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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ABSTRACT

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

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

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

1. Introduction

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

Larger, slower maturing and less fecund species, such as elasmobranchs, are more vulnerable to anthropogenic pressures than most teleost fish (Dulvy et al. 2000, Stevens et al. 2000, Ellis et al. 2011). Their life history traits lead to low rates of reproduction, and therefore low rates for population recovery (Dulvy et al., 2000; Stevens et al., 2000; Walker and Hislop, 1998). As a result of severe global declines observed during the late twentieth century (Dulvy et al., 2017; Stevens et al., 2000), conservation management measures were set up to protect elasmobranch species (e.g. added to IUCN red list, prohibited from commercial exploitation, country specific national action plans, etc.) (Dulvy et al., 2017). However, few studies have evaluated the effectiveness of such measures (Dulvy et al., 2017; Hutchings, 2000; Shiffman and Hammerschlag, 2016).

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

In this study, we used long-term fisheries dependent (2003 to 2018) and independent (1995 to 2018) data on skate abundance (the mean number of skate individuals observed per haul) and length. We analysed significant generalised additive mixed model derivative changes according to the implementation of a species-specific fisheries ban. We used the *Raja undulata* (undulate ray) fisheries ban, set up in 2009, prohibiting targeted fishing and bycatch landing (EC 43/2009; Ellis et al. 2012). Due to declines in *R. undulata* abundance, it was categorised under the IUCN red list as ‘Endangered’ (IUCN, 2019). The imposition of this ban was controversial with certain fishers due to high capture rates observed (ICES, 2018a & b). Consequently, *R. undulata* was removed from the prohibition list in 2015, and a small but annually increasing quota was permitted in the English Channel (112 in 2016 to 180 tonnes in 2018) and the Bay of Biscay (25 in 2016 to 30 tonnes in 2018) (EC 2015/960; ICES 2018a & b).

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

It was hypothesised that an increase in mean abundance would be observed in both species some time after the fisheries ban, as a result of their sympatric nature. It was also hypothesised that climate change would accentuate the increase in mean abundance of both species, and, in particular *R. undulata* given its warmer water preference (Sguotti et al., 2016). An immediate slight increase in size of both species was expected due the removal of targeted fishing of larger individuals. However, no overall long-term increase in mean size was expected due to the reintroduction of the quotas. Given the fishing effort data analysed was measured in days at sea for all species catch, by the gear types which caught skates (partly as bycatch), it was expected that the overall fishing effort would have remained more or less constant.

2. Method

2.1. Survey data

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

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

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

2.2. Skate abundance variations

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

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

clavata; accessed from ObsMer, CGFSs and published literature) (Ellis et al., 2012; Serra-Pereira et al., 2010) were removed to reduce zero inflation. To account for gear and area (ICES divisions) effects on skate abundance from the ObsMer data, both variables were incorporated into the model as random effects. To account for varying trawl durations using the CGFSs, swept surface area (km^2) was included in the model as an offset.

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

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

2.3. Climate change effects

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

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

2.4. Length variations

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

Other parameters to investigate potential fisheries induced evolution effects were not taken into consideration, due to insufficient biological information on maturity and age. Life history trait information is scarce in elasmobranchs and the baseline information which exists for these species varies greatly between regions (e.g. Ellis et al., 2005; Mccully et al., 2012).

2.5. Fishing effort changes

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

2.6. The Population Dynamic Model

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

2.6.1. Length at age and maturity estimations

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

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

here TL_t (cm) is total length expected at age, t is time (year), L_∞(cm) is the theoretical asymptotic length, exp is the exponential function, K is the growth rate and $t0$ is the theoretical age when length equals zero. The VBGF parameters were L_∞ = 108 cm, K = 0.25 - 0.27, t_{anchor} = 0.45. t_{anchor} replaces t_0 in the VBGF, and refers to the time of year where a new cohort is identified in each year.

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

2.6.2. Density dependent Leslie matrix model

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

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

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

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

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

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

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

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

3. Results

3.1. Skate abundance variations

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

3.2. Climate change effects

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

3.3. Length variations

For both species and both datasets, there was little if any mean length variation from the derivative plots in relation to the different management measures (Fig. S3). However, using both datasets a higher probability density function of small *R. undulata* (~20-40 cm) was observed before the ban than during or after, whereas the probability density function of larger individuals (~30-50 cm) evened out after the ban (Fig. 4.a). Fig S2, also shows larger *R. undulata* discarded during the ban than before, albeit landings still took place during the ban. For *R. clavata*, the results between the different dataset was mixed (Fig. 4.b).

