Determining long- term changes in a skate assemblage with aggregated landings and limited species data

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Abstract :

Sustainable fisheries management requires assessment of exploited populations and communities. Traditional fisheries stock assessment methods need species-specific input data, which for skates have only recently become available in Europe. To overcome this limitation, a Bayesian multispecies biomass production model was developed. In addition to aggregated landings, input data are short time series with species-specific information (landings and biomass indices). Applying the approach to four main skate species and a group of two skate species, all managed together in the Bay of Biscay (Northeast Atlantic), long-term changes in the skate assemblage composition were identified. Since the 1990s, Leucoraja naevus became increasingly dominant, while the contributions of the other three species (Raja brachyura, Raja clavata and Raja montagui) declined. The abundance of the grouped Leucoraja fullonica and L. circularis has also strongly decreased, suggesting long-term overexploitation. All species except this species group are expected to increase over the next decade under current harvest rates. Currently, the species considered here are managed under a single fishing quota making it unlikely that the group of the two most depleted species will recover soon. The multispecies modelling approach bears promise for other harvested assemblages for which only grouped harvest information is available for certain periods.

Keywords : community changes, fishing impacts, multispecies management, multispecies model, Rajiformes, species composition, vulnerable skates

Acknowledgements

Introduction

A major objective of ecosystem-based fisheries management is to maintain species and size diversity within exploited ecosystems (Livingston, Aydin, Boldt, Ianelli, & Jurado-Molina, 2005). Rajiformes, hereafter referred to as "skates", is a species-rich order containing some 382 species out of ca. 1209 elasmobranchs species and, whilst morphologically conservative, this order displays a range of life-history traits (Dulvy et al., 2017; WoRMS Editorial Board, 2017). Elasmobranchs display relatively low fecundity and high sensitivity to overfishing (Stevens, Bonfil, Dulvy, & Walker, 2000).

A lack of fishing limits, habitat loss, and climate change resulted in a decline of several elasmobranch populations around the world during the 20th century (Dulvy et al., 2014; Dulvy et al., 2017; Quéro & Cendrero, 1996). In the North Sea the European Union (EU) introduced fishing quotas for skates only in 1999, which were generalized to all EU Atlantic waters, including the Bay of Biscay, in 2009 (EC, 1999, 2009). This lack of management prior to 1999 led to changes in species composition: in the southern North Sea, the elasmobranch assemblage shifted from larger species to smaller and more productive species between 1902 and 2013 (Sguotti, Lynam, Garcia-Carreras, Ellis, & Engelhard, 2016). Similarly, a change in elasmobranch community composition over the last half century was found in the Adriatic Sea (Ferretti, Osio, Jenkins, Rosenberg, & Lotze, 2013). The main driver of this change was overexploitation (Barausse et al., 2014). In both areas the large bodied angel shark (*Squatina squatina,* Linnaeus, 1758) has been extirpated (Ferretti et al., 2013; Sguotti et al., 2016). This species was once also rather common in the Bay of Biscay (Quéro & Cendrero, 1996). Globally, predation release seems to have been an important driver for increases in certain skate species, with reduced fishing mortality playing a smaller role (see review in Ward-Paige, Keith, Worm, and Lotze (2012)).

In the last decade, the majority of reported landings of skates from the Bay of Biscay comprised four ray species: blonde ray *Raja brachyura* Lafont, 1871; thornback ray *Raja clavata* Linnaeus, 1758; spotted ray *Raja montagui* Fowler, 1910 and cuckoo ray *Leucoraja naevus* (Müller & Henle, 1841) (ICES, 2016). The main fisheries exploiting skates in the Bay of Biscay are trawl fisheries, which have represented 70% and 90% of landings of *R. clavata*, *L. naevus L. fullonica and L. circularis* respectively in recent years (ICES, 2017, 2018a). *R. clavata* is also caught by coastal small-scale longlining and netting. The more coastal *R. brachyura* and *R. montagui* are primarily landed by vessels using passive gears ((ICES, 2018d, 2018f)). The large contribution of trawling to catches of skates prevailed during and even before the study period (Du Buit, 1974; Letaconnoux, 1948) making skates primarily a bycatch of fisheries for the main bentho-demersal species such as hake, monkfishes, sole and megrim. Like elsewhere in European waters, fishing effort increased in the second half of the 20th century, generating harvest rates in excess of maximum sustainable yield (MSY) levels from the 1960s for numerous teleost stocks, and started decreasing at the turn of the 21st century (Fernandes & Cook, 2013; Mesnil, 2008). Two other skates species, sandy ray *Leucoraja circularis* (Couch, 1838) and shagreen ray *Leucoraja fullonica* (Linnaeus, 1758), are also present in recent landings with indications for higher past abundances at least in the northern part of the Bay of Biscay (Du Buit, 1974). These six species (*R. brachyura*, *R clavata*, *R. montagui*, *L. circularis*, *L. fullonica*, and *L. naevus*), were therefore considered in this study. Other Rajiformes occurring on the Bay of Biscay shelf and upper slope include undulate ray *Raja undulata* Lacepède, 1802; small-eyed ray *Raja microocellata* Montagu, 1818; white skate *Rostroraja alba* (Lacepède, 1803), *Dipturus batis* (Linnaeus, 1758) complex (blue skate composed of two species) and longnose skate *Dipturus oxyrinchus* (Linnaeus, 1758). These other species were not considered because they have either been subject to landing bans since 2009, occur at low abundance, or data are even more uncertain

than for the six species studied here. The studied species are small- to medium-sized skates occurring from shallow waters to the shelf break and have uncertain life history trait (Supporting information S1, Table S1.1).

