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

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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 (km<sup>2</sup>) 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),  $L_\infty$ (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,  $K = 0.25 - 0.27$ ,  $t_{\text{anchor}} = 0.45$ .  $t_{\text{anchor}}$  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  $\beta$  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 ( $\lambda$ ) is greater than one (Leslie, 1945). We found that, for an  
311 unfished population, the best-case scenario,  $\lambda$  is 1.06; so, the population is  
312 sustainable. When fishing was included in the model, reducing survival,  $\lambda$   
313 decreased. In particular, using this model, we identified that a fishing survival rate  
314 of less than 88% would reduce  $\lambda$  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

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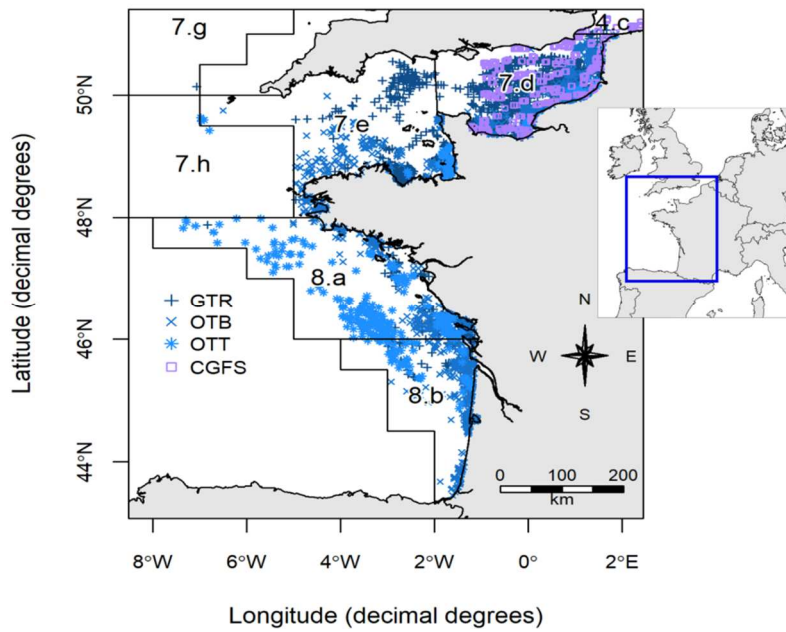
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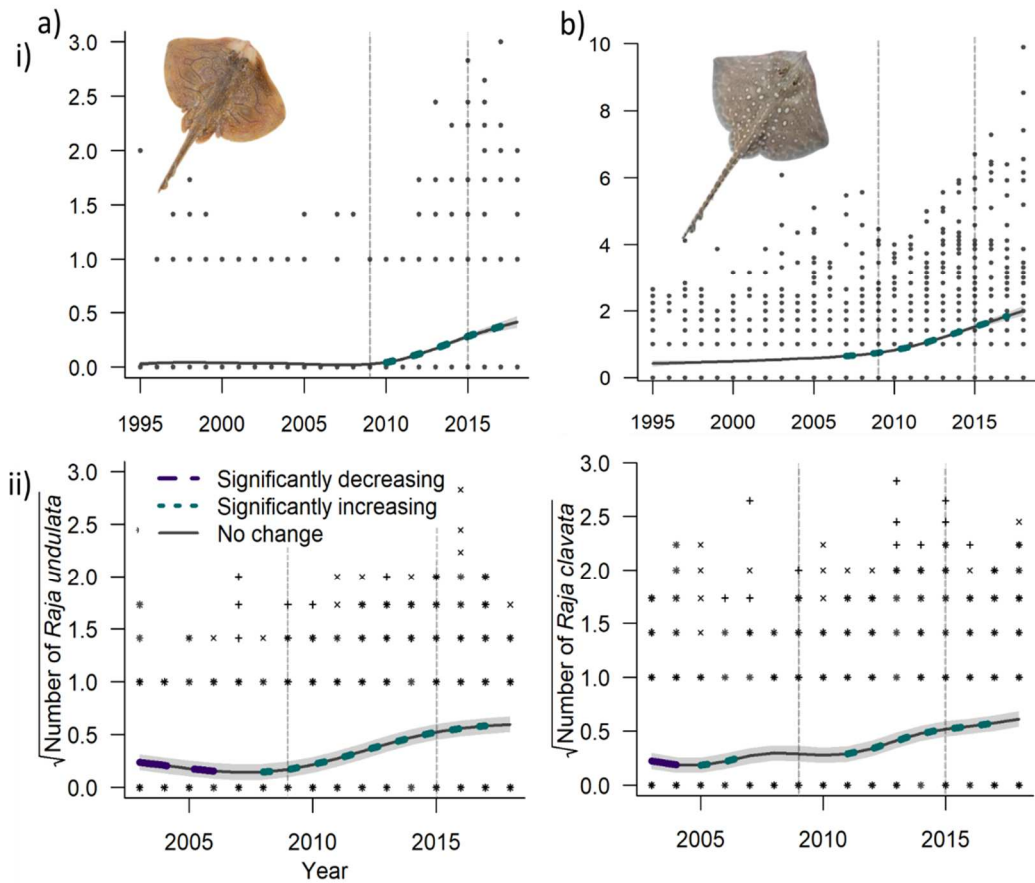
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2

