



# Patterns of extirpation. I. Changes in habitat use by thornback rays *Raja clavata* in the German Bight for 1902–1908, 1930–1932, and 1991–2009

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**ABSTRACT:** Abundance trends and distribution were analyzed for thornback rays *Raja clavata* in the German Bight (eastern central North Sea) for 3 periods: 1902–1908, 1930–1932, and 1991–2009. Abundances declined until 1932, and after 1991 only 4 specimens were encountered in the area during standard fisheries surveys. During the first period, thornback rays inhabited almost the entire German Bight, while a range reduction was observed for the second period and again after 1991. In the first period, thornback rays were negatively associated with gravel and mud, while no sediment parameter appeared to be significant in the 1930–1932 period. Temporal differences are interpreted as differential impacts of fisheries. At low fishing pressure, habitat associated with feeding grounds was occupied by thornback rays, while with increasing fishing pressure, in accordance with the interference hypothesis, less risky habitat was occupied and as such was less associated with feeding grounds, before fishing pressure ultimately caused extirpation. Local fishing mortality observed in all 3 periods exceeded the extinction level mortality ( $F_{\text{ext}} = 0.84$ ). The shift in habitat use is discussed with respect to the designation of marine protected areas based on distributions of species already under pressure.

**KEY WORDS:** Natura 2000 · North Sea · Trophic cascades · German Bight · Historic time series · Elasmobranchs

## INTRODUCTION

Significant changes in exploited marine populations appeared before any systematic collection of survey and fisheries information commenced. In particular, elasmobranch species were among the first to decline significantly (Jackson 2001, Ferretti et al. 2010) given their high vulnerability to fishing (Jennings et al. 1998, Dulvy et al. 2000, Rogers & Ellis 2000, Stevens et al. 2000, García et al. 2008).

Skate fisheries in the German Bight (Fig. 1) date back to the 15<sup>th</sup> century (Schnakenbeck 1928), and narrative fisheries information indicates that skates have always been an important by-catch in the coastal longline fisheries, with maximum catches of 1000 specimens d<sup>-1</sup> observed in the early 1800s on the German island of Amrum. Mainly 'Nagelrochen'

(thornback ray *Raja clavata*, a coastal species), but also 'Glattrochen' (mainly common skate *Dipturus batis*, from deeper waters offshore; see Heincke 1894) were landed from the German Bight. Whereas the elasmobranch fishery in the northern part of the German Bight ceased in the mid-1800s in favor of whaling in distant waters (Schnakenbeck 1928), it continued until 1907/8 in the southern area (Schnakenbeck 1928) after having peaked there in the mid-1890s in terms of the number of vessels involved in this fishery. Commercial catch indicators for the southern North Sea reveal declines already starting in the late 1880s (Lundbeck 1962), and by-catch and mortality analyses show consistently high pressure on elasmobranch populations in the North Sea until the present (Philippart 1998, Piet et al. 2009). Causes include demersal trawling that equally affects both

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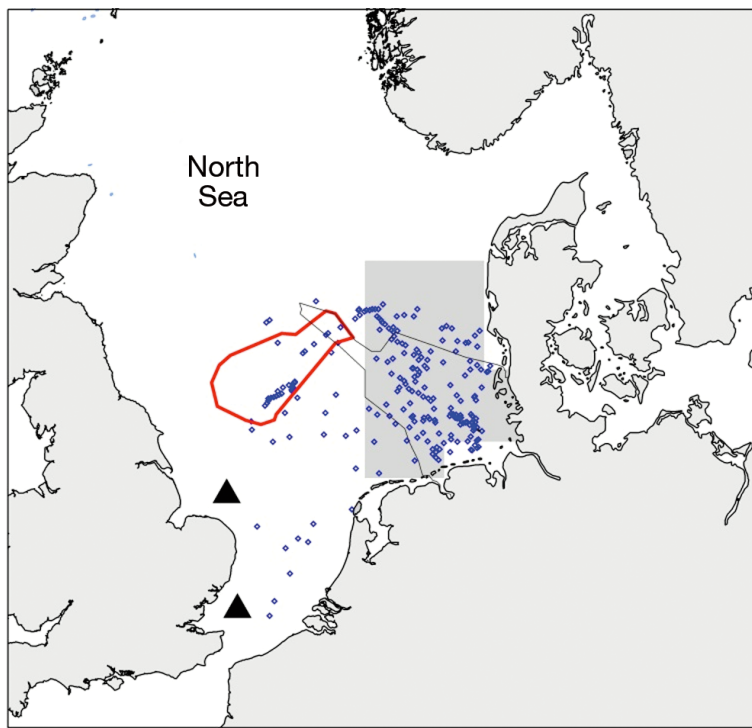


Fig. 1. North Sea area, including the German Exclusive Economic Zone (thin black line) and some present sub-populations of thornback rays *Raja clavata* (▲). Stations sampled in 1902–1908 mainly covering the German Bight are indicated in blue; the Dogger Bank area is outlined in red

skates and sharks in shelf sea areas, and longline fisheries in coastal and offshore waters, which pose a further threat to sharks (Stevens et al. 2000, Baum et al. 2003, Coelho et al. 2005).