Except for rare cases with very long survey time series (e.g. North Sea, Sguotti et al. (2016)), estimation of long-term time trends of skates has to rely on fishery-dependent data which unfortunately is hampered by low abundances commonly resulting in insufficient observations (Kuhnert, Griffiths, & Brewer, 2011). Whilst there have been improvements to the species-specific reporting of skate landings since 2009 (EC, 2009), landings prior to this were generally reported as "miscellaneous rays and skates" if not "miscellaneous sharks and rays". In order to investigate long term changes in the Bay of Biscay skate assemblage in such a data limited situation, a multispecies biomass model that uses historic landings aggregated across species and more recent species-specific landing and survey time series was developed. To account for uncertainty in landings and survey time series as well as in life history information, a Bayesian approach was used to fit the multispecies model. The effect of different data combinations and variants of prior information on species and composition time trends was explored. The main aim was to obtain robust estimates of time trends in a data limited situation which is rather common for species which are not the main target of fisheries and hence do not benefit from appropriate sampling and recording programs.

Methods

Data

All data are available in supporting information (Supporting information S3).

Commercial landings and fishery

Aggregated commercial landings for the studied species for the period 1950 to 2008 were derived from official landing statistics (see Supporting information S1). Species-specific landings were available for 2009-2016 and used to account for removals from the fishery and as data source to inform on recent species composition.

Biomass indices

Biomass indices were calculated for each species using data from the scientific bottom trawl survey (EVHOE - ÉValuation des ressources Halieutiques de l'Ouest de l'Europe) carried out in the Bay of Biscay from 1987 to 2016 (with missing years when the considered species were not observed or no survey was carried out) (Figure 1b-f; description of index calculation in Supporting Information S1). For *L. naevus* and the three *Raja* species, the time series was expanded using data from 1973 and 1976 collected with the same trawl and sampling plan (but limited to depths shallower than 200 m). For *L. fullonica* and *L. circularis*, as the number of individuals caught in the survey was small leading to very imprecise indices, data were combined into a single "other *Leucoraja* spp.*"* index and biomass indices were calculated using hauls from the Bay of Biscay and the adjacent Celtic Sea to cover the spatial distribution and increase the number of individuals caught. Consequently, biomass indices of *L. naevus* and *Raja* species were available for the years 1973, 1976 and 1987-2016 (including missing years) and for other *Leucoraja* spp. for 1997-2016 (including missing years).

Modelling

Model

The state-space biomass production model is a multispecies extension of the discrete-time model developed for thornback ray by Marandel, Lorance, and Trenkel (2016), see Table 1.

To overcome the lack of species-specific landings before 2009, the probability of aggregated landings having been from species e in year t was assumed to correspond to estimated biomass proportions in the previous year t-1. This assumption implies that there was no species-specific targeting before 2009 and fisheries selectivity for each species was constant over time and among species.

The observation model links population biomass to the biomass indices. Assuming landings are proportional to species biomasses, observed species-specific landings for 2009-2016 were also used to inform biomass composition for these years.

Model fitting and runs

The model was fitted using a Bayesian approach. Information on prior distributions and other technical issues can be found in the supporting information S1. In brief, informative priors were created for intrinsic growth rates r_e (Supporting information S1, Table S1.2) using life history parameters (McAllister, Pikitch, & Babcock, 2001) while uninformative priors were used for carrying capacities K_e (table 2). The prior for the process variance σ^2 was chosen to be moderately informative while the observation variances (τ^2 for biomass indices and ρ^2 for species composition in landings) were assumed known (Table 2). For survey catchabilities q_e the priors had most mass <0.5, for this Beta(1,3) was used for all species.

As no information was available concerning the initial relative biomass of each species in 1950, two sets of priors were tested for $Y0_e$ (see Table 1) corresponding to two depletion hypotheses (Table 2). For the BASE run, all species were assumed underexploited in 1950 (prior mode $Y0_e$=0.8) (see Table 2). For the EXPL run, all species were assumed fully exploited in 1950 (prior mode $Y0_e$=0.5). In addition, to evaluate the impact of corrections made of the aggregated landings (described in Supporting information S1) a third run called SHORT was carried out using a shorter time series during which little landings corrections

were made and biomass indices were available. The SHORT run used landings from 1973 and assumed all species were fully exploited in 1973. The BASE and the EXPL runs were compared using the DIC (Deviance Information Criterion) and residuals were inspected to assess model fit.

