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Distribution and life history trait models indicate vulnerability of skates

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ABSTRACT

Elasmobranchs are k-strategy species with low reproduction rate and slow growth lending to increased anthropogenic vulnerability. Specific management measures to improve the conservation of elasmobranchs can be problematic due to insufficient information on their biology and ecology. Here, three sympatric skates occupying north-eastern Atlantic waters, which have differing conservation status were studied within ICES divisions 4.c, 7.d–e, 7.f–h and 8a–b and d. Fisheries-dependent data on skate bycatch and a series of environmental variables were used to model spatio-temporal differences in habitat use between the three species.

Raja undulata, the undulate ray (IUCN red listed as 'Endangered') was observed to have a coastal distribution within the English Channel and the Bay of Biscay (ICES division 7.d–e and 8.a–b). *Raja clavata,* the thornback ray ('Near threatened'), had a broader distribution with higher presence in the eastern English Channel and the southern North Sea (ICES division 7.e and 4.c). *Raja montagui*, the spotted ray's probability of presence ('Least concerned') was higher off the coast of southern Ireland (ICES division 7.g). Seasonal and life-history trait differences were also observed.

From the fisheries-dependent data, wider skate distributions than previously studied were modelled. Although the species do co-occur, spatio-temporal differences between these species were observed. This study contributes to a greater understanding of skate habitat during their different life history stages, and indicates reasons for *R. undulata's* increased vulnerability than *R. clavata* and *R. montagui.* Information from the distribution models could be used for specific spatio-temporal management measures. Better understanding of the distribution of species can also help reduce bycatch of protected species such as *R. undulata*.

1. Introduction

From the range of anthropogenic activities that take place in on marine ecosystems, mobile demersal fishing activities have been identified as the most important cause for declines in species (Halpern et al., 2007) and loss of their habitat (Dulvy et al., 2003). Recent estimates indicate that large predatory fish, and in particular elasmobranch species, have declined by at least 90% worldwide (Myers and Worm, 2005). Depletion of top predators can also cause community changes through their 'top down' predation pressures on lower trophic levels (Myers and Worm, 2005; Stevens et al., 2000).

Elasmobranchs are slow growing, late maturing, k-strategy species' making them more vulnerable to exploitation than many fast reproducing r-strategy fish (Dulvy et al. 2000, Stevens et al. 2000, Ellis et al. 2011). During the late 20th century, declines in many elasmobranchs were recorded (Dulvy et al., 2017; Dulvy and Reynolds, 2002). As a result, numerous elasmobranchs were listed under the International Union for the Conservation of Nature (IUCN) red list category (IUCN, 2019) and prohibited from commercial exploitation (Ellis et al., 2012; Silva et al., 2012).

Within the European Union (EU), commercially important marine fish are managed through Total Allowable Catch (TAC), quotas and minimum landings sizes. Temporal and spatial fisheries closures or protected areas can also be introduced to protect 'essential fish habitats' (Elliott et al., 2016). Many elasmobranchs are, however, caught as bycatch, and certain fishers have claimed to see an increase in skates in recent years (Ellis et al., 2012; Silva et al., 2012). Quota restrictions for species which continue to be caught can stop vessels from fishing, even if they still have quota for their targeted species (Mortensen et al., 2018). Therefore, without good knowledge on their distributions during their different life history stages, efficiency of protection for red list species can be limited.

In this study, ecological terms relating to 'habitat' encompass the seabed and physico-chemical characteristics of an area occupied by a

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Table 1
Summary of model predictor variables. GNS = Set gillnets, GTR = Trammel nets, OTB = Otter beam trawls, OTT = Otter twin trawls, SDN = Danish seine nets.

Predictor variable	Description	Unit
Depth	Bathymetry data downloaded from EMODnet.	m
Salinity	At seabed, provided by Ifremer MARS3D hydrodynamic model at a 4 km resolution (Lazure and Dumas, 2008).	PSU ‰
Turbidity	At seabed, provided by Ifremer ECOMARS3D at a 4 km resolution.	g m^{-3}
Chlorophyll *a*		μg l^{1}
Sediment type	Broad-scale seabed habitat types (EUSeaMap) downloaded from EMODnet. Four classes were used according to grain size: mud (≤ 2mm), sand (> 2 and ≤ 4 mm), coarse grain (> 4 mm and 64 mm), and rock (> 64).	Categorical
Latitude Longitude	Obtained from ObsMer data.	Decimal degrees
Season	Winter = December-February, Spring = March-May, Summer = June-August, Autumn = September-November.	Categorical
Gear type	Skate presence absence data was obtained from five different metiers: GNS, GTR, OTB, OTT and SDN*.	Categorical

* SDN was not taken into consideration for *R. undulata* and GNS was not taken into consideration for *R. montagui*.

species during a particular stage in its ontogeny. To be able to manage species of conservation and commercial importance, knowledge of their habitat during their different life history stages is therefore essential to reduce bycatch and propose spatial management measures (Dulvy et al., 2003). To date, predictive distribution models for skates have been undertaken using scientific bottom trawl survey (SBTS) data which takes place at set periods during the year and within pre-determined locations (e.g. Martin et al. 2012; Sguotti et al. 2016). Fisheries-dependent data, is collected over the course of the year and within areas much closer to the coast. Therefore, although fisheries dependent data may be biased due to its targeted nature, it can be suitable to study data deficient species.

Several sympatric species of skate occur within north-eastern Atlantic waters. Here, three species were studied because of their sympatric geographical coverage (Ellis et al., 2004; Serra-Pereira et al., 2014), and because of their contrasting conservation status, indicating potential ecological trait differences. These skates include *Raja undulata,* the undulate ray which is classified as ‘Endangered’ under the IUCN redlist*, Raja clavata,* the thornback ray, classified as ‘Near threatened’, and *Raja montagui,* the spotted ray, classified as ‘Least concerned’ (IUCN, 2019). *R. undulata* was prohibited from being landed by the European Commission between 2009 and 2015 (EC 43/2009) but in 2016 a specific TAC for this species was reintroduced. All three species are caught as bycatch by a number of different gear types and have increased in abundance in recent years (ICES, 2017a and b, 2018a).