Initial attempts to assess elasmobranch populations in the North Sea began in the late 1990s some 50 yr after North Sea-wide elasmobranch catches reached their height in the 1950s (de Vooy & van der Meer 1998, Heessen 2003). Low economic value and apparent stability in aggregate elasmobranch landings may be seen as causes for this delayed response in the fisheries community (Dulvy et al. 2000, Stevens et al. 2000). Elasmobranch catches were often assigned to broader categories such as 'sharks and rays' but seldom to species level, and thus species-specific information on abundance trends was lost (Ferretti et al. 2010). In the Irish Sea, this practice disguised the extirpation of common skates, while other species increased in abundance (Brander 1981, Dulvy et al. 2000). North Sea survey data from the last 40 yr (Walker & Heessen 1996, Ellis et al. 2004, Daan et al. 2005) show an east–west gradient with significant elasmobranch aggregations in the western North Sea contrasting with the earliest available survey data from 1902–1909 for the southern North Sea which in-

dicated a much wider distribution at that time (Rijnsdorp et al. 1996, Rogers & Ellis 2000, Fock et al. 2014).

These data indicate that habitat use has changed significantly. However, habitat characteristics are mostly modeled from recent species distributions only (Maxwell et al. 2009, Martin et al. 2012, Pennino et al. 2013). Reconstruction of historical distributions is difficult (Ferretti et al. 2010) and is often inferred indirectly from commercial catch information, and thus depends on the quality of that information (e.g. lack of species determination data, see Walker & Heessen 1996). Given the importance of habitat information for elasmobranch conservation (Ward-Paige et al. 2012) in terms of adult habitat or nurseries (Baum et al. 2003, Robbins et al. 2006, Heupel et al. 2007, Bethea et al. 2009, Knip et al. 2012), historical knowledge on distribution patterns appears essential for further conservation measures, particularly in relation to the problem of shifting baselines (Baum & Myers 2004, Hoeksema et al. 2011).

This paper provides evidence of changes in habitat use by thornback rays *R. clavata* in the German Bight, taking into account the biological (provision of food) and abiotic (physical habitat) dimensions of habitats. I hypothesized that changes in spatial distribution and habitat use between these periods were subject to changes in fisheries in the area. As a corollary, changes in fisheries might generate conditions to re-establish local populations where they have become extirpated. The shift in habitat use is discussed with respect to the designation of marine protected areas (MPAs) based on distributions of species already under pressure.

## MATERIALS AND METHODS

### Rationale

Among the direct effects of fisheries on fished species are losses of the distributional ranges of species (Worm & Tittensor 2011) and losses of population diversity (Cardinale et al. 2011). This implies spatial effects at larger scales but also in relation to habitat utilization at smaller scales, for instance in relation to fine-scaled fisheries distributions. This is considered in terms of 3 hypotheses.

(1) Ideal free distribution (IFD) hypothesis: The use of space for populations may be described in terms of resource availability in habitat patches as IFD, where patches of poorer quality are less densely populated so that each individual gains an equal net fitness in the given assemblage of habitats (Fretwell & Lucas 1969). Increasing fish populations use a wider space (Rose & Leggett 1989, Swain & Wade 1993, Shepherd & Litvak 2004), including the use of poorer patches (Laurel et al. 2004). Declining populations will contract their ranges and concentrate in patches of higher quality, which in part is determined by food availability. Habitat selection changes with density, and the distribution within the entire area (Fig. 2, no. 1) and the relationship to potential feeding grounds as optimum habitats (Fig. 2, no. 2) are tested for IFD (concentration in habitats of higher quality with declining abundance). Feeding grounds are inferred from the present fishing grounds, given the relative spatial stability between 1924 and 2006 for shrimp, crustacean, and flatfish fisheries (Fock 2008). The diet of *Raja clavata* comprises mainly shrimp and brachyuran decapods, including brown shrimp *Crangon crangon*, and the proportion of fish prey is much smaller than for other skates (Farias et al. 2006, Demirhan et al. 2007).

(2) Interference hypothesis: Populations with interference, either from competitors or predators, will use poorer habitats if these are less 'risky,' mostly irre-

spective of resource availability (Rosenzweig 1981, Gilliam & Fraser 1987, Hugie & Dill 1994). This implies that spatial patterns can be understood as consequences of interference between ecosystem components (e.g. Fock & Greve 2002, Herr et al. 2009). Treating fisheries both as a competitor and a predator on fish stocks, information on the fisheries and fishing effort is investigated to explain the decline in the fish stock and the change in habitat use (Fig. 2, no. 3.) Lower association with preferred feeding grounds would indicate a shift into low quality but less risky habitats and is thus in contrast to the implications of the IFD hypothesis.

