hutchings, 2000). Until recently, fisheries management
447 measures are managed to “squeeze the last ‘sustainable’ fish” (Hilborn, 2007),
448 instead of applying extinction risk criteria (Fernandes et al., 2017; Musick, 1999)
449 and placing measures to prevent ‘shifting baselines’ (Pauly, 1995). Although the
450 reformed Common Fisheries Policy and other measures such as the Marine Strategy
451 Framework Directive have been working towards improving the state of fished
452 stocks (Fernandes et al., 2017; Fernandes and Cook, 2013), many species are still
453 fished above scientific advice or deemed as data deficient (Fernandes et al., 2017;
454 Fernandes and Cook, 2013).

455 The analysis of both fisheries dependent and independent data enabled life
456 history information to be evaluated, which could contribute to specific
457 management measures with minimum landing size thresholds based on maturity
458 (Barausse et al., 2014; Frisk et al., 2001). Furthermore, given the apparent high
459 discard survival rate of skates, their exemption from the CFP discard ban could
460 help population recovery. Although an increase in *R. undulata* was observed during
461 the ban, the mean number observed per trawl remains low and historic abundances
462 for this species is unknown. The results from the population dynamic model
463 indicate that the apparently steady population detected prior to the ban using the
464 CGFS and the ObsMer data, may instead have been a heavily depleted population in
465 slow decline.

466 To minimise impacts on the fishing industry whilst ensuring recovery of an
467 endangered species, we suggest that protected populations should be permitted to
468 reach a (relatively) steady state before evaluating appropriate quotas required.

469 This would allow potentially recovered stock levels to be estimated and stochastic
470 effects of environmental and anthropogenic pressures to be disentangled from the
471 implementation of management measures. A comprehensive understanding of the
472 dynamics of a population is essential in designing appropriate management
473 schemes.

474

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484

485

486 **Web reference**

487 IUCN. 2019. <https://www.iucnredlist.org/>. Downloaded on 09 January 2019.
488 Downloaded on 09 January 2019.

489 European Commission. 2009. EC 43/2009. [https://eur-lex.europa.eu/legal-
490 content/EN/TXT/?uri=CELEX%3A32009R0043](https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX%3A32009R0043)

491 ICES. 2018a. Undulate ray (*Raja undulata*) in divisions 7.d-e (English
492 Channel). <https://doi.org/10.17895/ices.pub.450>.

493 <http://www.ices.dk/sites/pub/Publication%20Reports/Advice/2018/2018/rju.27.7>
494 [de.pdf](#). Downloaded 02 February 2019.

495 ICES. 2018b. Undulate ray (*Raja undulata*) in divisions 8.a-b (northern and
496 central Bay of Biscay). <https://doi.org/10.17895/ices.pub.4502>.
497 <http://ices.dk/sites/pub/Publication%20Reports/Advice/2018/2018/rju.27.8ab.pdf>
498 Downloaded 02 February 2019

499 ICES. 2018c. Skates and rays in the Celtic Seas (ICES subareas 6 and 7 (ex-
500 cept Division 7.d)).
501 [http://ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20Report/acom/
502 2018/WGEF/20%20WGEF%20Report%202018_Section%2018%20Celtic%20Seas.pdf](http://ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20Report/acom/2018/WGEF/20%20WGEF%20Report%202018_Section%2018%20Celtic%20Seas.pdf).
503 Downloaded 08 November 2019.

504 ICES. 2018d. Thornback ray (*Raja clavata*) in subarea 8 (Bay of Biscay).
505 <https://doi.org/10.17895/ices.pub.4557>.
506 <http://www.ices.dk/sites/pub/Publication%20Reports/Advice/2018/2018/rjc.27.8>.
507 [pdf](#). Downloaded 02 February 2019.

508 ICES. 2018e. Thornback ray (*Raja clavata*) in division 7.e (western English
509 Channel). <https://doi.org/10.17895/ices.pub.4549>.
510 <http://www.ices.dk/sites/pub/Publication%20Reports/Advice/2018/2018/rjc.27.7e>
511 [.pdf](#). Downloaded 02 February 2019.

512 Simpson, G. (2019). [gavinsimpson's gists](https://gist.github.com/gavinsimpson/).
513 <https://gist.github.com/gavinsimpson/>. Downloaded 28 February 2019.

514 Zuur, AF, Leno, EN, Walker, NJ, Saveliev, AA, Smith, GM. 2009. Mixed
515 Effects Models and Extensions in Ecology with R. Springer-Verlag New York. ISBN
516 978-0-387-87458-6
517