The aims of this paper are therefore to: (1) Use fisheries-dependent data to map the spatio-temporal distribution of data deficient species (2) Compare the distribution of the three sympatric species during their different life history phases to understand why *R. undulata* is more vulnerable than the other two species. (3) Use the distribution models to identify management and conservation measures that may help reduce bycatch of endangered species in a fishery. To undertake this analysis, French fisheries observer data on skate bycatch and a variety of oceanographic variables were used to model their spatio-temporal distribution within the southern North Sea, the English Channel, the Bay of Biscay and the Celtic Sea. Since fisheries-dependent data is collected throughout the year, seasonal variation in habitat use was modelled. Life history trait differences in ontogeny and sex were also explored.

2. Methods

2.1. Study area and survey data

On board French fisheries observer data (ObsMer) were analysed from the southern North Sea, English Channel, Bay of Biscay and Celtic Sea (International Council for the Exploration of the Sea (ICES) division 4.c, 7.d, 7.e, 7.g and 7.h, 8.a and 8.b). Between 2015 and 2017 the French Atlantic netters and trawlers comprised of between 205 and 190 netters (0–10 m) respectively, and between 224 and 227 trawlers (10–18 m) respectively. Information on vessel numbers before and after this period were not available (EC, 2019). The ObsMer program was set up in 2003, under the European regulation 1639/2001. ObsMer data from 2009 to 2017 were used since the protocol to collect fisheries data was standardised across France in 2009, following the implementation of the Data Collection Framework. Within the national sampling plans, observers randomly select professional fishing boats to embark, and once aboard random hauls are sampled (Fauconnet et al., 2015). Information on fishing activity (time, latitude, longitude, gear, targeted species) and catch composition (landings and discards of fish and commercial invertebrates) are collected for each haul by scientific observers. For each haul, landed and discarded catch are identified (species), measured (cm), and whenever possible, sexed. Hauls that did not contain skate landings were taken into account to account for zero observations.

2.2. Predictor variables

A variety of fixed effect environmental variables that might have had an effect on the distribution of skates was explored. These included: depth (m), mean daily turbidity (g m^{-3}), chlorophyll *a* (μg l^{-1}) and salinity (PSU) at the seabed, sediment type (rock (R), coarse-grain (Cg), sand (S) and mud (M)), latitude and longitude (decimal degrees; Table 1).

Outliers were analysed with boxplots and explored by checking the raw data and mapping. Aberrant values were removed. Variations in the distribution of skates according to season (winter = December–February, spring = March–May, summer = June–August, autumn = September–November) were also explored to identify possible seasonal migratory behaviour. Biotic variables were not included in the model due to lack of information on such data. To account for variations in gear selectivity and reduce spatial autocorrelation, a random effect for gear was included in the models (Eqs. (1)–(3)) (Guillera-Arroita, 2017; Zuur et al, 2009).

2.3. Spatio-temporal modelling

Binomial generalised linear mixed models using a logistic regression with a logit or a complementary log–log link function were used to model and predict spatiotemporal distributions of the skates. Clog log links were used when there was a high percentage of zeros and the AIC was lower when fitting the model.

To reduce counting false zeros, both landed and discarded individuals that were considered. To reduce zero inflation, spatio-temporal biases and presence over estimations, only gear types with an even spatio-temporal coverage (set gillnet, trammel net, otter beam, and otter twin trawls, and Danish seine net for *Raja clavata*), and a skate bycatch of more than one percent of the total hauls were analysed, similar to Bourdaud et al., (2017). Data outside the known ranges of skate depth distributions (accessed from ObsMer and SBTS data, > 100 m for *R. undulata* and > 150 m for *R. clavata* and *R. montagui*) and

Table 2
Summary table of skate total number of presences per haul from 2009 to 2018 per ICES division.

Species	ICES division	Total number of hauls	Total presence	Percent presence (%)
R. undulata	7.d	3010	313	22
	7.e	1506	621	43
	8.a	1544	181	12
	8.b	1810	337	23
R. clavata	4.c	450	190	3
	7.d	8320	5310	75
	7.e	2413	947	13
	7.g	951	408	6
	8.a	2272	87	1
	8.b	2252	151	2
R. montagui	7.d	3545	113	12
	7.e	1253	209	22
	7.g	1407	456	48
	7.h	796	100	10
	8.a	2099	72	8

ICES divisions in which almost no skates were identified within, were removed to reduce zero inflation (Table 2).

The study area was downscaled and divided into a regular grid similar as recommended by (Keil et al., 2013; Liu et al., 2005; Trancart et al., 2014). For each grid cell, the central point was assigned a value of one if it contained an individual and a value of zero in the absence of an individual. A spatial resolution of 10 km^{2}was used to provide maximum detail.

Spearman's rank correlation was used to test for (multi) collinearity, and a variance inflation factors analysis of three or more was used to remove collinear variables. Variables were extracted from the grid cell centres. All possible combinations of interactions were explored and kept when significant. Post-hoc Tukey tests were performed to evaluate the within-subject effect of seabed type. All statistical modelling and mapping was undertaken within R CRAN free software (version 3.4.4; http://cran.r-project.org/).

$$\mathrm{Logit}(\mathrm{RU}_{ij}) = \beta_0 + \mathrm{Depth}_i\mathrm{:\ Season}_{ij} + \mathrm{Salinity}_i\mathrm{:\ Season}_{ij} + \mathrm{Latitude}_i + \mathrm{Sediment}_{ij} + \mathrm{Chlorophyll}_i + \mathrm{RE}(\mathrm{Gear}_{ij}) + \varepsilon \quad (1)$$

$$\mathrm{Logit}(\mathrm{RC}_{ij}) = \beta_0 + \mathrm{Depth}_i\mathrm{:\ Season}_{ij} + \mathrm{Latitude}_i + \mathrm{Longitude}_i + \mathrm{Sediment}_{ij} + \mathrm{RE}(\mathrm{Gear}_{ij}) + \varepsilon \quad (2)$$

$$\mathrm{Logit}(\mathrm{RM}_{ij}) = \beta_0 + \mathrm{Depth}_i\mathrm{:\ Season}_{ij} + \mathrm{Latitude}_i + \mathrm{Longitude}_i + \mathrm{Sediment}_{ij} + \mathrm{Turbidity}_i + \mathrm{Chlorophyll}_i\mathrm{:\ Season}_{ij} + \mathrm{RE}(\mathrm{Gear}_{ij}) + \varepsilon \quad (3)$$

where RU refers to *R. undulata*, RC, refers to *R. clavata* RM refers to *R. montagui* and RE refer to random effect.