Analyses

Changes in estimated species composition were studied in terms of the relative contribution of each species to total assemblage biomass. To evaluate the impact of fishing, harvest rates were calculated for each species by dividing estimated (known after 2009) landings by estimated biomass in each year (Table 1). Harvest rates where standardized by dividing them by the harvest rate leading to maximum sustainable yield harvest rates (Table 1).

To explore recovery potential under current (*status quo*) harvest rates, populations of all species, except *L. naevus* (no recovery needed), were simulated forward 10 years assuming constant harvest rates (mean for 2014-2016). To evaluate the effect of harvest reduction on species recovery constant harvest rates set at 0.5 *status quo* and no harvest were also simulated. The robustness of these projections was evaluated by comparing them to projections carried out starting from the fitted SHORT run and a shortened BASE run for which the 2016 data was removed.

The BASE run assuming underexploitation in 1950 was thought to be the most realistic run as French fishing power increased until the early 1990s (Mesnil, 2008). Further, hake, megrim and sole stocks (the only demersal stocks occurring in the Bay of Biscay with long time series assessed by ICES) were still above SSB$_{MSY}$ in the early 1980s (ICES, 2018b, 2018c, 2018e). Therefore results are presented primarily for the BASE run.

Results

Model runs

For all model runs posterior distributions for $Y0_e$ were identical to prior distributions indicating that the data did not permit estimating the initial depletion levels (Supporting information S2, Fig S.2.1). Model fits for the two depletion runs were identical (BASE DIC=1434; EXPL DIC=1434). Detailed results for the SHORT and the EXPL runs are provided in supporting information S2. Residuals of smoothed biomass indices and species-specific landings indicated satisfactory model fit (BASE run Figure S2.2 and S2.3).

Assemblage changes

Without exploitation, populations are expected to vary around their carrying capacity (K). In this situation, based on posterior mean estimates of K, the smallest species *L. naevus* was estimated to be the most abundant species (38% of assemblage biomass), followed by the other *Leucoraja spp.* (27%) and *R. clavata* (17%) (Figure 2a and Figure S2.4). *R. brachyura* and *R. montagui* were estimated to have the smallest biomass contributions (8% and 9% respectively).

The mean estimated species composition in 1950 was driven by the prior distributions for $Y0_e$ and hence similar to the unexploited situation (Figure 2b). Between 1950 and 1991 the estimated proportion of *L. naevus* remained constant with a small decrease in the 1970s, whilst *R. clavata* increased to 41%, thus becoming the dominant species (in biomass). After this *L. naevus* increasingly dominated the species composition, reaching 63% of the assemblage biomass in 2017. The estimated proportions of *R. brachyura* and *R. montagui* continuously decreased until 2010 and increased thereafter. The estimated proportion of other *Leucoraja* spp. decreased continuously over the study period. The species composition results

were insensitive to assumptions regarding initial depletion and time series length (see Figure S2.4 for results for EXPL and SHORT runs).

In the observed landings, the proportion of *L. naevus* decreased slightly from 78% in 2009 to 66% in 2016, while those of all other species except *R. clavata* increased (Figure 2c). The observed landings composition in 2009 was similar though not identical to the estimated assemblage composition in the same year.

Population changes

The estimated biomass of all species, except *L. naevus*, decreased generally between 1950 and around 2009 and increased over the most recent decade (Figure 3; Figure S2.5). *L. naevus* first decreased between 1950 and 1991 (-2.1% per year) and increased thereafter (+1.8% per year); the overall decrease between 1950 and 2017 was 20%. Its biomass in 2017 was estimated to be close to 64% of its carrying capacity (95 percentile interval: 46-83%). The decrease of *R. clavata* strongly accelerated after 1995 with the 2017 biomass being at around 40% of carrying capacity (95 PI: 25-55%). *R. montagui* decreased until 1995 (-1.94% per year), initially strongly, and increased after 2008 (+12% per year); its 2017 biomass was at 40% of carrying capacity (95 PI: 18-66%). *R. brachyura* followed a similar pattern with a strong decrease until 2009 (-1.65% per year) and an increase thereafter; the biomass in 2017 was estimated at 25% of carrying capacity (95 PI: 8-44%). Other *Leucoraja* spp. reached the lowest biomass in 2000 and increased to 8% (95 PI: 10-17%) in 2017.

Between 1950 and 1980 estimated annual landings for *R. clavata, L. naevus* and the other *Leucoraja* spp. were generally above 1 000 t, decreasing thereafter for all species (Figure 3, Figure S2.6). Until the early 1990s relative harvest rate estimates indicated overexploitation for all species, in particular other *Leucoraja* spp. (values >1 in Figure 3, Figure S2.7). After

2011 harvest rates were estimated to be at or below MSY values for all species except for the other *Leucoraja* spp.

The highest carrying capacity *K* was found for the small offshore *L. naevus*, followed by other *Leucoraja spp.* and *R. clavata*. *R. brachyura* and *R. montagui* had similar estimated *K* (Figure S2.8). However absolute values are uncertain as there was a negative correlation between estimates of *K* and survey catchability *q* as well as between *K* and intrinsic growth rates *r* (Figure S2.12). The informative priors for *r* were somewhat updated for all species: posterior estimates were larger than priors for *L. naevus* and *R. clavata* while for the other species posterior estimates were smaller (Figure S2.9). The fact that the data contained information on *r* implies that the estimated maximum sustainable yield values were not completely determined by *a priori* knowledge. For the process error σ^2 prior and posterior distributions were identical (Figure S2.10).