518 **References**

- 519 Ahmadia, G.N., Glew, L., Provost, M., Gill, D., Hidayat, N.I., Mangubhai, S.,
520 Purwanto, Fox, H.E., 2015. Integrating impact evaluation in the design and
521 implementation of monitoring marine protected areas. *Philos. Trans. R. Soc. B*
522 *Biol. Sci.* 370, 20140275. <https://doi.org/10.1098/rstb.2014.0275>
- 523 Barausse, A., Correale, V., Curkovic, A., Finotto, L., Riginella, E., Visentin, E.,
524 Mazzoldi, C., 2014. The role of fisheries and the environment in driving the
525 decline of elasmobranchs in the northern Adriatic Sea. *ICES J. Mar. Sci.* 71,
526 1593-1603. <https://doi.org/10.1093/icesjms/fst222>
- 527 Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens,
528 M.H.H., White, J.-S.S., 2009. Generalized linear mixed models: a practical
529 guide for ecology and evolution. *Trends Ecol. Evol.* 24, 127-135.
530 <https://doi.org/10.1016/j.tree.2008.10.008>
- 531 Bourdaud, P., Travers-Trolet, M., Vermard, Y., Cormon, X., Marchal, P., 2017.
532 Inferring the annual, seasonal, and spatial distributions of marine species from
533 complementary research and commercial vessels' catch rates. *ICES J. Mar. Sci.*
534 74, 2415-2426. <https://doi.org/10.1093/icesjms/fsx092>
- 535 Brander, K., 1981. Disappearance of common skate *Raia batis* from Irish Sea.
536 *Nature* 290, 48-49. <https://doi.org/10.1038/290048a0>
- 537 Caro, T., Eadie, J., Sih, A., 2005. Use of Substitute Species in Conservation Biology.
538 *Conserv. Biol.* 19, 1821-1826. [https://doi.org/10.1111/j.1523-](https://doi.org/10.1111/j.1523-1739.2005.00251.x)
539 1739.2005.00251.x
- 540 Clarke, J, Bailey, D.M., Wright, P.J., 2015. Evaluating the effectiveness of a
541 seasonal spawning area closure. *ICES J. Mar. Sci. J. du Cons.* 72, 2627-2637.
542 <https://doi.org/10.1093/icesjms/fsv144>

543 Clarke, J, Milligan, R.J., Bailey, D.M., Neat, F.C., 2015. A Scientific Basis for
544 Regulating Deep-Sea Fishing by Depth. *Curr. Biol.* 1-5.
545 <https://doi.org/10.1016/j.cub.2015.07.070>

546 Claudet, J., Guidetti, P., 2010. Improving assessments of marine protected areas.
547 *Aquat. Conserv. Mar. Freshw. Ecosyst.* 20, 239-242.
548 <https://doi.org/10.1002/aqc.1087>

549 Coelho, R., Erzini, K., 2006. Reproductive aspects of the undulate ray, *Raja*
550 *undulata*, from the south coast of Portugal. *Fish. Res.* 81, 80-85.
551 <https://doi.org/10.1016/j.fishres.2006.05.017>

552 Davidson, L.N.K., Krawchuk, M.A., Dulvy, N.K., 2016. Why have global shark and
553 ray landings declined: improved management or overfishing? *Fish Fish.* 17, 438-
554 458. <https://doi.org/10.1111/faf.12119>

555 Dowling, N.A., Smith, A.D.M., Smith, D.C., Parma, A.M., Dichmont, C.M.,
556 Sainsbury, K., Wilson, J.R., Dougherty, D.T., Cope, J.M., 2019. Generic
557 solutions for data-limited fishery assessments are not so simple. *Fish Fish.* 20,
558 174-188. <https://doi.org/10.1111/faf.12329>

559 Dulvy, N.K., Metcalfe, J.D., Glanville, J., Pawson, M.G., Reynolds, J.D., 2000.
560 Fishery stability, local extinctions, and shifts in community structure in skates.
561 *Conserv. Biol.* 14, 283-293. <https://doi.org/10.1046/j.1523-1739.2000.98540.x>

562 Dulvy, N.K., Sadovy, Y., Reynolds, J.D., 2003. Extinction vulnerability in marine
563 populations. *Fish Fish.* 4, 25-64. [https://doi.org/10.1046/j.1467-
564 2979.2003.00105.x](https://doi.org/10.1046/j.1467-2979.2003.00105.x)

565 Dulvy, N.K., Simpfendorfer, C.A., Davidson, L.N.K., Fordham, S. V., Bräutigam, A.,
566 Sant, G., Welch, D.J., 2017. Challenges and Priorities in Shark and Ray
567 Conservation. *Curr. Biol.* 27, R565-R572.

568 <https://doi.org/10.1016/j.cub.2017.04.038>

569 Elliott, S.A.M., Allan, B.A., Turrell, W.R., Heath, M.R., Bailey, D.M., 2018. Survival
570 of the fittest: Explanations for gadoid imbalance in heavily fished seas. *Aquat.*
571 *Conserv. Mar. Freshw. Ecosyst.* 1-8. <https://doi.org/10.1002/aqc.2926>

572 Elliott, S.A.M., Carpentier, A., Feunteun, E., Trancart, T., 2020. Distribution and
573 life history trait models indicate vulnerability of skates. *Prog. Oceanogr.* 181,
574 102256. <https://doi.org/10.1016/j.pocean.2019.102256>

575 Ellis, J.R., Cruz-Martínez, A., Rackham, B.D., Rogers, S.I., 2004. The Distribution of
576 Chondrichthyan Fishes Around the British Isles and Implications for
577 Conservation. *J. Northwest Atl. Fish. Sci.* 35, 195-213.
578 <https://doi.org/10.2960/J.v35.m485>

579 Ellis, J.R., Dulvy, N.K., Jennings, S., Parker-Humphreys, M., Rogers, S.I., 2005.
580 Assessing the status of demersal elasmobranchs in UK waters: A review. *J. Mar.*
581 *Biol. Assoc. United Kingdom* 85, 1025-1047.
582 <https://doi.org/10.1017/S0025315405012099>