2.4. Model evaluation

The model of best fit was identified by testing the mean deviance explained and the lowest Akaike Information Criterion (AIC) of the prediction by a bootstrap cross-validation. Pearson's residuals were extracted and the model's heteroscedasticity conditions verified. The accuracy of the model was tested by Area Under the Receiver Operating Curves (AUROC) and confusion matrices. AUROC and confusion matrices were employed to quantify the trade-off between specificity and sensitivity of the models and provide a value of prediction accuracy. For cross-validation, a random subset of 75% of the dataset was used for parameter estimation and the remaining 25% of observations were used for validation. Prediction error maps were also modelled to demonstrate at a spatial level, model prediction confidence. For models to exceed the evaluation criteria the P value needed to be < 0.01, and the AUROC and a confusion matrix score of > 0.7 (Hosmer et al., 2013). Model prediction uncertainty was computed by calculating the absolute difference between observed and predicted values. These errors were then estimated at the non-sampled locations by inverse distance weighted interpolation using the R package 'gstat'.

2.5. Skate life history trait variations in habitat use

Ontogenetic habitat variation was explored by modelling the explanatory variables according to their total length, using a general linear mixed model (Eqs. (4)–(6)).

$$\mathrm{RU\ \ length}_{ij} = \beta_0 + \mathrm{Depth}_i\mathrm{:\ Season}_{ij} + \mathrm{Salinity}_i\mathrm{:\ Season}_{ij} + \mathrm{Latitude}_i + \mathrm{Sediment}_{ij} + \mathrm{RE}(\mathrm{Gear}_{ij}) + \varepsilon \quad (4)$$

$$\mathrm{RC\ \ length}_{ij} = \beta_0 + \mathrm{Depth}_i\mathrm{:\ Season}_{ij} + \mathrm{Salinity}_i\mathrm{:\ Season}_{ij} + \mathrm{Sediment}_{ij} + \mathrm{Chlorophyll}_i + \mathrm{Turbidity} + \mathrm{RE}(\mathrm{Gear}_{ij}) + \varepsilon \quad (5)$$

$$\mathrm{RM\ \ length}_{ij} = \beta_0 + \mathrm{Salinity}_i\mathrm{:\ Season}_{ij} + \mathrm{Sediment}_{ij} + \mathrm{Turbidity}_i + \mathrm{RE}(\mathrm{Gear}_{ij}) + \varepsilon \quad (6)$$

The three skates were additionally divided according to two size classes: juveniles (≤ 25 cm; Eq. (7)), and mature (≥ 80 cm for *R. undulata*, ≥ 75 cm for *R. clavata* and ≥ 65 cm for *R. montagui*; Eqs. (8)–(10)), to investigate potential essential skate habitat. The size classes were based upon density frequency plots and existing literature (Coelho and Erzini, 2006; Ellis et al., 2012; Koop, 2005; McCully et al., 2012; Serra-Pereira et al., 2015, 2014). Presence absence models by sex were also explored (Eqs. (11)–(16)). When a very low presence of a particular length group or sex was observed, ICES divisions and gear types with low presence data (Table 1) were removed to reduce the zero inflation. When skates were not observed over a particular sediment type (e.g. mud and rock for both juvenile *R. undulata*), these categories was removed from the analysis to improve logistic model convergence.

$$\mathrm{Juvenile\ \ RU}_{ij} = \beta_0 + \mathrm{Depth}_i\mathrm{:\ Season}_{ij} + \mathrm{RE}(\mathrm{Gear}_{ij}) + \varepsilon \quad (7)$$

$$\mathrm{Mature\ \ RU}_{ij} = \beta_0 + \mathrm{Depth}_i\mathrm{:\ Season}_{ij} + \mathrm{Salinity}_i + \mathrm{Sediment}_{ij} + \mathrm{RE}(\mathrm{Gear}_{ij}) + \varepsilon \quad (8)$$

$$\mathrm{Mature\ \ RC}_{ij} = \beta_0 + \mathrm{Depth}_i\mathrm{:\ Season}_{ij} + \mathrm{Longitude}_i + \mathrm{Sediment}_{ij} + \mathrm{Chlorophyll}_i + \mathrm{RE}(\mathrm{Gear}_{ij}) + \varepsilon \quad (9)$$

$$\mathrm{Mature\ \ RM}_{ij} = \beta_0 + \mathrm{Depth}_i\mathrm{:\ Season}_{ij} + \mathrm{Sediment}_{ij} + \mathrm{RE}(\mathrm{Gear}_{ij}) + \varepsilon \quad (10)$$

$$\mathrm{Female\ \ RU}_{ij} = \beta_0 + \mathrm{Depth}_i\mathrm{:\ Season}_{ij} + \mathrm{Salinity}_i\mathrm{:\ Season} + \mathrm{Sediment}_{ij} + \mathrm{RE}(\mathrm{Gear}_{ij}) + \varepsilon \quad (11)$$

$$\mathrm{Male\ \ RU}_{ij} = \beta_0 + \mathrm{Depth}_i\mathrm{:\ Season}_{ij} + \mathrm{Sediment}_{ij} + \mathrm{RE}(\mathrm{Gear}_{ij}) + \varepsilon \quad (12)$$

$$\mathrm{Female\ \ RC}_{ij} = \beta_0 + \mathrm{Depth}_i\mathrm{:\ Season}_{ij} + \mathrm{Salinity}_i\mathrm{:\ Season}_{ij} + \mathrm{Longitude}_i + \mathrm{Sediment}_{ij} + \mathrm{Chlorophyll}_i + \mathrm{RE}(\mathrm{Gear}_{ij}) + \varepsilon \quad (13)$$

$$\text{Male } \mathrm{RC}_{ij} = \beta_0 + \mathrm{Depth}_i\text{: }\mathrm{Season}_{ij} + \mathrm{Longitude}_i + \mathrm{Sediment}_{ij} + \mathrm{Chlorophyll}_i + \mathrm{RE}(\mathrm{Gear}_{ij}) + \varepsilon \quad (14)$$

$$\text{Female } \mathrm{RM}_{ij} = \beta_0 + \mathrm{Depth}_i\text{: }\mathrm{Season}_{ij} + \mathrm{Salinity}_i + \mathrm{Sediment}_{ij} + \mathrm{Turbidity}_i + \mathrm{RE}(\mathrm{Gear}_{ij}) + \varepsilon \quad (15)$$

$$\text{Male } \mathrm{RM}_{ij} = \beta_0 + \mathrm{Depth}_i\text{: }\mathrm{Season}_{ij} + \mathrm{Salinity}_i + \mathrm{Sediment}_{ij} + \mathrm{Turbidity}_i + \mathrm{RE}(\mathrm{Gear}_{ij}) + \varepsilon \quad (16)$$

3. Results

33,408 hauls (including presences and absences) were used over nine years for all three species. The presence of *R. undulata* was recorded in 1452 of 7870 hauls, the presence of *R. clavata* was observed in 7093 in 16,658 hauls and *R. montagui* were observed in 950 of 9100 hauls (Table 2).