Short-term projections

Projecting the two depleted species and the grouped species ($Y_{e,2017}$<0.4) forwards indicated that under current harvest rates *R. clavata* and *R. montagui* are expected to increase above 50% of carrying capacity (corresponding to the MSY biomass level) within the next five years (Figure 4). Even without fishing the other *Leucoraja* spp. are not expected to increase much by 2028 (from 8% of carrying capacity in 2018 to 12% in 2028). Under *status quo* harvesting *R. brachyura* is predicted to increase to 41% (PI 16-66) of carrying capacity within ten years, halving the harvest rate would make it reach the same depletion level within around seven years.

The projections results for the SHORT run and the shortened BASE run were generally similar, thus confirming the robustness of projections, except that *R. clavata* is predicted to take around three years longer for the shortened BASE run to reach MSY biomass (Figure

S2.11). For *R. montagui* the SHORT run estimated population biomass to be already at MSY level in 2017.

Discussion

Understanding changes in exploited elasmobranch communities is challenging, as it requires disentangling the effects of exploitation and changes in predation, competition and environmental conditions, in a data limited situation (Ferretti et al. 2013). To overcome the data limitation for skates in the Bay of Biscay, in particular the lack of species-specific landings for most of the time period, a Bayesian approach simultaneously modelling all species was developed. Applying this approach indicated that the total biomass of the six considered skate species has declined strongly in the Bay of Biscay since the 1950s. In 2017, only *L. naevus* was estimated to be above 50% of its carrying capacity; three species (*R. brachyura, R. montagui* and *R. clavata)* were estimated to be between 20 and 40% of their carrying capacity while the grouped other *Leucoraja* spp. were estimated to be <10%. Whilst the actual values are uncertain, the relative order of species should be more robust. Comparable composition changes have been reported in the Irish Sea, where *L. naevus* increased and *R. clavata* and *R. montagui* decreased between the early 1960s and the 1990s (Dulvy, Metcalfe, Glanville, Pawson, & Reynolds, 2000).

The assemblage composition in 1950 might have been close to what would be expected without fishing. In contrast, since the 1990s the small offshore *L. naevus* increasingly dominated the assemblage, while the contribution decreased for the populations of medium-sized species, the offshore other *Leucoraja* spp. and the coastal *R. brachyura*. For all species, harvest rates throughout most of the 67 years were larger than those leading to maximum sustainable fisheries yield, indicating overfishing by coastal fisheries as well as fisheries on the continental slope as a major factor for their strong decline. While *L. naevus* is also found

on the continental slope, its higher intrinsic growth rate compared to the other *Leucoraja* spp. might explain why it sustained exploitation better. For *R. clavata,* the wide bathymetric distribution, from coastal to the upper continental slope (Supplementary information S1, Table S1.1), might have created refuges from fishing, as there is little targeted skate fishing, except in coastal areas. Analysing data from the Celtic Sea, Shephard, Gerritsen, Kaiser, and Reid (2012) concluded that the spatial heterogeneity of fishing created refuges for elasmobranchs in this area. To evaluate the potential refuge effect in the Bay of Biscay, an analysis of the spatial overlap of fishing and species distributions would be needed. Unfortunately, the spatial coverage of the bottom trawl survey was insufficient in coastal waters for the data to be useable for such an analysis. Further, the insufficient coverage of coastal waters might have hampered derivation of robust biomass indices for *R. brachyura* and *R. montagui* which are primarily found in coastal waters. Hence the results for these two species should be interpreted with caution. Further, as the spatial distribution of *L. circularis* and *L. fullonica* extends further offshore than the survey area, any changes in spatial distribution will have biased biomass indices. However, we do not know of any evidence for such changes.

Prior to the 2000s, skate catches were mostly unmanaged in European waters. The total allowable catch (TAC) for Rajiformes, introduced in 2009 in the study area, may not have been limiting from the start but has been reduced from 6400 t in 2009 to 3400 t in 2016 with this TAC covering both the Bay of Biscay and the western Iberian shelf. As a reaction to the limited catch opportunities, some fishers' producer organisations and governments have added various rules, such as a cap on landings per trip and minimum landing sizes. For example in France, skates smaller than 45 cm total length cannot be landed (JORF, 2017) and are therefore discarded at sea. As skates have been considered to be amongst the fish species that might survive discarding (Depestele, Desender, Benoit, Polet, & Vincx, 2014; Knotek,

Rudders, Mandelman, Benoit, & Sulikowski, 2018; Morfin, Mehault, Benoit, & Kopp, 2017), discarding rather than landing all catches may have helped reduce fishing mortality. If this effect is sufficiently large, it should lead to an increase in biomass, though with some delay (Collie, Rochet, & Bell, 2013). Thus, the biomass increases observed in recent years for most species might at least partially be due to reduced fishing mortality caused by increased discarding in addition to reduced fishing fleet capacity (Mesnil, 2008). Unfortunately there is a lack of discard information to test this hypothesis.