583 Ellis, J.R., McCully, S.R., Brown, M.J., 2012. An overview of the biology and status
584 of undulate ray *Raja undulata* in the north-east Atlantic Ocean. *J. Fish Biol.*
585 80, 1057-1074. <https://doi.org/10.1111/j.1095-8649.2011.03211.x>

586 Ellis, J.R., Morel, G., Burt, G., Bossy, S., 2011. Preliminary observations on the life
587 history and movements of skates (Rajidae) around the Island of Jersey,
588 western English Channel. *J. Mar. Biol. Assoc. United Kingdom* 91, 1185-1192.
589 <https://doi.org/10.1017/S0025315410001906>

590 Enberg, K., Jørgensen, C., Dunlop, E.S., Heino, M., Dieckmann, U., 2009.
591 Implications of fisheries-induced evolution for stock rebuilding and recovery.
592 *Evol. Appl.* 2, 394-414. <https://doi.org/10.1111/j.1752-4571.2009.00077.x>

593 Fauconnet, L., Trenkel, V.M., Morandeau, G., Caill-Milly, N., Rochet, M.-J., 2015.
594 Characterizing catches taken by different gears as a step towards evaluating
595 fishing pressure on fish communities. *Fish. Res.* 164, 238-248.
596 <https://doi.org/10.1016/j.fishres.2014.11.019>

597 Fernandes, P.G., Cook, R.M., 2013. Reversal of Fish Stock Decline in the Northeast
598 Atlantic. *Curr. Biol.* 23, 1432-1437. <https://doi.org/10.1016/j.cub.2013.06.016>

599 Fernandes, P.G., Ralph, G.M., Nieto, A., García Criado, M., Vasilakopoulos, P.,
600 Maravelias, C.D., Cook, R.M., Pollom, R.A., Kovačić, M., Pollard, D., Farrell,
601 E.D., Florin, A.-B., Polidoro, B.A., Lawson, J.M., Lorange, P., Uiblein, F.,
602 Craig, M., Allen, D.J., Fowler, S.L., Walls, R.H.L., Comeros-Raynal, M.T.,
603 Harvey, M.S., Dureuil, M., Biscoito, M., Pollock, C., McCully Phillips, S.R., Ellis,
604 J.R., Papaconstantinou, C., Soldo, A., Keskin, Ç., Knudsen, S.W., Gil de Sola,
605 L., Serena, F., Collette, B.B., Nedreaas, K., Stump, E., Russell, B.C., Garcia,
606 S., Afonso, P., Jung, A.B.J., Alvarez, H., Delgado, J., Dulvy, N.K., Carpenter,
607 K.E., 2017. Coherent assessments of Europe's marine fishes show regional
608 divergence and megafauna loss. *Nat. Ecol. Evol.* 1, 1-8.
609 <https://doi.org/10.1038/s41559-017-0170>

610 Frisk, M.G., Miller, T.J., Fogarty, M.J., 2001. Estimation and analysis of biological
611 parameters in elasmobranch fishes: a comparative life history study. *Can. J.*
612 *Fish. Aquat. Sci.* 58, 969-981. <https://doi.org/10.1139/f01-051>

613 Froese, R., Winker, H., Coro, G., Demirel, N., Tsikliras, A.C., Dimarchopoulou, D.,
614 Scarcella, G., Probst, W.N., Dureuil, M., Pauly, D., 2019. A new approach for
615 estimating stock status from length frequency data. *ICES J. Mar. Sci.* 76, 350-
616 351. <https://doi.org/10.1093/icesjms/fsy139>

617 Halpern, B.S., Selkoe, K.A., Micheli, F., Kappel, C. V, 2007. Evaluating and ranking

618 the vulnerability of global marine ecosystems to anthropogenic threats.
619 *Conserv. Biol.* 21, 1301-1315. <https://doi.org/10.1111/j.1523->
620 [1739.2007.00752.x](https://doi.org/10.1111/j.1523-1739.2007.00752.x)

621 Heath, M.R., Neat, F.C., Pinnegar, J.K., Reid, D.G., Sims, D.W., Wright, P.J., 2012.
622 Review of climate change impacts on marine fish and shellfish around the UK
623 and Ireland. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 22, 337-367.
624 <https://doi.org/10.1002/aqc.2244>

625 Heino, M., Godø, O., 2002. Fisheries-induced selection pressures in the context of
626 sustainable fisheries. *Bull. Mar. Sci.* 70, 639-656.

627 Henry, E., Brammer-Robbins, E., Aschehoug, E., Haddad, N., 2019. Do substitute
628 species help or hinder endangered species management? *Biol. Conserv.* 232,
629 127-130. <https://doi.org/10.1016/j.biocon.2019.01.031>

630 Hilborn, R., 2007. Moving to sustainability by learning from successful fisheries.
631 *Ambio A J. Hum. Environ.* 36, 296-303. <https://doi.org/10.1579/0044->
632 [7447\(2007\)36](https://doi.org/10.1579/0044-7447(2007)36)

633 Hordyk, A.R., Prince, J.D., Carruthers, T.R., Walters, C.J., 2019. Comment on “A
634 new approach for estimating stock status from length frequency data” by
635 Froese et al. (2018). *ICES J. Mar. Sci.* 76, 457-460.
636 <https://doi.org/10.1093/icesjms/fsy168>