3.1. Skate presence absence distribution models

The three species of skate were observed to have overlapping but differing distributions (Figs. 1 and 2). *R. undulata* had a coastal distribution, with a higher presence off the east of Brittany (ICES division 7.e, 43%; Fig. 2.a; Table 2). *R. clavata's* distribution was mainly concentrated to the east of the English Channel and the southern North Sea (ICES division 7.d and 4.c, 75%; Fig. 2.b; Table 2). *R. montagui*'s distribution was highest within ICES division 7.g (south of Ireland; Fig. 2.c, 48%; Table 2). *R. undulata* and *R. clavata* had a reduced presence in winter (Fig. 2.a and b). Whereas, *R. montagui's* distribution was the broadest in winter, extending down to ICES division 7.h, even with less trawls occurring in winter (Fig. 2.c).

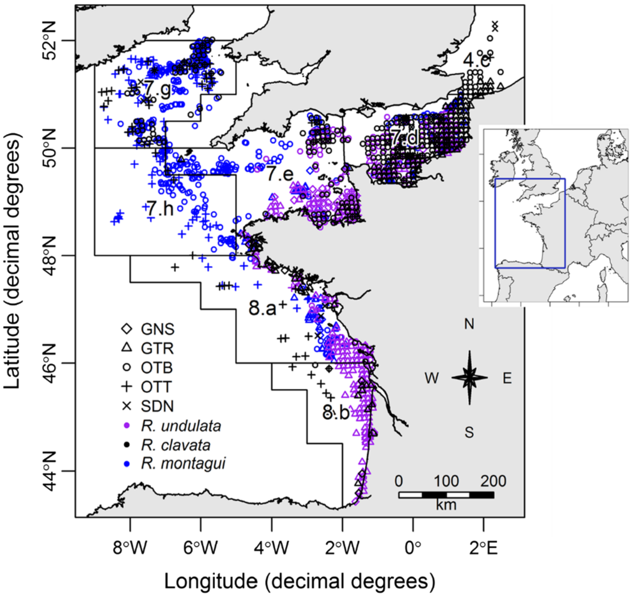

Fig. 1. Location of the study area with fishing vessel presence hauls of *Raja undulata* (purple), *Raja clavata* (black) and *Raja montagui* (blue) between 2009 and 2017. The different shaped points represent the different gear types: set gillnets (GNS, ◊), trammel nets (GTR, △), otter beam trawls (OTB, ○), otter twin trawls (OTT, +) and Danish seine nets (SDN, X). Black solid lines delineate ICES statistical divisions and their coded name. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

In general prediction errors associated with each habitat map (Fig. S1) were higher in areas where individuals were caught more frequently, suggesting higher probability of occurrence in these areas. Prediction errors were lower in areas where individuals were less frequently captured, indicating a good model certainty in the area that the species were modelled but absent.

Predictor variables influencing the habitat of the three species were mainly reflected by that of their spatial (X, Y and Z) distribution. *R. undulata* was observed in shallower (mean = 28.77 ± SD 18.06 cm), more coastal waters than *R. clavata* and *R. montagui* (mean = 39.97 ± SD 27.58 cm; mean = 80.31 ± SD 30.39 cm consecutively) (Fig. 2; Fig. S2-S4). A higher presence of *R. clavata* was observed over coarse-grain (Fig. S3). No obvious sediment preference was observed for the *R. undulata* presence absence model (Fig. S2). *R. montagui* seemed to avoid mud (Fig. S4). A negative relationship between chlorophyll *a* concentration and *R. undulata* and *R. montagui* presence was observed (Fig. S2 and Fig S4). *R. montagui* was also observed in areas of lower chlorophyll consenrtration in winter and a positive relationship with turbidity was observed for *R. montagui* (Fig. S4).

All models exceeded the evaluation criteria. Model prediction accuracy was greater for *R. montagui* and *R. clavata* (Table 3). All AUROC scores were classified as 'acceptable' or above (Table 3; Hosmer et al., 2013).

3.2. Skate life history trait differences

For all three species, larger individuals were observed in deeper or more saline waters, and over more rugose sediments than smaller individuals (Table 4; Fig. S5-S7).

Juvenile (< 25 cm) *R. clavata* and *R. montagui* presence were not modelled due to the inability to reduce zero inflation to less than 90%. Presence of juvenile *R. undulata* (< 25 cm) was only modelled in ICES division 7.d and 7.e and at depths below 80 m, using otter beam and twin trawls. A higher presence was observed in shallower waters spring and winter than the other seasons (Fig. 3; Fig. S8.a).

The probability of presence of mature *R. undulata* (> 80 cm) was modelled in ICES division 7.e and 7.e (Fig. 4a). The probability of presence of mature *R. clavata* (> 75 cm) was modelled in ICES division 4.c, 7.d 7.e and 7.g using trammel nets, otter beam trawls and Danish seine nets (Fig. 4b). Whereas the probability of presence of mature *R. montagui* (> 65 cm) was modelled in 7.e and 7.g, and only trammel nets were used (Fig. 4c). Mature *R. undulata* presence was lower in winter (Fig. 4a), mature *R. clavata* presence was lower in spring (Fig. 4b) and mature *R. montagui* presence was lowest in summer (Fig. 4c).

When comparing the differing environmental variables between genders, only the depth season interaction differed between sex for the three species (Fig. S11). Fewer males than females were observed for *R. clavata* and *R. montagui*. Male *R. clavata* was not modelled in 8.a and 8.b, and male *R. montagui* was only modelled in ICES divisions 7.e, 7.g and 7.h, using otter beam, twin trawls, and trammel nets (Fig. 5). *R. undulata* females were observed further offshore in summer and autumn and slightly closer to the coast in winter than males (Fig. 5a; Fig. S11.a). *R. clavata* females were also observed in slightly higher presence further offshore in summer and autumn (supplementary information Fig. S11.b). *R. montagui* male presence was much lower in summer with highest males presence further offshore in spring (Fig. 5.c; Fig. S11.c).