(3) Habitat specialization hypothesis: Habitat use is strongly specialized and density independent. Habitat selection between periods of different abundance appears to be similar.

### Survey data

Fisheries survey data from 3 historical periods (1902–1908, 1919–1923, 1930–1932) were available from otter board trawl surveys of FRV 'Poseidon I' (Fock et al. 2014). Historical samples encompass samples from the German Bight proper and the German Exclusive Economic Zone (EEZ), except for the first period, when samples from the Dogger Bank area farther west were also available (Fig. 1). Subsequent to a standardization procedure (Fock et al. 2014), historical data were compared to Quarter 1 and Quarter 3 (of the year) ICES International Bottom Trawl Survey (IBTS) data from 1991–2009 (see Rijnsdorp et al. 1996) taken from rectangles representing the German Bight and the coastal zone (Fig. 1). To account for uneven survey coverage, a mixed model with negative binomial error distribution with log link function was applied to calculate mean abundance and CIs, with space as a random effect and year as a fixed effect (SAS procedure GLIMMIX, Fock et al. 2014).

### Testing for changes in distribution

#### Spatial distribution and range reduction

Spatial distributions were calculated using all samples from a selected period (Ellis et al. 2004, Daan et al. 2005) applying universal kriging to account for non-stationarity in data. Catch data from 1930 were applied to evaluate results for the German Bight against North Sea-wide distributions (Table 1). A

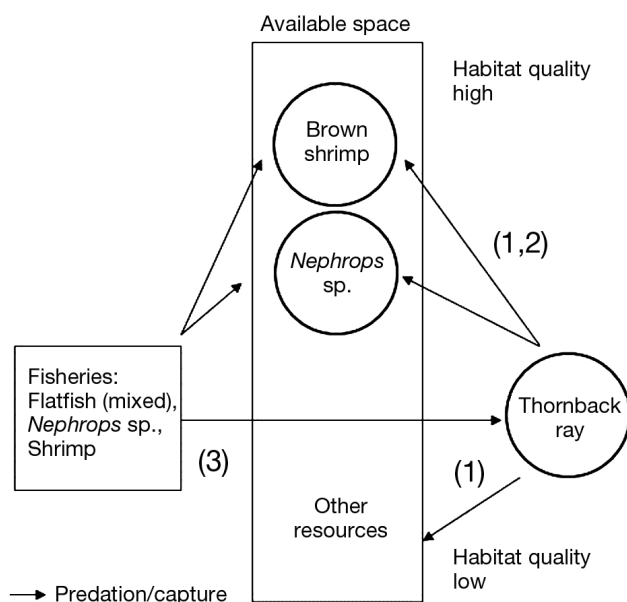


Fig. 2. Conceptual model for the analysis of changes in habitat use by thornback rays *Raja clavata* in the German Bight. Numbers refer to working hypotheses, 1: ideal free distribution; 2: interference; 3: habitat specialization. For details, see 'Rationale' in the 'Materials and methods'

range reduction was indicated by a significant increase in unoccupied cells between 2 periods with declining abundance, applying a chi-square test (SAS Institute 2010, see Worm & Tittensor 2011).

### Changes in habitat use

Changes in habitat use were described by a habitat model for each period 1902–1908 and 1930–1932, comprising 4 sediment types as variables (mud, sand, muddy sand, and gravel, see Fock et al. 2011) and water depth ([www.emodnet-hydrography.eu](http://www.emodnet-hydrography.eu)). Step-wise logistic regression (procedure LOGISTIC, SAS Institute 2010) was applied to binary scaled kriging scores calculated as integers and ceiled to 1. This reduces the influence of small kriging scores subject to the interpolation procedure. The modeling of presence-absence is comparable to the first stage in habitat modeling as outlined by Lauria et al. (2011, and references therein) and Martin et al. (2012). Probability of occurrence  $\pi$  can be backcalculated as:

$$\text{logit}(\pi) = \log\left(\frac{\pi}{1-\pi}\right) = \alpha + \beta x \quad (1)$$

i.e. the negative parameter  $\beta$  of the explanatory variable  $x$  decreases the probability of occurrence. Overall model fit is assessed using Akaike's information criterion (AIC), which adjusts the negative likelihood of the model to the number of terms used. Because data change between subsequent periods, AIC cannot be applied to compare models between different periods, so that model evaluation is based on their ensemble of significant model parameters and on the deviance criterion. Deviance >1 indicates overdispersion of data, i.e. variance in the data is greater than is predicted by the model, and deviance <1 indi-

cates variance much lower than predicted by the model. Models with strong over- or underdispersion indicate that the model setup is not adequate (SAS Institute 2010).