637 Hunter, A., Speirs, D.C., Heath, M.R., 2015. Fishery-induced changes to age and
638 length dependent maturation schedules of three demersal fish species in the
639 Firth of Clyde. *Fish. Res.* 170, 14-23.
640 <https://doi.org/10.1016/j.fishres.2015.05.004>

641 Hutchings, J.A., 2000. Collapse and recovery of marine fishes. *Nature* 406, 882-885.
642 <https://doi.org/10.1038/35022565>

643 Hutchings, J.A., Reynolds, J.D., 2004. Marine Fish Population Collapses:
644 Consequences for Recovery and Extinction Risk. *Bioscience* 54, 297-309.
645 [https://doi.org/10.1641/0006-3568\(2004\)054\[0297:MFPCCF\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054[0297:MFPCCF]2.0.CO;2)

646 Leslie, P.H., 1945. On the use of matrices in certain population mathematics.
647 *Biometrika* 33, 183-212. <https://doi.org/10.1093/biomet/33.3.183>

648 Levin, S.A., Goodyear, C.P., 1981. Analysis of an age-structured fishery model. *J.*
649 *Math. Biol.* 12, 263-263. <https://doi.org/10.1007/BF00276134>

650 Lotze, H.K., 2006. Depletion, Degradation, and Recovery Potential of Estuaries and
651 Coastal Seas. *Science* (80-.). 312, 1806-1809.
652 <https://doi.org/10.1126/science.1128035>

653 Martin, C.S., Vaz, S., Ellis, J.R., Lauria, V., Coppin, F., Carpentier, A., 2012.
654 Modelled distributions of ten demersal elasmobranchs of the eastern English
655 Channel in relation to the environment. *J. Exp. Mar. Bio. Ecol.* 418-419, 91-
656 103. <https://doi.org/10.1016/j.jembe.2012.03.010>

657 McCully, S.R., Scott, F., Ellis, J.R., 2012. Lengths at maturity and conversion
658 factors for skates (Rajidae) around the British Isles, with an analysis of data in
659 the literature. *ICES J. Mar. Sci.* 69, 1812-1822.
660 <https://doi.org/10.1093/icesjms/fss150>

661 McCully, S.R., Scott, F., Ellis, J.R., 2012. Lengths at maturity and conversion
662 factors for skates (Rajidae) around the British Isles, with an analysis of data in
663 the literature. *ICES J. Mar. Sci.* 69, 1812-1822.
664 <https://doi.org/10.1093/icesjms/fss150>

665 Mildenberger, T.K., Taylor, M.H., Wolff, M., 2017. TropFishR : an R package for
666 fisheries analysis with length-frequency data. *Methods Ecol. Evol.* 8, 1520-
667 1527. <https://doi.org/10.1111/2041-210X.12791>

668 Moura, T., Figueiredo, I., Farias, I., Serra-Pereira, B., Coelho, R., Erzini, K., Neves,
669 A., Gordo, L.S., 2007. The use of caudal thorns for ageing *Raja undulata* from
670 the Portuguese continental shelf, with comments on its reproductive cycle.
671 Mar. Freshw. Res. 58, 983-992. <https://doi.org/10.1071/MF07042>

672 Musick, J.A., 1999. Criteria to Define Extinction Risk in Marine Fishes: The
673 American Fisheries Society Initiative. Fisheries 24, 6-14.
674 [https://doi.org/10.1577/1548-8446\(1999\)024<0006:CTDERI>2.0.CO;2](https://doi.org/10.1577/1548-8446(1999)024<0006:CTDERI>2.0.CO;2)

675 Parma, A.M., Hilborn, R., Orensanz, J.M., 2006. The good, the bad, and the ugly:
676 learning from experience to achieve sustainable fisheries. Bull. Mar. Sci. 78,
677 411-427.

678 Pauly, D., 1995. Anecdotes and the shifting baseline syndrome of fisheries. Trends
679 Ecol. Evol. 10, 430. [https://doi.org/10.1016/S0169-5347\(00\)89171-5](https://doi.org/10.1016/S0169-5347(00)89171-5)

680 Perry, R.I., 2010. Potential impacts of climate change on marine wild capture
681 fisheries: an update. J. Agric. Sci. 149, 63-75.
682 <https://doi.org/10.1017/S0021859610000961>

683 Perry, R.I., Cury, P., Brander, K., Jennings, S., Möllmann, C., Planque, B., 2010.
684 Sensitivity of marine systems to climate and fishing: Concepts, issues and
685 management responses. J. Mar. Syst. 79, 427-435.
686 <https://doi.org/10.1016/j.jmarsys.2008.12.017>

687 Serra-Pereira, B., Erzini, K., Figueiredo, I., 2015. Using biological variables and
688 reproductive strategy of the undulate ray *Raja undulata* to evaluate
689 productivity and susceptibility to exploitation. J. Fish Biol. 86, 1471-1490.
690 <https://doi.org/10.1111/jfb.12653>

691 Serra-Pereira, B., Farias, I., Moura, T., Gordo, L.S., Santos, M., Figueiredo, I.,
692 2010. Morphometric ratios of six commercially landed species of skate from

693 the Portuguese continental shelf, and their utility for identification. *ICES J.*
694 *Mar. Sci.* 67, 1596-1603. <https://doi.org/10.1093/icesjms/fsq056>