Predation release is another factor which has been used to explain community changes (Myers, Baum, Shepherd, Powers, & Peterson, 2007; Shepherd & Myers, 2005; Ward-Paige et al., 2012). Several large elasmobranch species have declined in the Bay of Biscay, including *S. squatina* (Quéro & Cendrero, 1996), *D. batis* complex and *R. alba*. Stomach content information collected in the English Channel in the 1930s indicated that large (>120 cm) *D. batis* feed on both *R. montagui* and *L. naevus* (Pinnegar, 2014). Hence predation release might be a potential explanation for the more recent increase in *L. naevus* and *R. montagui,* though perhaps to a different degree for the two species. Large and small skates may also have overlapping feeding niches (Smale & Cowley, 1992), which could have led to competition release.

Assuming constant intrinsic population growth rates and carrying capacities over several decades is clearly a simplification. Changes in environmental conditions, habitat, competition and predation might have modified both parameters. Also, changes in the species composition of the benthos in favour of scavengers such as some gastropods, may modify predation rates on substrate-attached skate eggs (Lucifora & Garcia, 2004). Further, different factors are likely to have affected the six species in different ways. However, the developed model included a process error which accommodates unknown changes in r and K when estimating biomasses.

The multi-species Bayesian model provided an effective way for integrating aggregated landings with species-specific biomass indices and life history information (informative prior distributions for intrinsic growth rates) to study long-term changes for species which could not be investigated otherwise due to insufficient data, or only making even stronger assumptions.

Given the problem of aggregated landings is widespread (Reuter et al., 2010), we believe the approach has potential for being applied in other areas. To the best of our knowledge, only few published studies have modelled the abundance of data poor stocks abundance based on aggregated catches (but see Bell, Fogarty, and Collie (2014)). However, the suitability of the approach critically depends on the assumption of landings having been roughly proportional to biomasses (and vice versa for years with species-specific landings). This assumption might be relaxed if proxies of fisheries targeting are available. In this case, a model estimating the relative fisheries catchability of each species (or species group) could be developed.

Survey indices were smoothed after initial runs showed problems with model fitting. To improve raw indices and avoid the need for smoothing, survey spatial coverage and the number of hauls would need to be adapted to the spatial distribution and low density of skate species. For example, *R. brachyura* and *R. montagui* are primarily inshore species mostly abundant by depth <40m (Quéro & Vayne, 1997) while the EVHOE survey is mainly further offshore (Poulard & Trenkel, 2007). In contrast, the depth range (Supporting information S1, Table S1.1) *L. circularis* and *L. fullonica,* which were modelled as other *Leucoraja* spp., is well covered by the survey (around 90% of hauls are between 80m and 600m). Thus for these species the sampling plan might be well adapted in terms of spatial coverage, though not in terms of number of hauls.

In conclusion, the group of other *Leucoraja* spp. and *R. brachyura* were found to have decreased strongly during the study period and to have too high current harvest rates making them the primary species of concern for management. In contrast, abundant species, in particular *L. naevus*, seem to be able to sustain the current levels of harvesting.

Supporting information

Supporting information S1, S2 and S3 are available at the online version of the article.

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Tables

Table 1. Model equations, parameter description and variable distributions.

Model equations	Description	Distributions
General	*e* species *t* year	
Process model Population dynamics 1950 to 2008: $$Y_{e,t+1} \sim N\left((r_e + 1)Y_{e,t} - r_e Y_{e,t}^2 - \frac{C_{e,t}}{K_e},\ \sigma^2\right)$$ $$Y_{e,t} = \frac{B_{e,t}}{K_e}$$ $$Y_{e,1} = Y0_e$$ Predicting landings 1950 to 2008: $$\boldsymbol{C}_t \sim Multi(\boldsymbol{p}_t, C_{tot,t})$$ $$p_{e,t} = \frac{B_{e,t-1}}{\sum_e B_{e,t-1}}$$ Population dynamics 2009 to 2016: $$Y_{e,t+1} \sim N\left((r_e + 1)Y_{e,t} - r_e Y_{e,t}^2 - \frac{l_{e,t}}{K_e},\ \sigma^2\right)$$	$Y_{e,t}$ relative biomass $Y0_e$ relative biomass in 1950 σ^2 variance for relative biomass $B_{e,t}$ absolute biomass r_e intrinsic growth rate K_e carrying capacity $C_{e,t}$ predicted landings $p_{e,t}$ probability of landings being from species *e* $C_{tot,t}$ observed aggregated landings $l_{e,t}$ observed landings by species	Y: truncated normal ($Y_{e,t} \geq 0$) C: multinomial
Observation model Biomass index 1973 (1997) to 2016: $$I_{e,t} \sim N(q_e B_{e,t}, \tau_e^2)$$ Landings proportions 2009 to 2016 $$l_{e,t} \sim N\left(\frac{B_{e,t-1}}{\sum_e B_{e,t-1}} C_{tot,t}, \rho^2\right)$$	$I_{e,t}$ biomass index q_e survey catchability τ_e^2 variance of biomass index ρ^2 variance of landings proportions	I: truncated normal ($I \geq 0$) l: truncated normal ($l \geq 0$)
Harvest rates $$h_{e,t} = C_{e,t}/B_{e,t}$$ $h_{MSY} = r_e/2$	$h_{e,t}$ harvest rate h_{MSY} maximum sustainable yield harvest rate	

Table 2: Prior distributions and data used for model runs.