3.4.Fishing effort changes

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

3.5. The population dynamic model

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

Fishing survival and juvenile discard survival were varied in order to match the behaviour of the CGFS and ObsMer data (Fig. 2.a.i-ii; Fig 6). Similar recovery dynamics to the real data were only observed for *R. undulata* when the fishing ban increased juvenile discard survival (Table 3; Fig. 6iii.b-c). However, the rapid decline after the end of the ban predicted by the population dynamic model (Fig. 6), was not observed within the real data. The sensitivity analysis demonstrated that the recovery dynamics were highly sensitive to juvenile survival rates and fishing survival, and somewhat sensitive to fecundity, while being relatively insensitive to the other model parameters (Fig. S1).

4. Discussion

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

4.1. Abundance changes

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

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

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

4.2. Climate change effects

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

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

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

4.3. Length changes

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

4.4. Use of fisheries dependent and independent data

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

4.5.Fishing effort

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

4.6. The population dynamics model

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

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

4.7. Implications for conservation and management

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

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

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

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

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

Acknowledgements

This study was funded by the French marine fisheries and aquaculture administration (DPMA). We are grateful to DPMA, the 'Systeme d'Information Halieutique', and all those who were involved in collecting and compiling on-board fisheries observer data (ObsMer) and Channel Ground Fish Data. We would like to thank the reviewers for their valuable contribution. The authors would also like to thank Gavin Simpson for his advice with regard to generalised additive mixed models derivative analysis and Philippe Bryère (ARGANS) for access to high resolution PATHFINDER temperature data.

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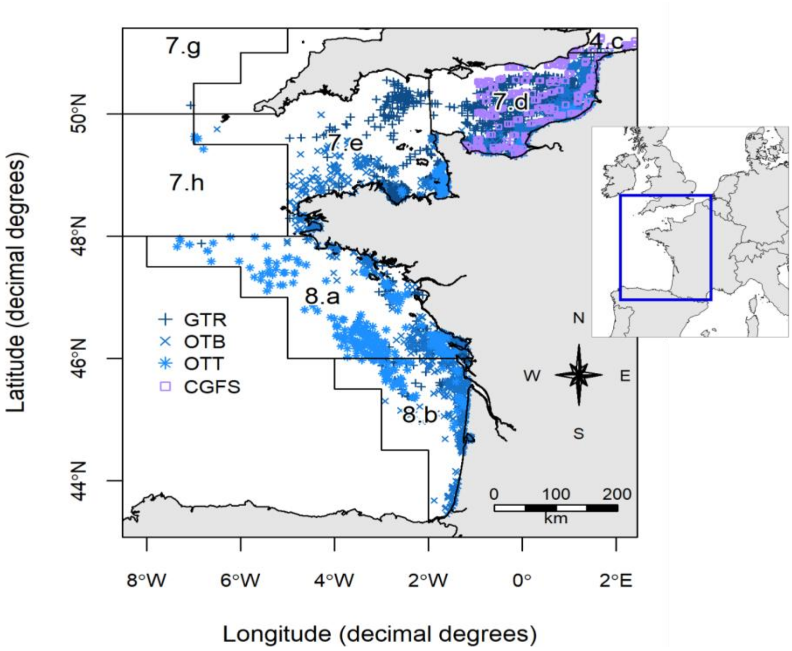

Fig. 1. Presence points of *Raja undulata* and *Raja clavata* fisheries dependent ObsMer gear types and fisheries independent Channel Ground Fish Surveys (CGFS), represented different coloured symbols: CGFS, □, Trammel nets (GTR, +), Otter Beam Trawls (OTB, X), Otter Twin Trawls (OTT, ∗). Black solid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