### Association with feeding grounds

Principal fishing grounds as outlined by Fock (2008) for known target species were defined as potential feeding grounds for thornback rays with respect to flatfish, shrimp, and Norway lobsters *Nephrops norvegicus* (see Figs. S1 & S2 in the Supplement at [www.int-res.com/articles/suppl/n025p197\\_supp.pdf](http://www.int-res.com/articles/suppl/n025p197_supp.pdf)). Association between feeding grounds and thornback ray populations is measured by the Morisita-Horn overlap index  $C_{MH,f}$ , following the approach applied by Herr et al. (2009, and details therein):

$$C_{MH,f} = \frac{2 \sum p_p p_f}{\sum p_p^2 + \sum p_f^2} \quad (2)$$

with  $p$  denoting the proportion of thornback rays or feeding grounds by grid cell ( $3 \times 3$  nautical miles, n miles) and calculated for the periods 1902–1908 and 1930–1932. Subscripts  $p$  and  $f$  denote values for thornback rays and feeding grounds, respectively. A test statistic is derived from permutations, and thornback rays can be positively (>random), independent from (random), or negatively associated (<random) with a habitat.

### Testing for the cause: age-based fishing mortality of *R. clavata*

Fishing mortality is assessed against reference conditions as applied for sustainable fisheries (maximum

Table 1. Comparison of local survey and regional commercial catch rates (in numbers per catch day) for select elasmobranchs. Commercial catch rates taken from Lundbeck (1937). Survey catch data are for the German Bight; data and conversion to catch day are taken from Fock et al. (2014). See Fig. 1 for a delineation of the German Bight. Commercial catches are for German steam trawlers

Species	1902–1923	1930			
	Survey catches	Southern North Sea Commercial catches	Survey catches	Central North Sea Commercial catches	Northern North Sea Commercial catches
<i>Dipturus batis</i>	2.2	0.2	0.4	1.4	6
<i>Amblyraja radiata</i>	5.8	11.7 <sup>b</sup>	9	1.7 <sup>b</sup>	0.05 <sup>b</sup>
<i>Raja clavata</i>	25		3		
<i>Squalus acanthias</i> <sup>a</sup>	17	8	1.2	56	192

<sup>a</sup>Commercial catches did not distinguish between *S. acanthias* and tope shark *Galeorhinus galeus*, the second most common species in the catches (Lundbeck 1937)

<sup>b</sup>Commercial catches did not distinguish between *A. radiata* and *R. clavata*

sustainable yield,  $F_{MSY}$ ) and fisheries leading to extinction (maximum sustainable mortality,  $F_{ext}$ ).

Following the approach of ter Hofstede & Rijnsdorp (2011), the 3 study periods are interpreted as periods with contrasting fishing regimes. Period 1 comprises the years 1902–1908 with relatively low fishing pressure, where some 17 % of the area was untrawled (ter Hofstede & Rijnsdorp 2011, Fock et al. 2014). Period 2 (1930–1932) represents a period of increased fishing effort, with new coastal fisheries of shrimp and fish for industrial purposes commencing in the mid-1920s, and total trawling effort tripling from the early 1920s to 1930–1932 (Fock 2014). Period 3 (1991–2009) can be described as a period with high fishing pressure (ter Hofstede & Rijnsdorp 2011).

Instantaneous fishing mortality  $F$  is the difference between total mortality  $Z$  and natural mortality  $M$ . Fishing mortality is defined as local mortality  $F_L$  according to Zhou & Griffith (2008), since it cannot be assumed that thornback rays in the German Bight represent the entire stock. Local mortality refers to an unknown proportion of the entire stock in area  $j$ ,  $p_j$ :

$$F = p_j F_L \quad (3)$$

A von Bertalanffy growth function (VBGF) was adopted to calculate age from size in survey catches (Caillet et al. 2006, Natanson et al. 2006), with VBGF parameters for the Irish Sea taken from Gallagher et al. (2005; data in Kadri et al. 2014 from the Mediterranean result in a smaller size-at-age unlikely for North Sea conditions). Size at hatch was assumed as minimum size in samples. Survey catches provided size ranges, modal lengths (often multiple), and single length measurements. Length distributions were derived according to the following procedure. For the available size ranges, specimens were uniformly distributed between the minimum and maximum limits. When modal lengths were provided, these were added to the uniform distribution, the 2 smallest modal lengths were given 10-fold weight, and further modal lengths were given triple weights. Single

measurements were not changed, and 84.5 % of the variability of the onboard weight measurements was captured by this protocol.