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.

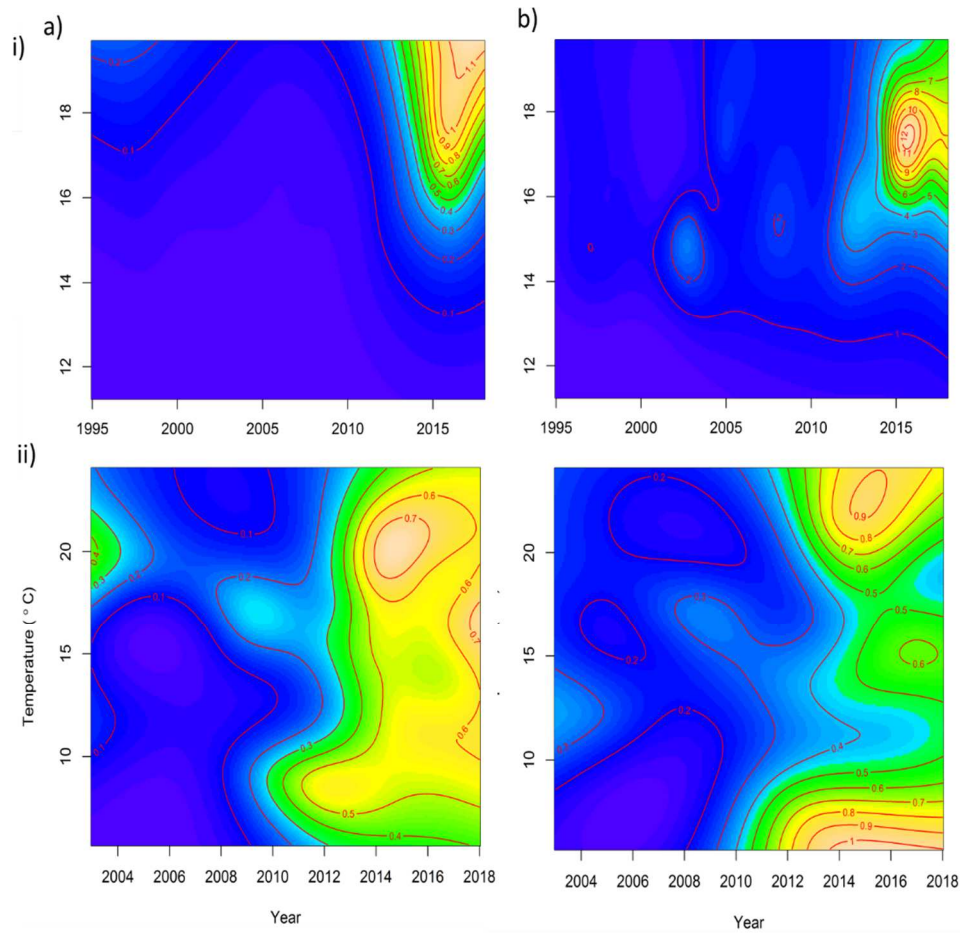
8 *1 column fitting figure*



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*

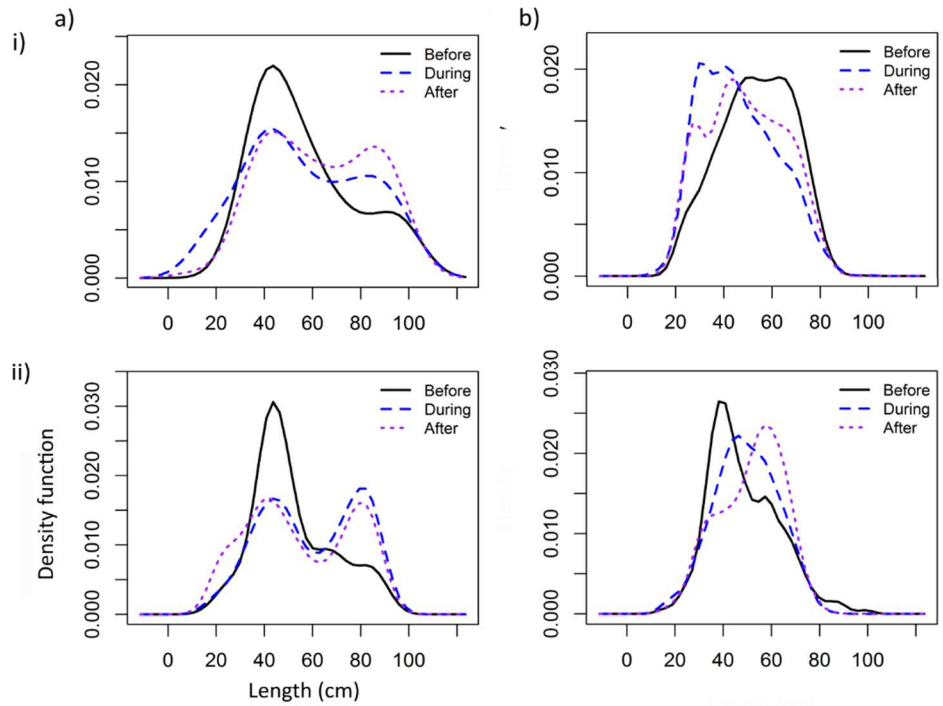


19

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*



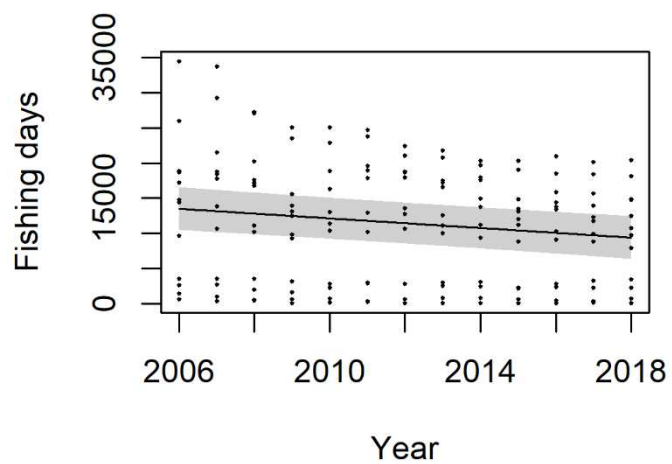
26

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

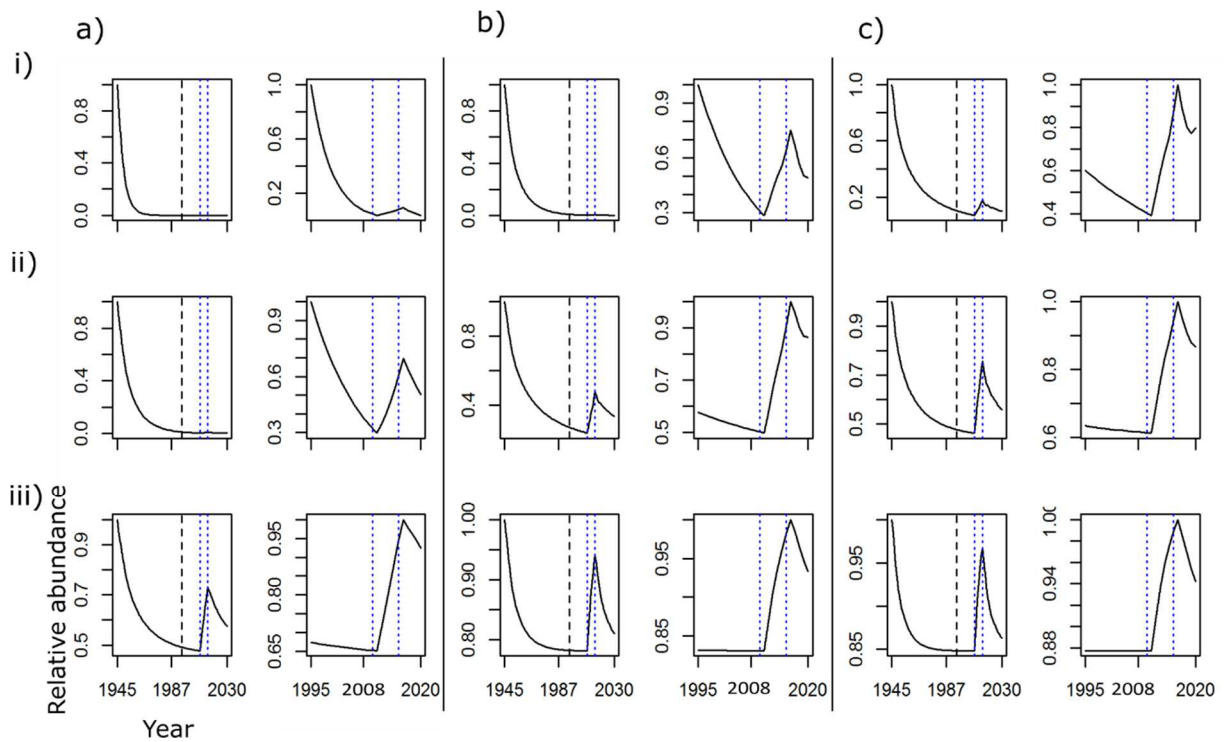


33

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*

1 **Table 1.** Details of statistical models used to understand the effect of time and temperature on *Raja undulata* and *Raja clavata*  
2 mean abundance using both the Channel Ground Fish Survey (CGFS) and ObsMer data. Akaike Information Criterion (AIC), Sea  
3 Surface Temperature (SST, °C), Swept Surface Area (SSA, km<sup>2</sup>), Random Effect (RE).

Species	Dataset					