695 Sguotti, C., Lynam, C.P., García-Carreras, B., Ellis, J.R., Engelhard, G.H., 2016.
696 Distribution of skates and sharks in the North Sea: 112 years of change. *Glob.*
697 *Chang. Biol.* 22, 2729-2743. <https://doi.org/10.1111/gcb.13316>

698 Shiffman, D.S., Hammerschlag, N., 2016. Shark conservation and management
699 policy: a review and primer for non-specialists. *Anim. Conserv.* 19, 401-412.
700 <https://doi.org/10.1111/acv.12265>

701 Simpfendorfer, C.A., Heupel, M.R., White, W.T., Dulvy, N.K., 2011. The
702 importance of research and public opinion to conservation management of
703 sharks and rays: a synthesis. *Mar. Freshw. Res.* 62, 518-527.
704 <https://doi.org/10.1071/MF11086>

705 Stevens, J., Bonfil, R., Dulvy, D.K., Walker, P.A., 2000. The effects of fishing on
706 sharks, rays, and chimaeras (chondrichthyans), and the implications for marine
707 ecosystems. *ICES J. Mar. Sci.* 57, 476-494.
708 <https://doi.org/10.1006/jmsc.2000.0724>

709 Underwood, A.J., 1992. Beyond BACI: the detection of environmental impacts on
710 populations in the real, but variable, world. *J. Exp. Mar. Bio. Ecol.* 161, 145-
711 178.

712 Underwood, A.J., 1994. On beyond BACI: Sampling designs that might reliably
713 detect environmental disturbances. *Ecol. Appl.* 4, 3-15.
714 <https://doi.org/10.2307/1942110>

715 Walker, P.A., Hislop, J.R.G., 1998. Sensitive skates or resilient rays? Spatial and
716 temporal shifts in ray species composition in the central and north-western
717 North Sea between 1930 and the present day. *ICES J. Mar. Sci.* 55, 392-402.

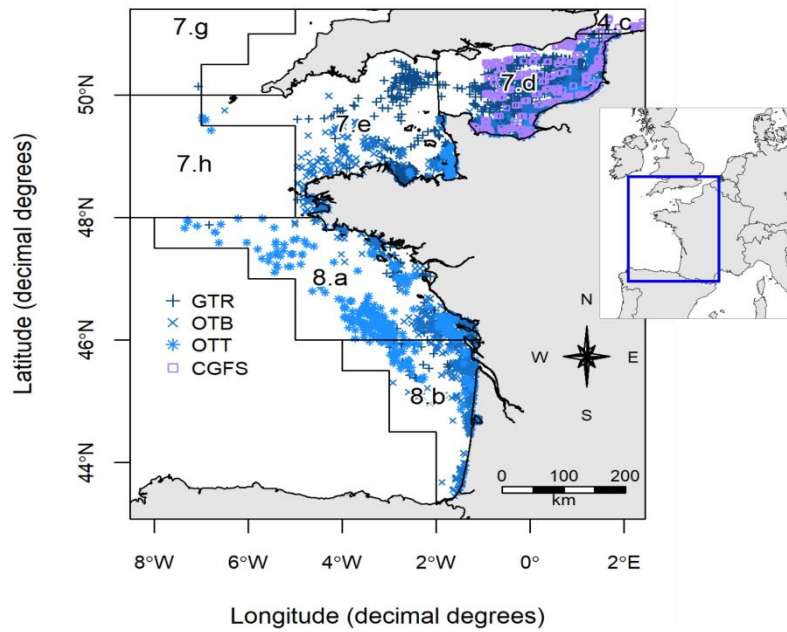
718 <https://doi.org/10.1006/jmsc.1997.0325>

719 Ward-Paige, C.A., Keith, D.M., Worm, B., Lotze, H.K., 2012. Recovery potential
720 and conservation options for elasmobranchs. *J. Fish Biol.* 80, 1844-1869.
721 <https://doi.org/10.1111/j.1095-8649.2012.03246.x>

722 Worm, B., Davis, B., Kettner, L., Ward-Paige, C.A., Chapman, D., Heithaus, M.R.,
723 Kessel, S.T., Gruber, S.H., 2013. Global catches, exploitation rates, and
724 rebuilding options for sharks. *Mar. Policy* 40, 194-204.
725 <https://doi.org/10.1016/j.marpol.2012.12.034>

726 Wright, P.J., Trippel, E.A., 2009. Fishery-induced demographic changes in the
727 timing of spawning: consequences for reproductive success. *Fish Fish.* 10, 283-
728 304. <https://doi.org/10.1111/j.1467-2979.2008.00322.x>