The more conservative estimate for natural mortality from Ryland & Ajayi (1984), i.e.  $M = 0.16$ , was applied, as compared to 0.14 in Philippart (1998). Local mortality was estimated as  $F_L = Z_L - M$  as the average for ages 1 to 7 over the entire period to account for uncertainty in the abundance estimates ( $F_{Lbar1-7}$ , applying length-based age estimates). Applying cohort-based catch curve analysis (Hilborn & Walters 1992),  $Z_L$  values by age and year were calculated by subtracting  $\ln(a_{year,age})$  from  $\ln(a_{year+1,age+1})$ , where  $a$  is the age-specific survey catch per unit effort (CPUE), reiterated 1000 times given the survey age composition and the survey abundances resampled proportional to survey CIs (see Fig. 3, and Table S1 in the Supplement at [www.int-res.com/articles/suppl/n025p197\\_supp.pdf](http://www.int-res.com/articles/suppl/n025p197_supp.pdf)). For the years 1904, 1905, and 1922,  $Z_L$  was calculated as 3 yr and 2 yr mortality between years with available age composition and divided by 3 and 2, respectively.

$F_{MSY}$  was derived from a non-equilibrium stochastic surplus production model (Hilborn & Walters 1992, see Text S1 in the Supplement at [www.int-res.com/articles/suppl/n025p197\\_supp.pdf](http://www.int-res.com/articles/suppl/n025p197_supp.pdf)), based on pentadal data from 1894 to 1930 under the assumption that effort and catches in this period represented a fully developed fishery in the German Bight (Lundbeck 1962, his Table 2). The  $F_{ext}$  estimate is 0.84 (García et al. 2008).

## RESULTS

### Trends

During 1902–1923, thornback rays were the most common elasmobranch species in the study area (Table 1). Abundance of thornback rays declined almost steadily towards 1932 (Fig. 3), when starry rays

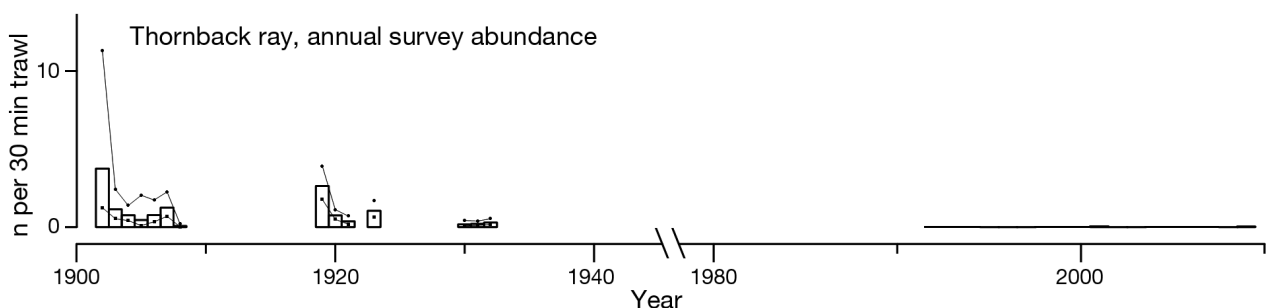


Fig. 3. Survey trends for thornback rays *Raja clavata* in the German Bight. Means (bars) and upper and lower CI (lines) are indicated



*Amblyraja radiata* became more abundant. Survey and commercial catch rates were much the same for the period 1930–1932 with regard to common skates *Dipturus batis* (0.2–0.4 specimens per catch day) and starry and thornback rays, accounting for about 12 specimens per catch day as a species group (Table 1). As indicated by CIs, abundance estimates, in particular for the first period (1902–1908), are subject to higher uncertainty. In the period 1991–2009, thornback rays became virtually extirpated in the study area, with only 4 specimens caught during IBTS surveys. Commercial catches show that the abundance of starry and thornback rays declined further toward the northern North Sea, while the elasmobranch assemblage there was dominated by common skates and spiny dogfish *Squalus acanthias*.

The age composition (see Table S1 in the Supplement at [www.int-res.com/articles/suppl/n025p197\\_supp.pdf](http://www.int-res.com/articles/suppl/n025p197_supp.pdf)) reveals that the oldest specimens were encountered in 1902 (age 7) and 1919 (age 8). Maximum age in survey catches subsequently declined to age 2 in 1932.

### Spatial distribution and range reduction

Thornback rays were distributed throughout almost the entire German Bight in the period 1902–1908 (Fig. 4), although a gradient towards the eastern and northeastern areas was evident. Peak

abundance was modeled for coastal waters. For 1902–1908, the abundance of thornback rays over the Dogger Bank was only apparent in the northern section ('a' in Fig. 4). An additional patch was located in deeper waters in the central German Bight both in 1902–1908 and 1930–1932 ('b' in Fig. 4). A third aggregation similar in both periods was found to be associated with coastal waters in the eastern part of the German Bight ('c' in Fig. 4). Overall, the change in distribution from period 1 (1902–1908) to period 2 (1930–1932) can be described as a range reduction. The portion of unoccupied space cells increased from 51.7 % in 1902–1908 to 75.5 % in 1930–1932, yielding a highly significant difference (chi-squared < 0.001). For the third period 1991–2009, almost 100 % of cells were unoccupied due to near-0 abundance.