4. Discussion

Here, species distribution models were explored to identify the habitat of three sympatric skate species of different conservation status. As a result of the fisheries-dependent data, a wider distribution of the three skates was possible to model. Results revealed that although all three species of skates overlapped in distribution, large spatio and temporal

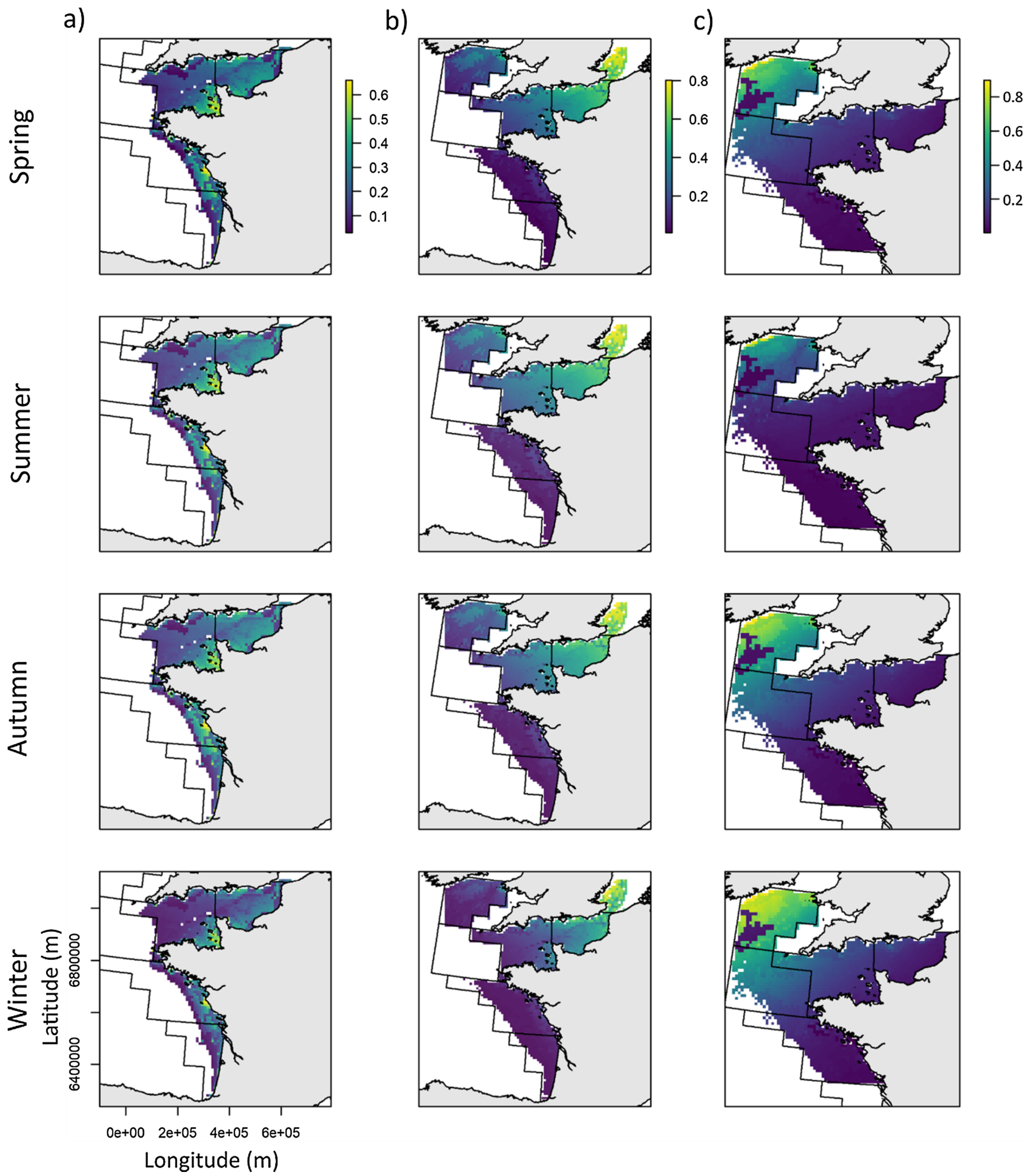

Fig. 2. (a) *Raja undulata* (b) *Raja clavata* and (c) *Raja montagui* prediction maps (10 km^2 cells) per season (three month period). The legend represents the probability of presence. Black solid lines delineate ICES statistical divisions.

differences existed between species. *Raja undulata* had a coastal distribution with the highest presence in the western English Channel. *Raja clavata* had a higher presence in the Eastern English Channel and *R. montagui* presence was highest off the coast of southern Ireland.

4.1. *Use of fisheries-dependent data*

To date, habitat models for north-eastern Atlantic water skates have been undertaken on an ICES division scale using SBTS data (Martin et al. 2012; Sguotti et al. 2016). However, SBTSs do not take place close to the shore, where many skates are fished. Furthermore, ICES division 7.e (where the skates studied have been caught), does not have a history of annual SBTS due to historically poor spatial coverage (Ellis et al., 2011). Such biases may lead to an under estimation of skates abundance and elasmobranch in general (Maxwell and Jennings, 2005), and a poor understanding of their essential habitat. The use of fisheries-dependent data enabled the area within 7.d, more coastal and temporal distribution to be modelled.

Studies using fisheries dependent data are not common due to the biases of fisheries data (i.e. targeting a species rather than sampling randomly) (Pennino et al., 2016). However, measures were implemented into the model to reduce spatio-temporal bias and presence over estimations. For example, mixed binomial models were used to reduce the effect of gear catchability, and only gear types with an even spatio-temporal coverage were selected. Furthermore, the fishery observed data used did not target skates, and therefore removes spatial bias resulting from over estimation of abundance.

Fisheries-dependent and independent data comparative studies (e.g. Bourdaud et al., 2017; Pennino et al., 2016), have shown that distribution models using such data are complementary and coherent to

Table 3
Discriminatory power of the 10 km^2 gridded statistical models in relating species presence absence to the measured environmental variables.