Run	Species	Landings	*r*~Beta mode, sd	*Y0*~Beta mode, sd	*K*~Uniform min,max	*1/σ²*~Gamma mode, sd
BASE	*L. naevus*	1950-2016	0.132, 0.05	0.8, 0.10	2000, 800 000	400,1
	R. clavata		0.105, 0.05	0.8, 0.10	2000, 250 000	400,1
	R. montagui		0.114, 0.05	0.8, 0.10	2000, 250 000	400,1
	R. brachyura		0.091, 0.05	0.8, 0.10	2000, 250 000	400,1
	Other Leucoraja spp.		0.098, 0.05	0.8, 0.10	2000, 250 000	400,1
EXPL	*L. naevus*	1950-2016	as above	0.5, 0.10	as above	as above
	R. clavata			0.5, 0.10		
	R. montagui			0.5, 0.10		
	R. brachyura			0.5, 0.10		
	Other *Leucoraja* spp.			0.5, 0.10		
SHORT	*L. naevus*	1973-2016	as above	0.5, 0.10	as above	as above
	R. clavata			0.5, 0.10		
	R. montagui			0.5, 0.10		
	R. brachyura			0.5, 0.10		
	Other *Leucoraja* spp.			0.5, 0.10		

Figure legends

FIGURE 1. a) Aggregated landings in tonnes for the Rajidae Species (Rajidae, Rajiformes, *Raja* spp, *L. naevus, L. circularis, L. fullonica, R. clavata, R. brachyura and R. montagui*) from (ICES 2017, 2016, 2011) and specific landings for *R. brachyura*, *R. clavata*, *R. montagui*, *L. naevus* and the other *Leucoraja* spp. from (ICES 2016). Survey biomass indices and smoothed indices for (b) *R. montagui*, (c) *R. brachyura*, (d) other *Leucoraja* spp*., (e) L. naevus* and (f) *R. clavata*.

FIGURE 2. a) Species composition at carrying capacity for the five studied species; b) Mean estimated species composition between 1950 and 2017; c) Observed species composition in landings between 2009 and 2016.

FIGURE 3. Estimated relative biomass between 1950 and 2017 (top row), landings (tonnes) between 1950 and 2016 (middle row) and relative harvest rates between 1950 and 2016 (bottom row) for the studied ray species (mean values with 95% percentile bands). Dashed horizontal lines for relative harvest rates correspond to maximum sustainable yield (h_{MSY}).