1 column fitting figure

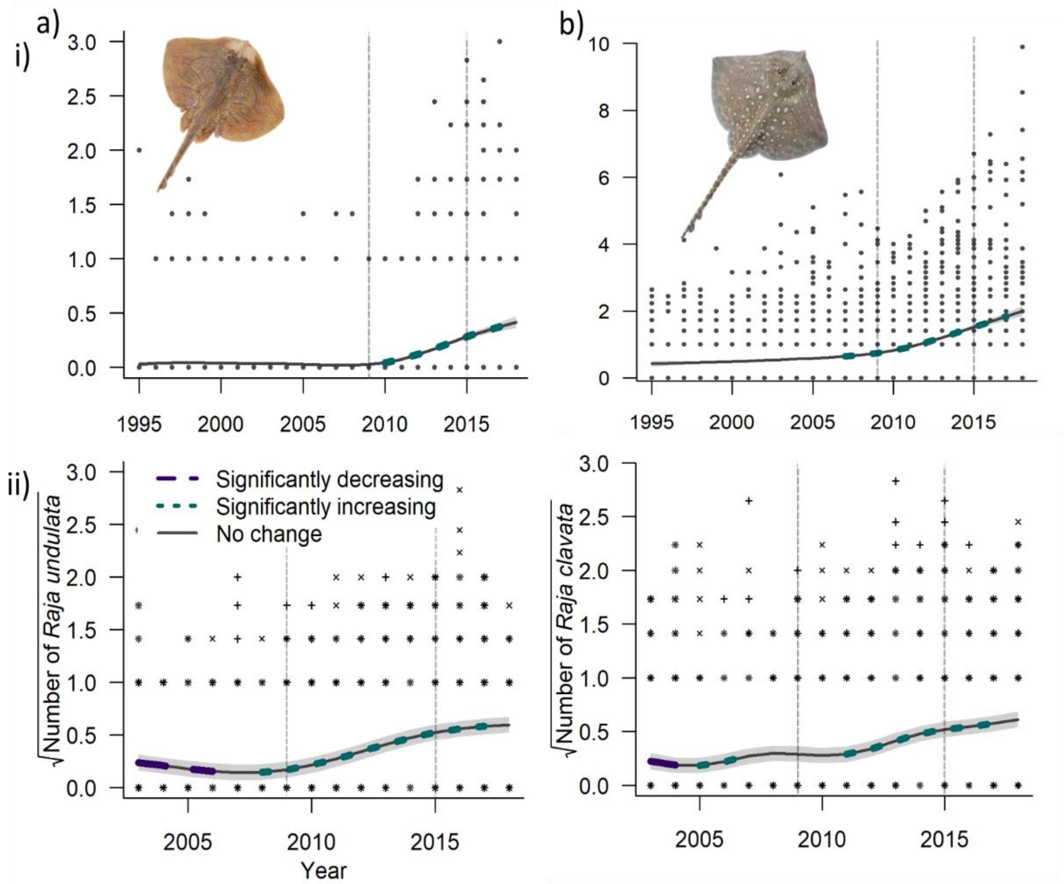

Fig. 2. The square root mean number of a) *Raja undulata* b) *Raja clavata* per haul, from i) 1995 to 2018 using Channel Ground Fish Survey data and ii) 2003 to 2018, using ObsMer data. Each response variable is fitted with a general additive mixed-effect model versus year. The fitted line is black,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