Model	Species	Sample number	% 0	AUROC	Confusion matrix	Model P < value
PA	*R. undulata*	2472	70	0.72	0.71	0.001
	R. clavata	3455	73	0.81	0.79	0.001
	R. montagui	8624	88	0.83	0.90	0.001
Juvenile	*R. undulata*	1641	81	0.91	0.92	0.001
	R. clavata					
	R. montagui					
Mature	*R. undulata*	4031	84	0.79	0.83	0.001
	R. clavata	5829	78	0.79	0.79	0.001
	R. montagui	1263	83	0.83	0.82	0.001
Female	*R. undulata*	8922	76	0.76	0.79	0.001
	R. clavata	13,971	76	0.79	0.78	0.001
	R. montagui	9200	81	0.84	0.81	0.001
Male	*R. undulata*	7255	80	0.70	0.79	0.001
	R. clavata	8621	72	0.70	0.72	0.01
	R. montagui	3147	77	0.79	0.79	0.01

Table 4
Summary of the model of best fit predictor variables effect for the length models for each species. R = rock, Cg = course grain, S = sand, M = mud. A = autumn, Sp = spring, Su = summer, W = winter, ↑ = increase, ↓ = decrease.

Species	Predictor variable	Effect	P value
R. undulata	Depth: Season	↑ Au & Sp > Su & W	0.0001
	Salinity: Season	↑ W & Su > Au & Sp	0.0001
	Latitude	↓	0.0001
	Sediment type	R > Cg > S & M	0.0001
R. clavata	Depth: Season	↑	0.0001
	Salinity: Season	↑	0.0001
	Sediment type	Cg & R > S & M	0.001
	Chlorophyll *a*	↓	0.0001
	Turbidity	↓	0.001
R. montagui	Salinity: Season	↑ Sp > A & W > Su	0.0001
	Sediment type	Cg > S	0.0001
	Turbidity	↓	0.0001

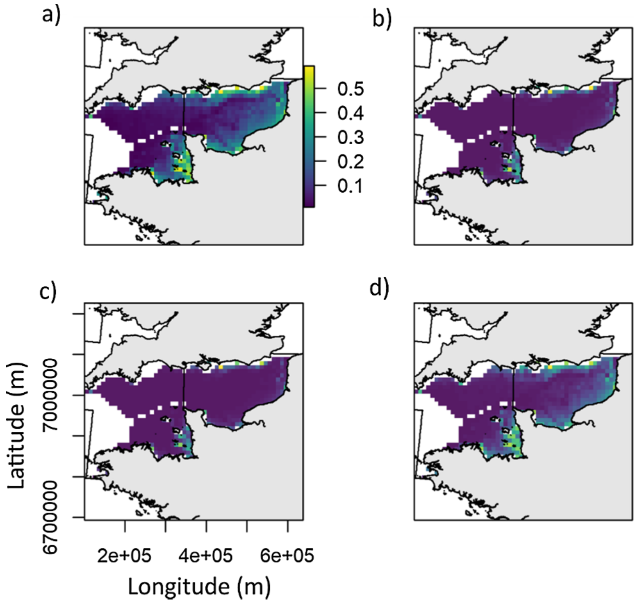

Fig. 3. Juvenile *Raja undulata* predicted distribution maps (10 km^2 cells) per season (a) spring (b) summer (c) autumn and (d) winter. The legend represents the probability of presence. Black solid lines delineate ICES statistical divisions.

independent models. The use of dependent data can provide more insight into species' temporal behaviour as a result of the data collected throughout the year (Bourdaud et al., 2017; Pennino et al., 2016). Furthermore, fisheries-dependent data is a relatively abundant and cheap method to acquire data on fish and therefore ideal for data deficient species.

4.2. Life history trait differences demonstrating the need for specific management measures

Raja undulata had a coastal distribution, with the highest presence off the coast of north-east Brittany (ICES division 7.e). *Raja clavata,* the thornback ray's distribution was greatest within the eastern English Channel (ICES division 7.d). *Raja montagui*, the spotted-ray's distribution was concentrated to the south of Ireland (ICES division 7.g). Similar distributions in *R. clavata* and *R. montagui* were observed by Silva et al. (2012) between 2002 and 2010, using observer data from English-registered commercial vessels around the British Isles. Coelho and Erzini (2006), Moura et al. (2007) and Ellis et al. (2011) also observed coastal distributions in *R. undulata* within English and Portuguese waters.

The southern offshore migration observed in *R. montagui* during winter months and the shallower more coastal distributions of *R. undulata* and *R. clavata* may be a result of decreased temperature. Global warming climate change-driven effects have been found to influence the distribution of *R. clavata* and *R. montagui* in the North Sea, where both species were found to have a preference for warmer temperatures (Sguotti et al., 2016). Temperature was not modelled due to collinearity with season. The higher presence of *R. montagui* in winter than summer months may benefit the survival of this species, as a result of reduced number of fishing hauls in winter.

Few studies have undertaken ontogenetic shift habitat models due to the complexities involved (Robinson et al., 2011; Seitz et al., 2014). Results from *R. undulata's* length-based models highlight potential spatio-temporal nursery habitats in coastal areas within ICES division 7.e during springtime. The latter results are in line with previous research which highlight estuaries and inshore areas as important nursery areas for *R. undulata* (e.g. Moura et al. 2007; Ellis et al. 2012; Serra-Pereira et al. 2014). Particular spatial-temporal patterns for mature skates were not observed from the generic models, other than deeper waters with more rugose sediment type (e.g. coarse grain and rock).

Spatio-temporal sex variations were observed for the skates studied. Presence of female *R. undulata* and *R. clavata* were slightly higher in offshore waters in summer and autumn than for males. Whereas for *R. montagui*, a lower male presence was observed in summer. Information on the life cycle of skates is sparse and varied between regions (e.g. Ellis et al., 2012, 2004; Serra-Pereira et al., 2014; Walker et al., 1997). Reproduction of *R. undulata* is supposed to occur between winter and spring, with egg-laying occurring shortly after (Moura et al., 2007; Serra-Pereira et al., 2015). Whereas, the reproductive strategy for *R. clavata* and *R. montagui* is supposed to peak in summer (Koop, 2005; Serra-Pereira et al., 2011). The offshore female migration observed may be a form of size and sex segregation. Size and sex segregation have been observed in other species (e.g. Gadoids, *Dissostichus eleginoides*, the Patagonian toothfish and other species of skate), and may help maximise juvenile survival and avoid competition (Elliott et al., 2017; Hoff, 2010; Péron et al., 2016).