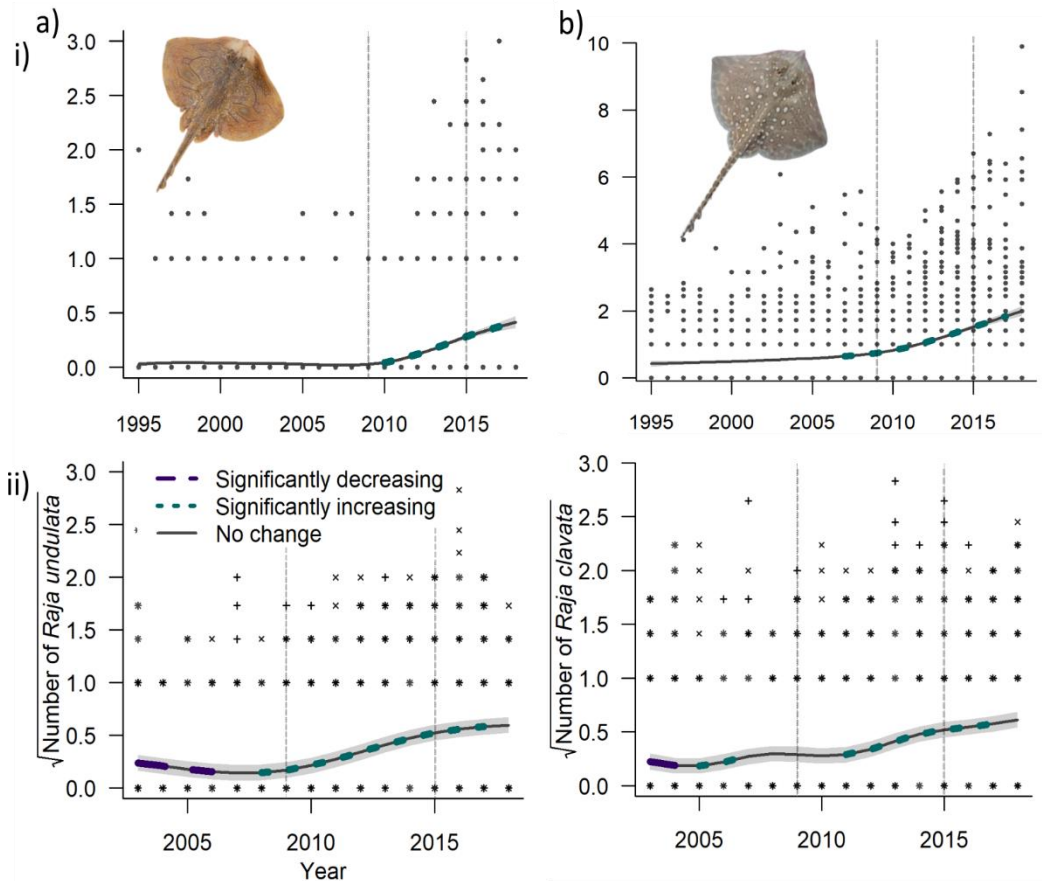
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2

3 **Fig. 1.** Presence points of *Raja undulata* and *Raja clavata* fisheries dependent
 4 ObsMer gear types and fisheries independent Channel Ground Fish Surveys (CGFS),
 5 represented different coloured symbols: CGFS, □, Trammel nets (GTR, +), Otter
 6 Beam Trawls (OTB, x), Otter Twin Trawls (OTT, *). Black solid lines delineate ICES
 7 statistical divisions and their coded name.