1.5 column fitting figure

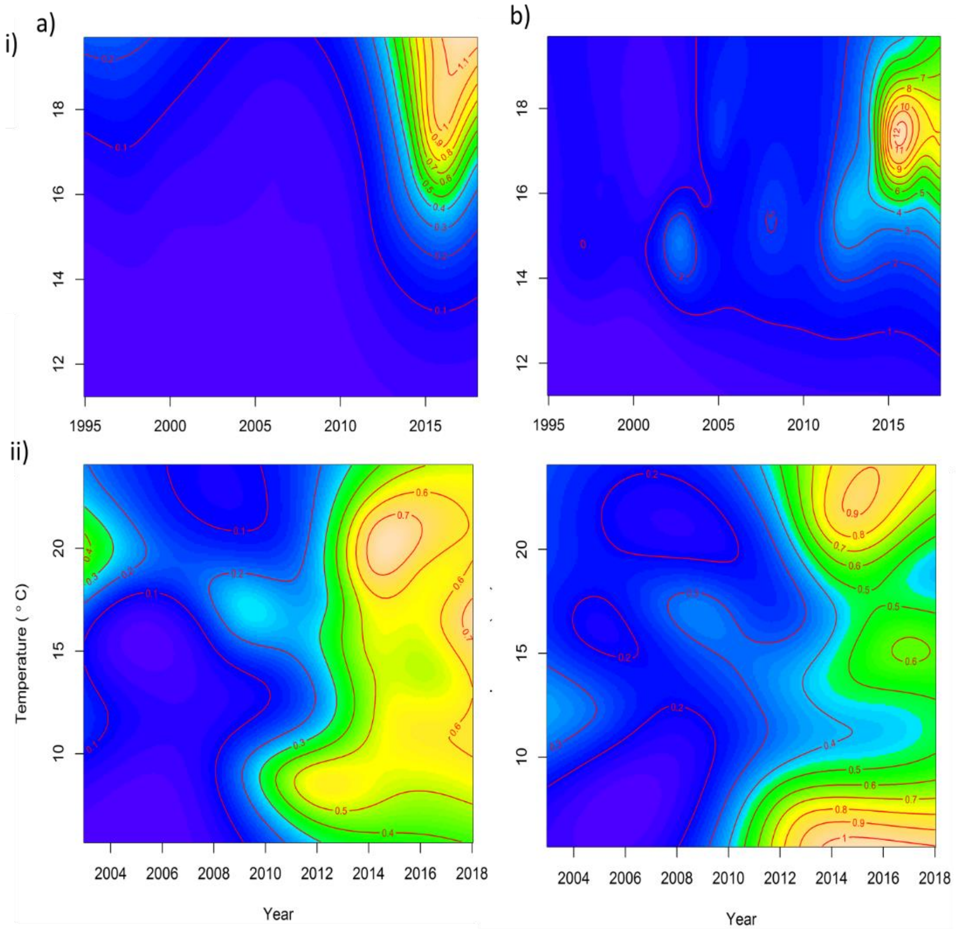

Fig. 3. Contour plots of the effect of temperature and time on the mean abundance of i) *Raja undulata* and ii) *Raja clavata* using a) Channel Ground Fish Survey data and b) ObsMer data. Contours highlight relative abundance, Lighter colours represent higher mean number of individuals observed and darker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

1.5 column fitting figure

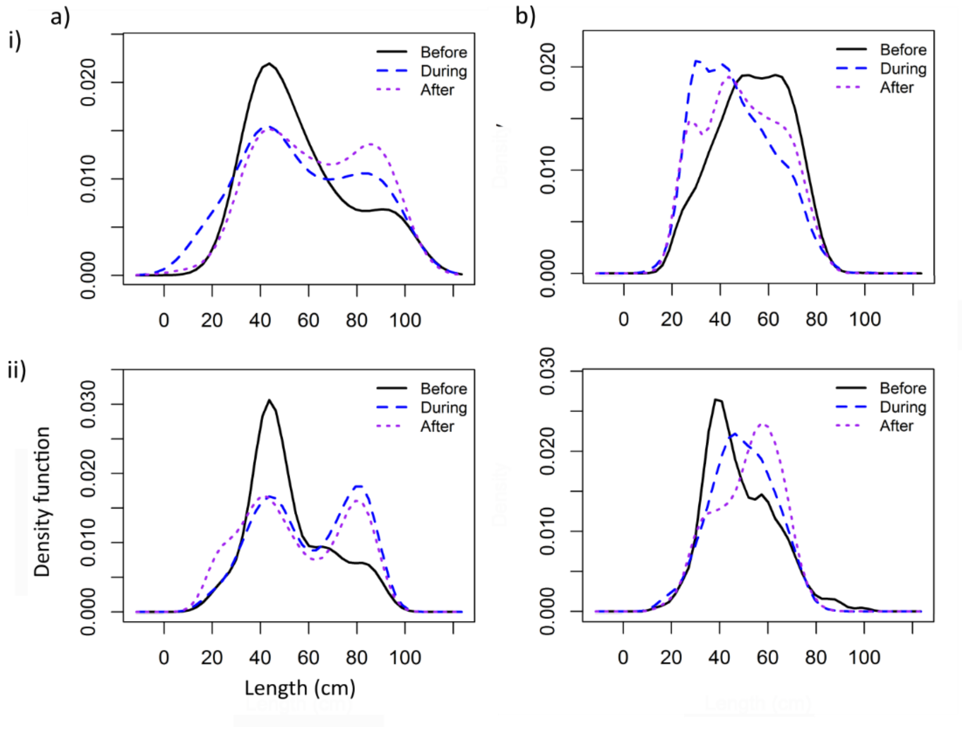

Fig. 4. Kernel smoothed probability density length plots for a) *Raja undulata* and b) *Raja clavata* using ObsMer data before (2003 – 2008), during (2009 – 2014) and after (2015 – 2018) the *R. undulata* fisheries ban.