### Habitat model

The habitat model revealed significant differences between 1902–1908 and 1930–1932 (Table 2). No model was developed for 1991–2009. The difference in deviance between 1902–1908 (deviance = 0.68) as compared to 1930–1932 (deviance = 0.09) reveals a poorer model fit for the latter period, indicating that sediment and depth characteristics were of less significance in determining the distribution of thornback rays. For 1902–08, distribution was negatively associated with gravel, mud, and depth, whereas in

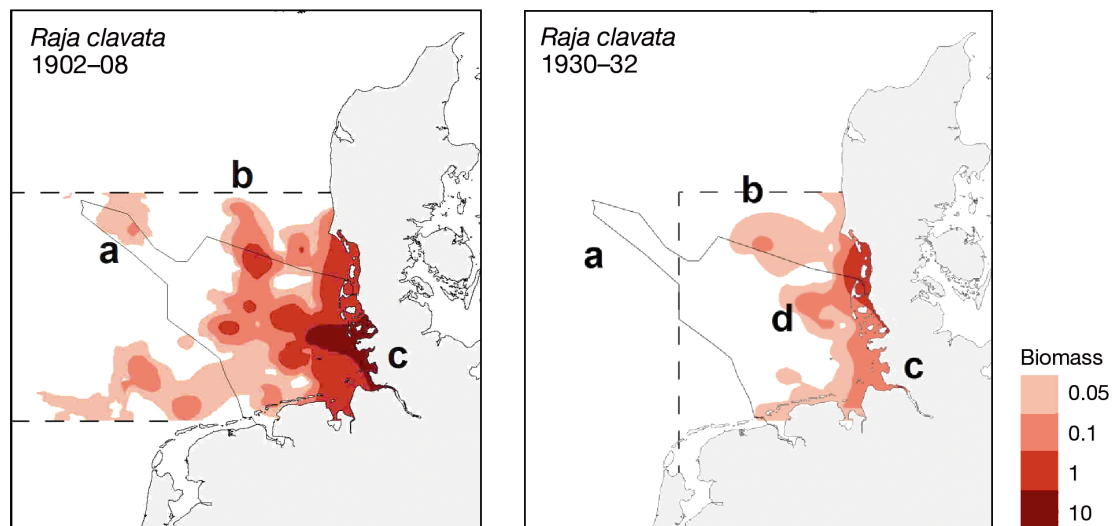


Fig. 4. Historical distribution patterns of thornback rays *Raja clavata*. Left panel covers the period 1902–1908 including the Dogger Bank area (see Fig. 1); right panel covers the period 1930–1932. Due to low abundances in particular after 1991, no data are depicted for the period 1991–2009. The German EEZ is delineated by the thin black line. Biomass contours in kg per 30 min trawling (survey catch per unit effort): 0.05–0.1–1–10. a: Dogger Bank; b: deeper central German Bight; c: eastern German Bight; d: Sylt outer reef

Table 2. Parameterization of the thornback ray *Raja clavata* habitat model for period 1 (1902–1908) and period 2 (1930–1932). No model was calculated for period 3 due to near-0 abundances. AIC: Akaike's information criterion; (–) parameter not estimated

Parameter	1902–1908			1930–1932		
	Esti- mate	Lower 95% CI	Upper 95% CI	Esti- mate	Lower 95% CI	Upper 95% CI
AIC	921			106		
Deviance	0.68			0.09		
Number of samples	136			147		
Intercept	–1.40	–1.88	–0.93	0.41	–0.73	1.56
Depth	–0.11	–0.13	–0.10	–0.20	–0.29	–0.12
Muddy sand	–			–		
Gravel	–1.35	–2.34	–0.29	–		
Mud	–1.22	–1.78	–0.64	–		
Sand	–			–		

1930–1932, only depth appeared to be a significant parameter without significant contributions of sediment parameters. This is contrary to hypothesis 3.

#### Association with feeding grounds

Patches of higher abundance observed in the deeper central ('b' in Fig. 4) and the eastern German Bight ('c' in Fig. 4) can be seen in conjunction with available crustacean food for thornback rays. Three different feeding grounds are considered, each identified through their main fisheries patterns, i.e. principal fishing areas (Table 3). Overlap with shrimp grounds was significant but declined from 1902–1908 (0.55) to 1930–1932 (0.48). The overlap with Norway lobster grounds also declined, but in general was smaller than for shrimp grounds and was insignificant in 1930–1932. No difference was apparent between periods with regard to association with flatfish fishing grounds, and overlap was not sufficient to explain any positive association. The negative trend for feeding grounds of preferred diet indicates a shift into less favorable habitats. This is in support of hypothesis 2.