The species and ontogenetic differences observed within the distribution models undertaken, demonstrate the importance of specific management measures. The more inshore distribution of *R. undulata* (particularly during their vulnerable juvenile stages), than *R. clavata* and *R. montagui*, may expose *R. undulata* to increased anthropogenic pressure (Costanza, 1999; Halpern et al., 2008b, 2008a). Coastal waters are subject to a wider range of marine and terrestrial related pressures such as agricultural run offs, a wider range of fishing activities, aggregate dredging, etc. Whether conservation effort should be focused on mature females or juveniles is a long standing debate in many species

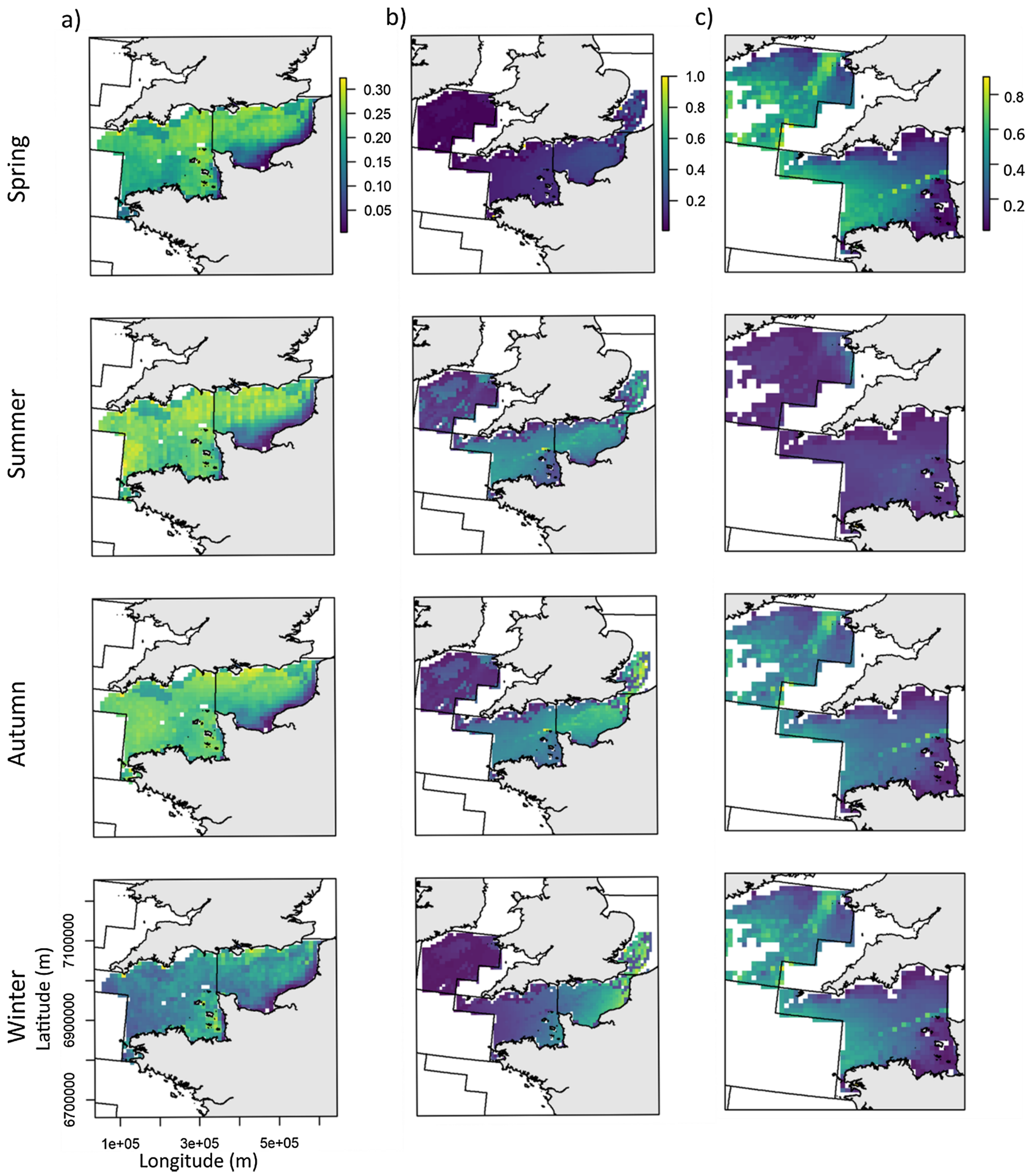

Fig. 4. Mature (a) *Raja undulata* (b) *Raja clavata* (c) *Raja montagui* predicted distribution maps (10 km^2 cells) per season (three month period). The legend represents the probability of presence. Black solid lines delineate ICES statistical divisions.

(e.g. turtles) (James et al., 2005). Frisk et al. (2002) found that reducing juvenile skate mortality yielded in the greatest population growth rate. Given the temporal and ontogenetic shift variation observed in *R. undulata*, spatio-temporal management measures during particular life history stages (i.e. juvenile stages), may be of benefit to its conservation.

More detailed essential habitat analyses are required. Stable isotope analysis can provide detailed understanding of species' spatial movement in addition to trophic structures, according to their nitrogen and carbon signatures (e.g. Hussey et al., 2015b). The later would provide more detailed understanding of potential biotic interactions. Telemetry studies can also provide information on species' movement during reproductive, spawning and nursery stages, which would provide key information to be able to protect species during their essential life history phases (e.g. Hussey et al., 2015a). These methods are, however, more costly and time consuming.

4.3. Implications for management and conservation

Although *R. undulata* and *R. clavata* are IUCN red listed species, their stocks have increased in recent years (ICES, 2017a; 2018a). An increase in TAC within French waters is being discussed for *R. undulata* (ICES, 2018b). Stocks can, however, fluctuate largely from year to year, so caution should be taken before reintroducing TACs to protected species.