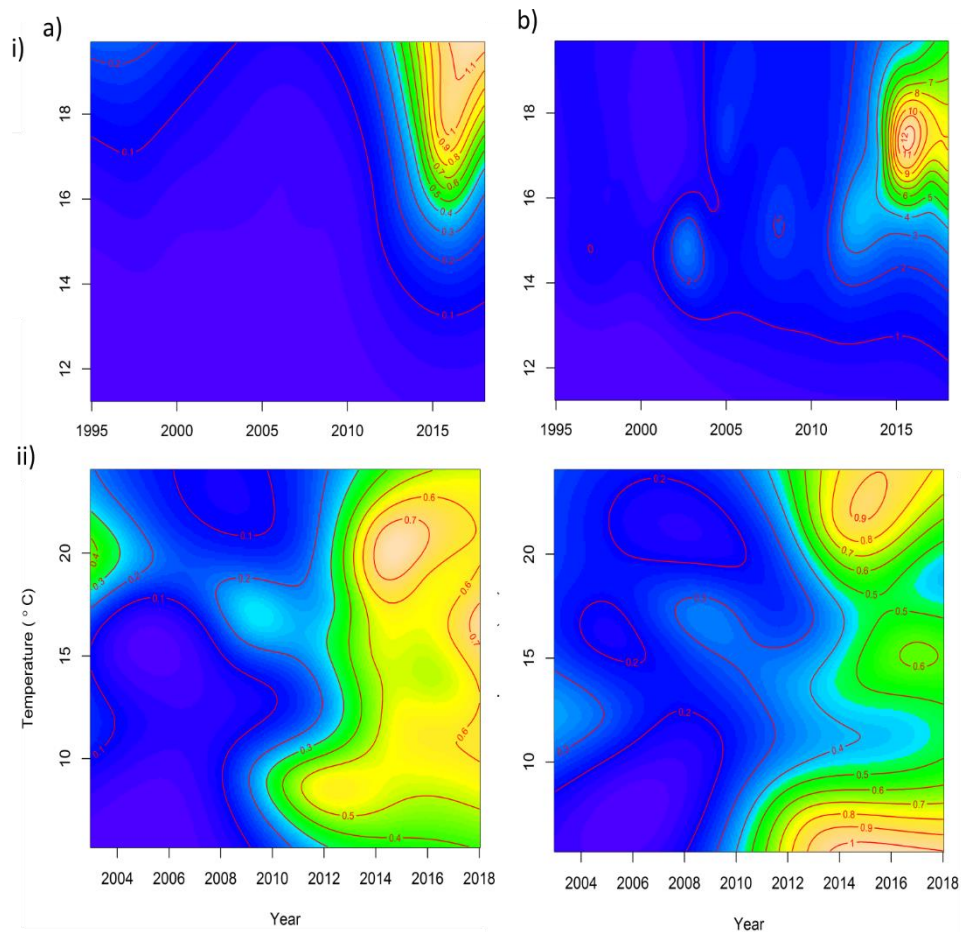
8 *1 column fitting figure*



9

10 **Fig. 2.** The square root mean number of a) *Raja undulata* b) *Raja clavata* per haul,
 11 from i) 1995 to 2018 using Channel Ground Fish Survey data and ii) 2003 to 2018,
 12 using ObsMer data. Each response variable is fitted with a general additive mixed-
 13 effect model versus year. The fitted line is black, and 95% confidence intervals are
 14 shaded in grey. Derivative significant increases are highlighted by blue dashed lines
 15 and significant decreases in purple dashed lines. The vertical dashed black line
 16 indicates the 2009 *R. undulata* ban and the 2015 relax in prohibition. + = GTR, x =
 17 OTB, * = OTT.

18 *1.5 column fitting figure*

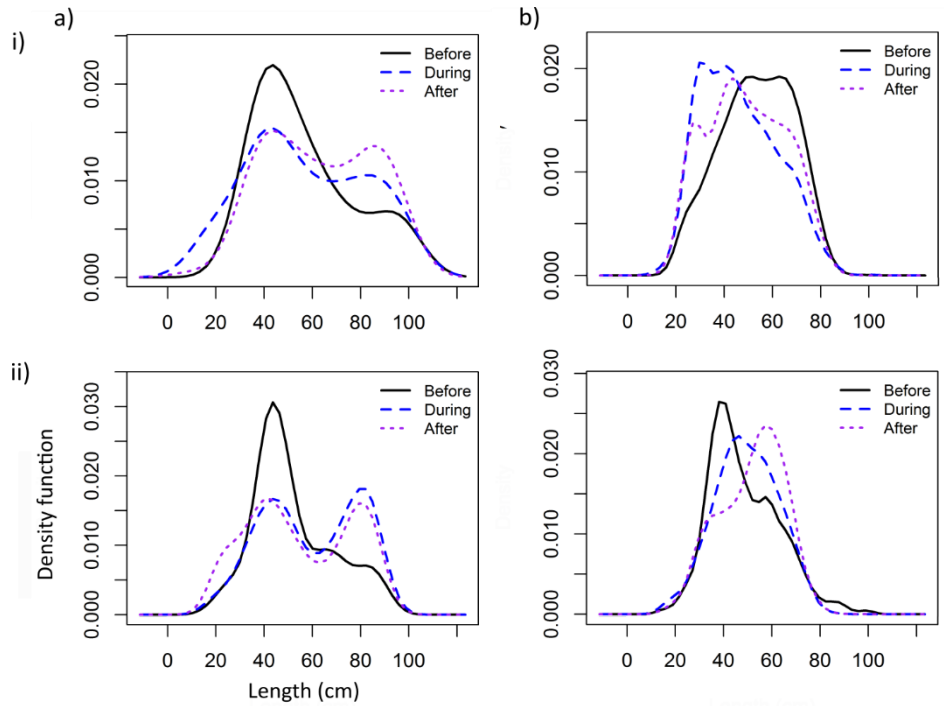


19

20 **Fig. 3.** Contour plots of the effect of temperature and time on the mean
 21 abundance of i) *Raja undulata* and ii) *Raja clavata* using a) Channel Ground Fish
 22 Survey data and b) ObsMer data. Contours highlight relative abundance, Lighter
 23 colours represent higher mean number of individuals observed and darker colours
 24 represent lower mean number of individuals observed.

25

1.5 column fitting figure



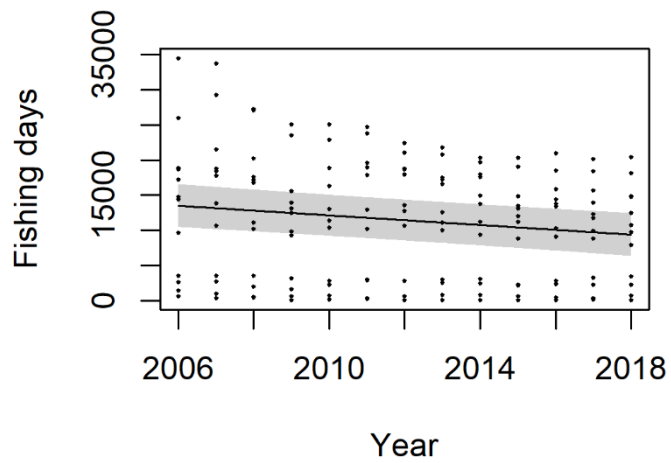
26

27 **Fig. 4.** Kernel smoothed probability density length plots for a) *Raja undulata* and b)
 28 *Raja clavata* using ObsMer data before (2003 - 2008), during (2009 - 2014) and after
 29 (2015 - 2018) the *R. undulata* fisheries ban.