FIGURE 4. Projected relative biomass for three species and the species group under three harvest regimes (coded with color and linetype) (mean values with 95% percentile bands).
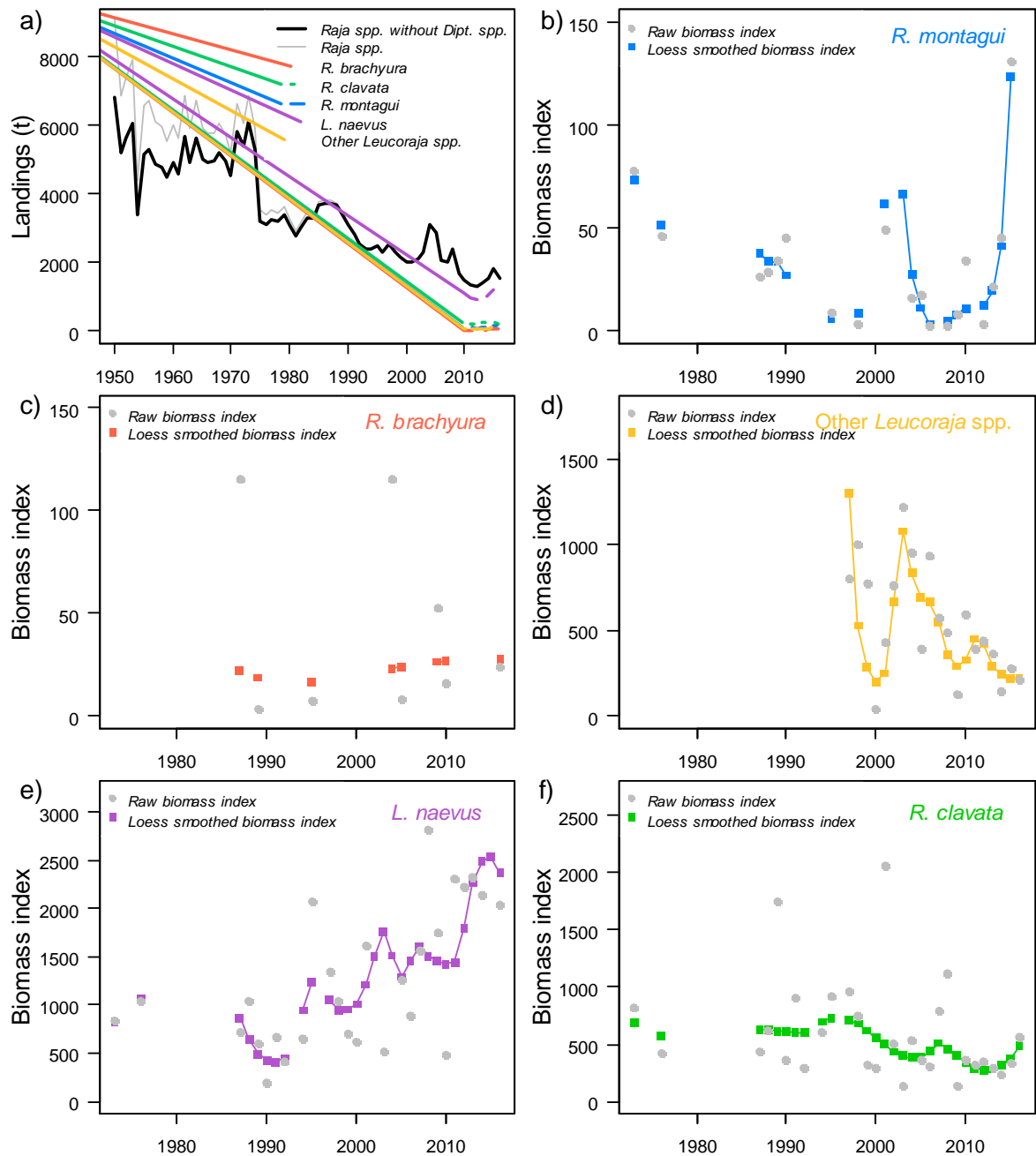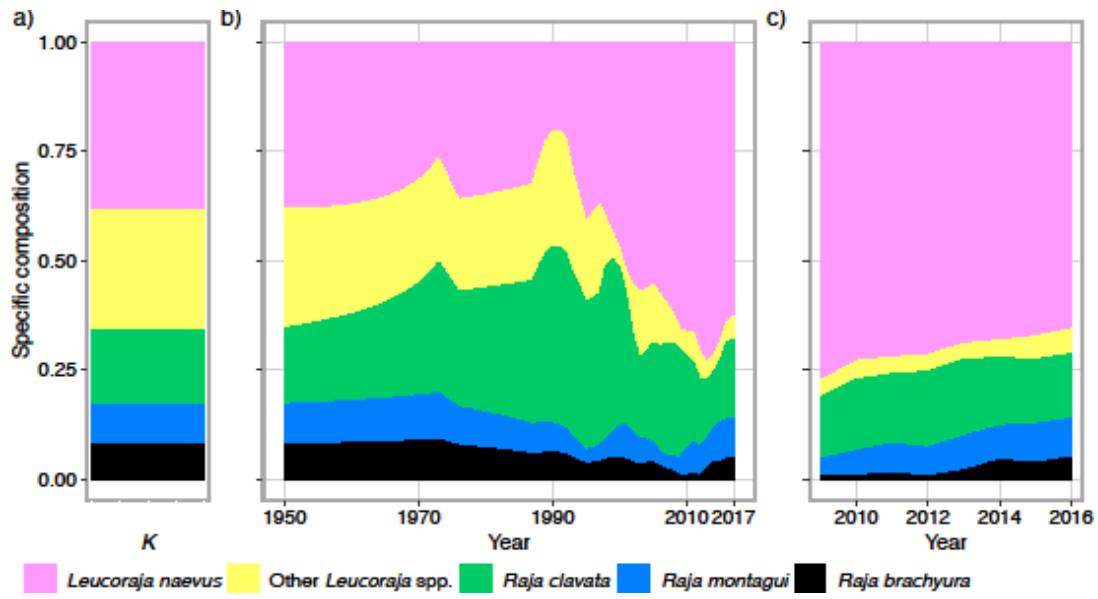
Figures

FIGURE 1. a) Aggregated landings of Rajiformes in tonnes from (ICES 2017, 2016, 2011) and species-specific landings for *Raja brachyura*, *R. clavata*, *R. montagui*, *Leucoraja naevus* and *L. fullonica* and *L. circularis* grouped as other *Leucoraja* spp. from (ICES 2016). Survey biomass indices and smoothed indices for (b) *R. montagui*, (c) *R. brachyura*, (d) other *Leucoraja* spp*., (e) L. naevus* and (f) *R. clavata*.