High bycatch rates in species can prevent fishing vessels from going out and fishing their targeted catch (Mortensen et al., 2018). Examples of targeted species in which bycatch of skates occur include that of sole, monkfish, cuttlefish and mixed demersal fisheries. Under the European Union Common Fisheries Policy, bycatch restrictions are being

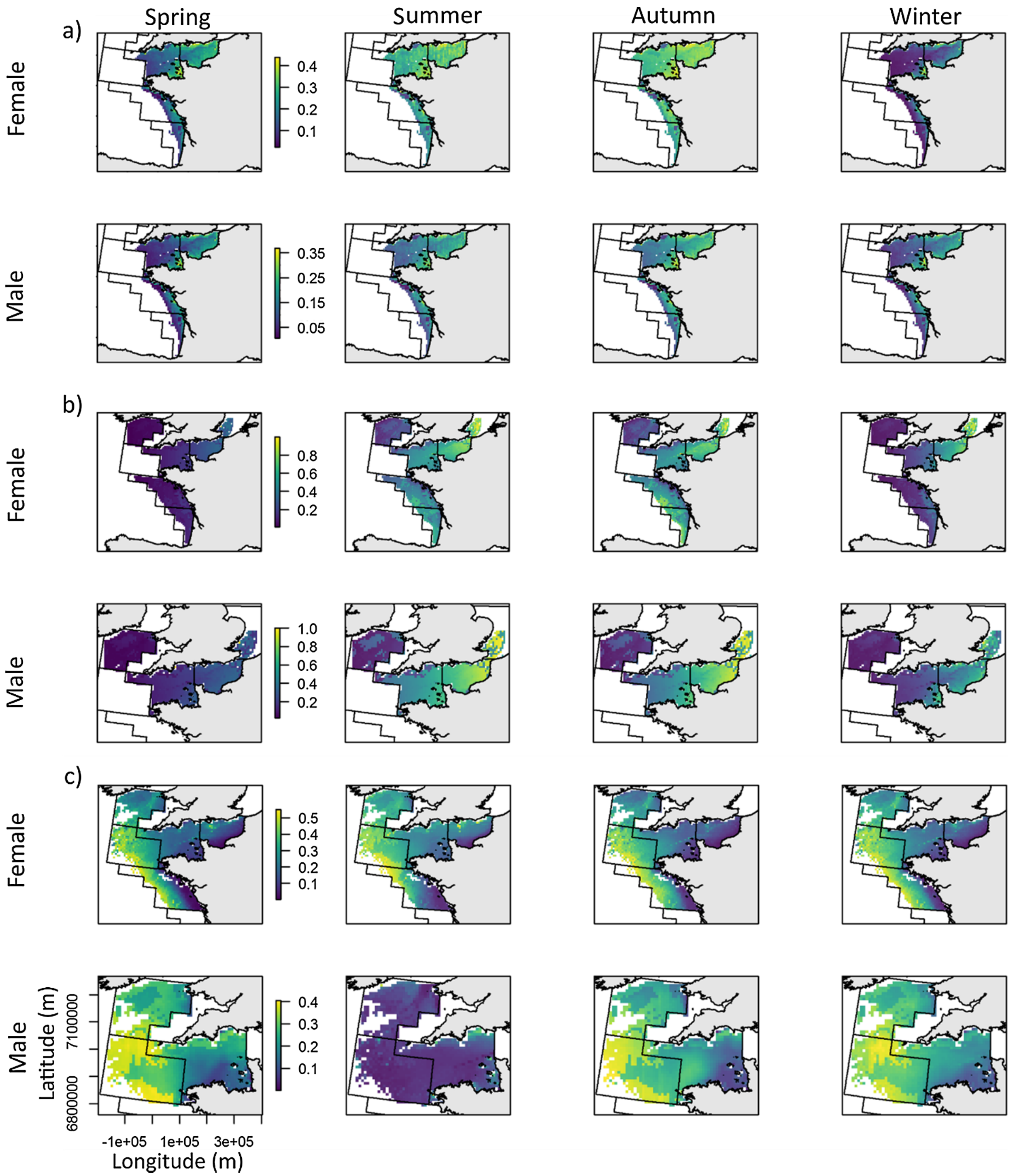

Fig. 5. Female and male (a) *Raja undulata* (b) *Raja clavata* (c) *Raja montagui* predicted distribution maps (10 km^2 cells) per season. The legend represents the probability of presence. Black solid lines delineate ICES statistical divisions.

implemented so that all species with TAC are required to be landed and not discarded (EC 1380/2013; Mortensen et al., 2018). At present (2019), there is an exemption of the landings obligation for skates based on their supposedly high survival rate. More detailed studies on skate discard survival are required.

Through the understanding of species distributions during their different life history stages and in particular using fisheries-dependent data, the avoidance of bycatch of the species in question can be undertaken (Ellis et al., 2017). Here, *R. undulata* were observed closer to the coast with particular hotspots along French and Southern English coasts than the other two species of skate. Given the ontogenetic shift variation, bycatch of *R. undulata* could be minimised by avoiding fishing activity during certain times of the year at set locations (i.e. during springtime or within hotspot coastal areas).

Implementation of protective spatial measures has been criticised due to the 'unintended consequences' displacement activities (e.g. additional damage to the marine environment and non-targeted species, lack of focal species recovery, economic losses) (Hilborn et al., 2004; Kaiser, 2005). Nonetheless, carefully planned fisheries spatial and or temporal closures, focusing on 'essential fish habitats' and avoiding areas where fishing effort is high, can prevent 'unintended consequences' through stock recovery (Hiddink et al., 2006; Kaiser, 2005).

4.4. Conclusion

Within this study the distribution of three supposedly sympatric species of skate with different conservation status were modelled on a wider scale than has been previously undertaken. Results expose the large variation in habitat use between species, demonstrating the importance of species-specific management measures. The inshore habitat use of *R. undulata* may lend this species to be more vulnerable than other species of skate found within Eastern Atlantic waters as a result of the increased coastal anthropogenic activity. In addition, the wider spatial distribution of *R. clavata* and *R. montagui* may lend these skates to being more resilient to anthropogenic activities. More detailed studies need to be undertaken to understand the effect of fishing pressure on these species, including thresholds to which they can tolerate. Given the supposedly high bycatch rate in *R. undulata*, more detailed analysis in abundance trends are required.

To reduce bycatch of *R. undulata*, knowledge provided here on their spatio-temporal distribution is essential. The latter could help fishers avoid areas with high concentrations of the species in question. We recommend the use of fisheries observer data in conjunction with knowledge from fisheries-independent surveys, to widen our ecological knowledge of species of conservation and commercial importance. Undertaking spatio-temporal distribution models at different life history stages can help understand reasons for the vulnerability of species, whilst reducing their bycatch.

Declaration of Competing Interest

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.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2019.102256.

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