30 *1.5 column fitting figure*

31

32

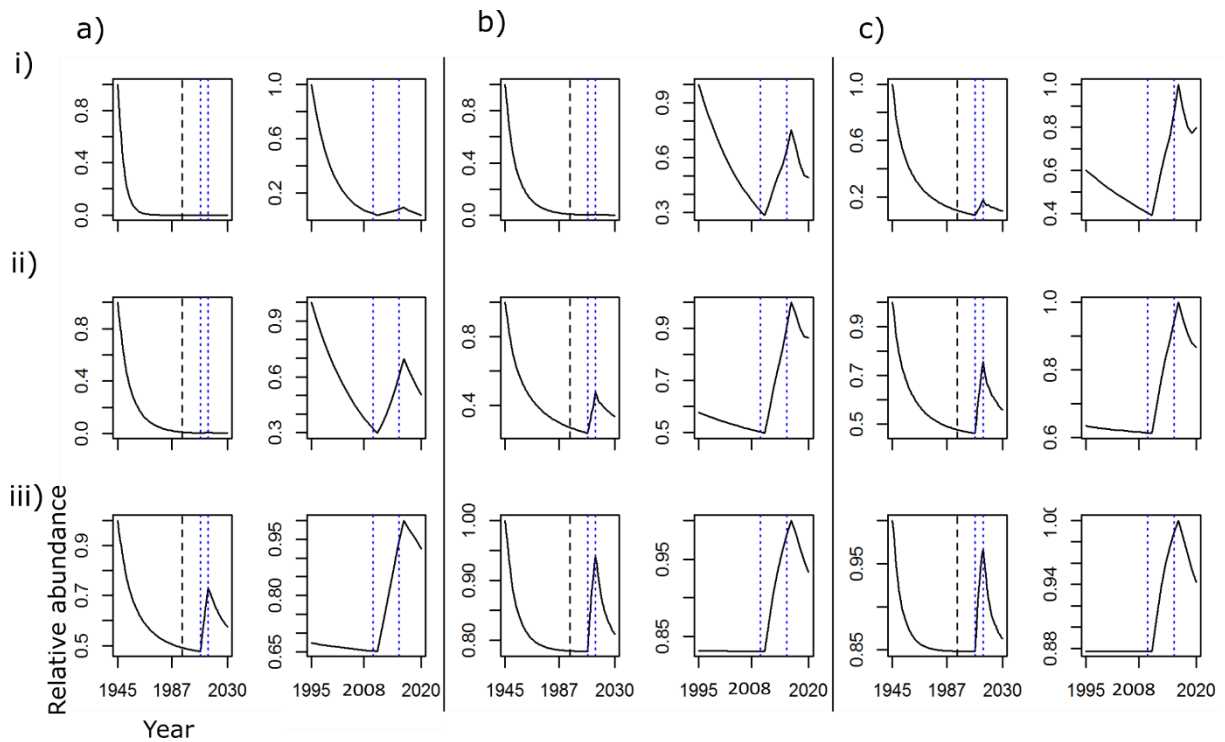


33

34 **Fig. 5.** Fishing pressure (days at sea per gear type and region) from 2006 to 2018.

35 The fitted line is black, and 95% confidence intervals are shaded in grey.

36 *1 column fitting figure*



38

39 **Fig. 6.** *Raja undulata* population dynamic results from the age-structured density
 40 dependent Leslie matrix model, with fishing mortality at i) 30%, ii) 20% and iii) 10%
 41 and juvenile discard survival at a) equivalent to fishing mortality, b) increasing
 42 figures between fishing mortality and 100% survival (Table 3) and c) 100% survival.
 43 The vertical dotted blue lines indicate the 2009 *R. undulata* ban and the 2015 relax
 44 in prohibition. The vertical black dashed line indicates 1995. Two figures for each
 45 scenario have been plotted to better understand temporal trends at the different
 46 scales (1945 - 2030 and 1995 - 2018).

47 *double column fitting figure*



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Table

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Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

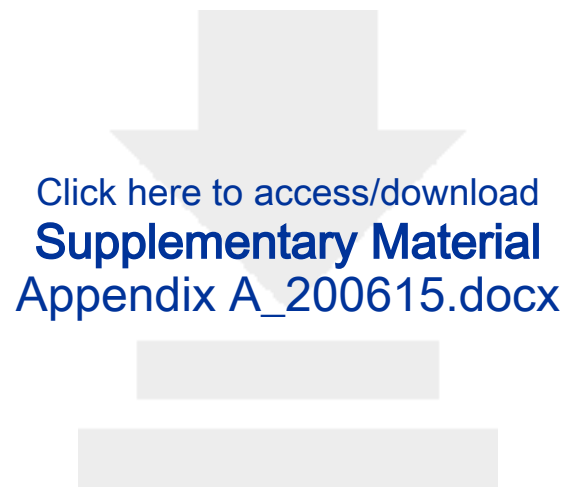
CRedit author statement

Elliott S. A. M: Conceptualization, Methodology, Formal analysis, Data curation, Writing - Original Draft, Writing - Review & Editing, Visualization. **Bearup D:** Methodology support, Software, Validation, Writing - Review & Editing. **Carpentier A:** Writing - Review & Editing, Funding acquisition. **Larivain A:** Writing - Review & Editing. **Trancart T:** Writing - Review & Editing, Funding acquisition. **Feunteun E:** Resources, Writing - Review & Editing, Supervision, Project administration, Funding acquisition.



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Supplementary Material
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