FIGURE 2. a) Species composition at carrying capacity for the five studied species; b) Mean estimated species composition between 1950 and 2017; c) Observed species composition in landings between 2009 and 2016.
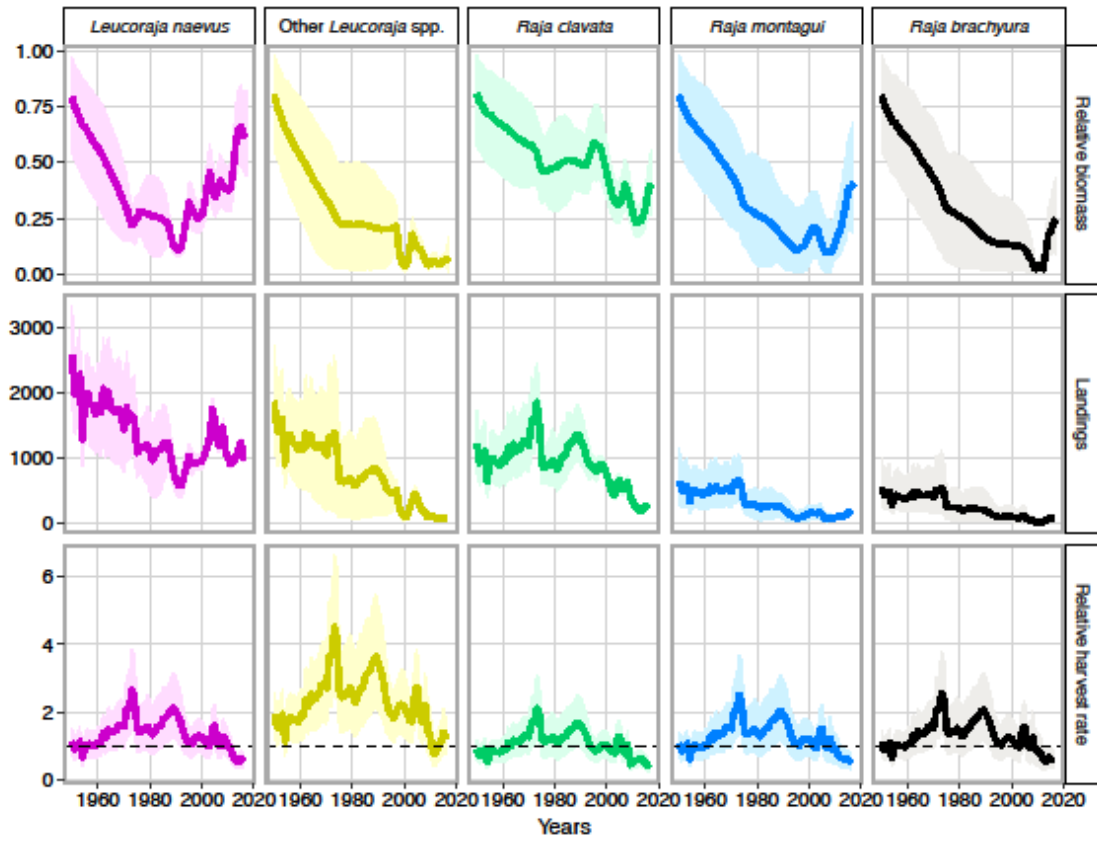
FIGURE 3. Estimated relative biomass between 1950 and 2017 (top row), landings (tonnes) between 1950 and 2016 (middle row) and relative harvest rates between 1950 and 2016 (bottom row) for the studied ray species (mean values with 95% percentile bands). Dashed horizontal lines for relative harvest rates correspond to maximum sustainable yield.
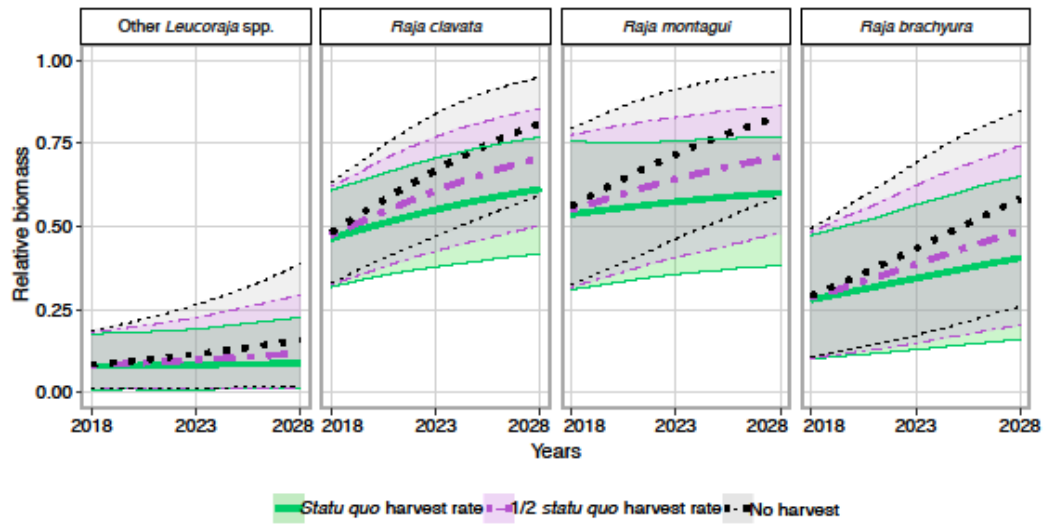
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