1.5 column fitting figure

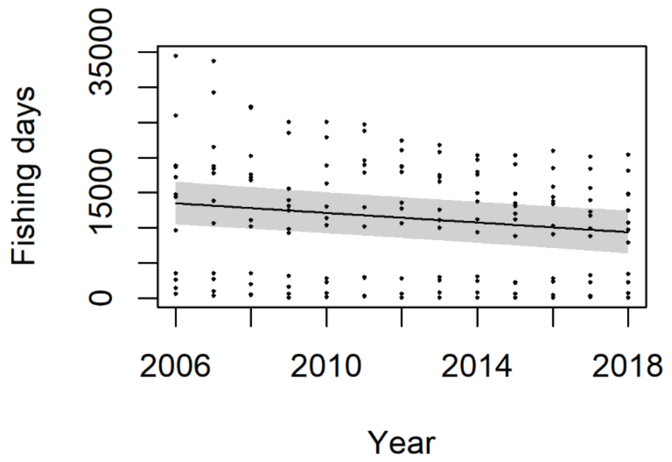

Fig. 5. Fishing pressure (days at sea per gear type and region) from 2006 to 2018. The fitted line is black, and 95% confidence intervals are shaded in grey.

1 column fitting figure

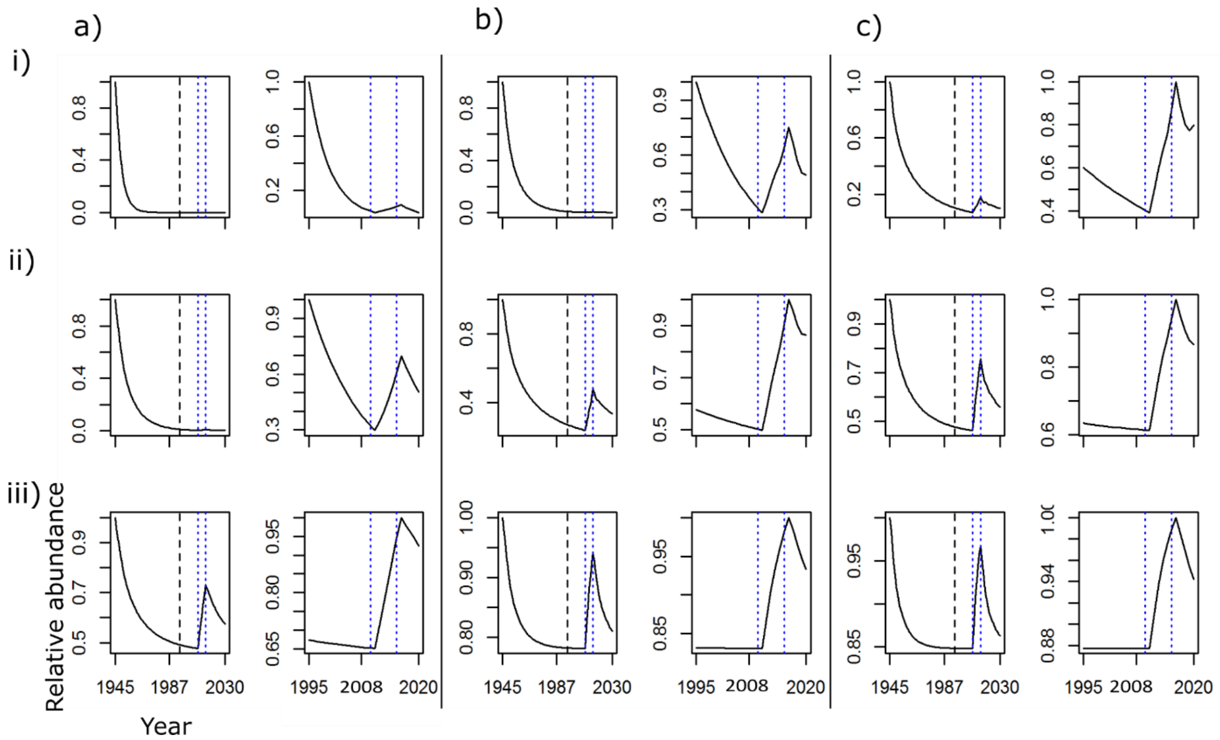

Fig. 6. *Raja undulata* population dynamic results from the age-structured density dependent Leslie matrix model, with fishing mortality at i) 30%, ii) 20% and iii) 10% and juvenile discard survival at a) equivalent to fishing mortality, b) increasing figures between fishing mortality and 100% survival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

double column fitting figure

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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