Table 3. Association of thornback rays *Raja clavata* with feeding grounds during period 1 (1902–1908) and period 2 (1930–1932), and corresponding randomized test statistics

Association with	Period		5 <sup>th</sup> – 95 <sup>th</sup> percentiles of the randomized test statistic	
	1902–1908	1930–1932	1902–1908	1930–1932
Shrimp grounds	0.55	0.48	0.04–0.15	0.04–0.17
Flatfish grounds	0.03	0.027	0.07–0.17	0.08–0.18
<i>Nephrops</i> grounds	0.19	0.09	0.07–0.17	0.08–0.18

#### Fishing pressure

In the period 1902–1932, fishing mortality was determined as  $F_L = 1.03$ , with  $F_L = 1.35$  for 1902–1908 and  $F_L = 0.71$  for 1919 to 1932. For the period 1985–2006, Piet et al. (2009) reported an average effort-based harvest rate of 71% for the North Sea main fishing grounds ( $F = 1.2$ ), which appears more reliable than the moderate estimates of exploitation rate by Walker & Hislop (1998) of 30%, based on already declined survey CPUEs in a confined area of the southern North Sea. The value from Piet et al. (2009) was applied to further assess the trend for

thornback rays. With reference conditions of  $F_{MSY} = 0.04$  and  $F_{ext} = 0.84$ , local fishing mortality both in the historical period and at the present time exceed the maximum sustainable level, generating a strong enough momentum for thornback rays to become extirpated in the German Bight. Commercial CPUE data for skates collapsed in the 1920s and are in support of identifying fisheries as the main driver of the decline (Lundbeck 1962). This is in support of hypothesis 2.

#### DISCUSSION

This study shows how habitat modeling and fisheries information can be combined to analyze the extirpation process for thornback rays in the German Bight. Three hypotheses were qualitatively tested: (1) the IFD hypothesis (high quality habitats at lower population density); (2) the interference hypothesis (low quality habitats at lower population density); and (3) the habitat specialization hypothesis (habitat use is density independent). The results are in clear support of hypothesis 2, indicating a range reduction at reduced abundance paralleled by an intermediate move into habitats of poorer quality but of apparently lower risk of being caught (less related to preferred fishing grounds, see Fig. 2) before the fishing pressure on this stock, i.e. interference, forced it to final extirpation. This is supported by estimated historical trawling distributions (Fock 2014) indicating that part of the area occupied by thornback rays in 1930–1932 was less intensively trawled than surrounding areas ('d' in Fig. 4).

### Effects of fisheries and food availability

Fishing mortality is usually assessed against trends in catches and survey abundance (McAuley et al. 2007). As in this case with only observational, i.e. survey, data resolved to catch-at-age, and pentadal commercial data without information on catch composition, the use of dynamic modeling is impaired and the 2 types of information are applied separately. Catch curve models make the tacit assumption of a constant  $M$ , of unchanging catchability in the fisheries affecting the stock, and widely ignore density-dependent effects such as migration and depensation effects at low densities (Hilborn & Walters 1992, Dulvy et al. 2003, Swain & Chouinard 2008) and thus may be misleading with respect to  $F$  (see Cortés 2007). However, taking into account the high sensitivity to fishing (Robbins et al. 2006), any probable change in  $M$  must appear small as compared to the estimated local fishing mortality  $F_L$ . Available estimates for  $M$  differ only little. The  $F_{MSY}$  reference level was obtained by means of a surplus production model. The use of surplus production models for elasmobranchs has been criticized given that such models are unable to account for delayed responses in the long-lived species (Benson et al. 2001). In this study,  $F_{MSY}$  was calculated on pentadal averages and therefore appears capable of picking up changes in the thornback ray stock, given that with an age at maturity of 6.2 to 10 yr, each 5 yr period covers 1 generation fairly well.

Local fishing mortality observed in the periods 1902–1932 ( $F_L = 1.03$ ), and 1985–2006 ( $F = 1.2$ , Piet et al. 2009) exceeded the extinction level mortality ( $F_{ext} = 0.84$ ) and thus is sufficient to explain the extirpation of thornback rays in the German Bight. In this analysis,  $F_L$  also apparently declined with decreasing catch rates after 1919 ( $F_L$  in the period 1930–1932 was about 0.66), reflecting changes in catchability at low species densities. The  $F_{MSY} = 0.04$  may be deemed tentative but indicates that only very modest fishing mortality is tolerable for this species before stock status deteriorates, and it is in line with average elasmobranch rebound rates of 4.9% (Worm et al. 2013). This underpins the role of fisheries in determining the distribution of thornback rays, as evidenced by the significant range reduction indicated during the 3 periods 1902–1908, 1930–1932, and 1991–2009 with almost 0 abundance during the latter period. Fishing mortality is driven by a considerable increase in fishing power in the area, ranging from relatively low values and 17% of untrawled area in 1902–1908, to high fishing pressure in 1991–2009 (ter Hofstede & Rijnsdorp 2011, Fock 2014, Fock et al.