	CGFS			ObsMer		
Model	AIC	Adjusted R2	Model	AIC	Adjusted R2	
<i>R. undulata</i>	s(Year) + s(SST) + offset(SSA)	1573	0.11	s(Year) + s(SST) + RE(Gear) + RE(Area)	25928	0.15
	s(Year, SST) + offset(SSA)	<b><u>1566</u></b>	<b><u>0.12</u></b>	s(Year, SST) + RE(Gear) + RE(Area)	<b><u>25723</u></b>	<b><u>0.16</u></b>
	s(Year) + offset(SSA)	<b>1587</b>	<b>0.10</b>	s(Year)+ RE(Gear) + RE(Area)	<b>25965</b>	<b>0.15</b>
	s(SST) + offset(SSA)	1785	0.06	s(SST) + RE(Gear) + RE(Area)	27593	0.05
<i>R. clavata</i>	s(Year) + s(SST) + offset(SSA)	14343	0.15	s(Year) + s(SST) + RE(Gear) + RE(Area)	39682	0.15
	s(Year, SST) + offset(SSA)	<b><u>14229</u></b>	<b><u>0.15</u></b>	s(Year, SST) + RE(Gear) + RE(Area)	<b><u>39552</u></b>	<b><u>0.16</u></b>
	s(Year) + offset(SSA)	<b>14498</b>	<b>0.13</b>	s(Year)+ RE(Gear) + RE(Area)	<b>39952</b>	<b>0.125</b>

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$s(\text{SST}) + \text{offset}(\text{SSA})$	16551	0.04	$s(\text{SST}) + \text{RE}(\text{Gear}) + \text{RE}(\text{Area})$	40876	0.035
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5 **Table 2.** Density dependent population dynamic model parameters.

Model parameter	Value	Age	Size	Survival	Age	Size	Survival
Max fecundity	70 eggs	0-1	13	0.25	6-7	93	0.9
Maturity	Age-5	1-2	35	0.35	7-8	96	0.9
Density effect	$1.5 \times 10^{-6}$	2-3	65	0.4	9-10	99	0.9
Age-4+ fishing survival	0.7-0.9	3-4	74	0.5	10-11	101	0.8
Age-0-3 discard survival (see table 3)	0.8-1	4-5	82	0.6	11-12	103	0.0
		5-6	88	0.9			

6

7 **Table 3.** *Raja undulata* age-0-3 discard survival during the periods of time when  
8 fishing was permitted relating to Figure 5.b.i-iii).

Discard survival by age			
Fishing survival	Age-0-1	Age-1-2	Age-2-3
0.7	1	0.9	0.80
0.8	1	0.95	0.9
0.9	1	0.975	0.95

9