2014). The range reduction for thornback rays coincided with a change in habitat use, and significant differences were indicated between habitat models for 1902–1908 and 1930–1932 in terms of sediment parameters applied in either model. Thus, sediment properties during 1930–1932 did not definitively determine the distribution of thornback rays. The deviance statistic for the 1930–1932 habitat model indicates that the model was underparameterized. Fishing effort distribution could be an additional parameter to explain thornback ray distribution. A new fishery, i.e. the coastal shrimp fisheries (Fig. S3 in the Supplement at [www.int-res.com/articles/suppl/n025p197\\_supp.pdf](http://www.int-res.com/articles/suppl/n025p197_supp.pdf)) developed in the 1920s and increased fishing pressure in the coastal area. This particular increase (Fock 2014) could be the cause for a weaker presence of thornback rays in coastal waters in the period 1930–1932 ('c' in Fig. 4), causing the stock to move into off-coastal and more northerly areas. This was paralleled by a weaker association with the shrimp feeding grounds. Likewise, high densities in the first period 1902–1908 in deeper offshore areas ('b' in Fig. 4) indicated a significant association with *Nephrops* feeding grounds, but this association became insignificant in the period 1930–1932. Despite examples for range contractions (e.g. Worm & Tittensor 2011), responses to fishing mortality in terms of changes in habitat quality are only known for a few species (e.g. *Solea solea*, Engelhard et al. 2011).

In the present study, thornback rays were negatively associated with gravel and mud in the first period (1902–1908), while no sediment parameter appeared to be significant in period 2 (1930–1932). The preference for gravel as indicated by Martin et al. (2012) could be interpreted as an effect of reduced fisheries, since these areas are less targeted by the trawling fisheries for flatfish, similar to the shift of thornback rays to less risky habitat ('d' in Fig. 4). Areas populated by thornback rays in UK waters (Maxwell et al. 2009) experience less fishing activity than surrounding areas (see Stelzenmüller et al. 2008). In accordance with Maxwell et al. (2009) and Martin et al. (2012) this study indicates that depth is a major factor. Sediment was an important predictor, with thornback rays preferring sandy shallow and coastal areas and areas with gravel (Martin et al. 2012), or being negatively associated with mud (Maxwell et al. 2009).

### Implications for recovery potential

Fisheries were identified as the main driver of change, with high fishing mortality of thornback rays



and collapsing skate CPUE statistics in the 1920s (Lundbeck 1962). Spatially unconstrained fisheries in the area are likely among the factors hindering a re-establishment of thornback rays. Accordingly, spatial differences in fishing pressure can be applied to help explain the differences in habitat models published elsewhere (Maxwell et al. 2009, Martin et al. 2012). In line with this argument, local extirpation of thornback rays in the eastern North Sea (in Wolff 2000, Dulvy et al. 2003) and the Adriatic Sea (Sifner et al. 2009) has been attributed to fishery exploitation.

Thus, aiming to re-establish elasmobranchs based on present or most recent distribution figures primarily involves the identification of habitats less subjected to fisheries. This may be seen as the spatial equivalent of the shifting baselines problem in elasmobranch research (see Baum & Myers 2004) and may draw effort into the conservation of second-best habitats. The question remains whether such habitats can provide sufficient means to sustain a local

population. In this case, areas that were populated during period 2 (1930–1932) which were proven to be less risky at that time could be installed as MPAs with appropriate fisheries regulations. One MPA is currently being planned under the EU Habitats Directive (see Pedersen et al. 2009a) for the German EEZ (Fig. 5, Sylt outer reef). It encompasses an area of some 5000 km<sup>2</sup>, which in conjunction with the stepping stones available to immigrate from existing populations along the English east coast (Fig. 1), appears likely to enable recovery. In line with modeling studies (Wiegand et al. 2011), a fishing ban had a significant positive effect for thornback rays in a 500 km<sup>2</sup> protected area in the English Channel (Blyth-Skyrme et al. 2006), and even locally reduced fishing effort may provide effective refuges for elasmobranchs (Shephard et al. 2012).

### Implications for ecosystem functioning

Due to the high abundance of elasmobranchs and in particular thornback rays in the German Bight at the beginning of the last century (see Lundbeck 1937, Fock et al. 2014) as compared to recent catch figures (Pedersen et al. 2009b), understanding changes in this species in the southern North Sea are crucial to track changes in ecosystem functioning. The high proportion of crustaceans in the diet of thornback rays points to the role of thornback rays for food web structure in all 3 periods, and trophic cascade effects as consequences of elasmobranch removal must be considered important (Ferretti et al. 2010). Thus, to improve the ecological status of the marine environment as a major goal of modern maritime policies such as the European 'Marine Strategy Framework Directive' with regards to food web structure (MSFD, 2008/56/EC, Descriptor 4), elasmobranch conservation is of paramount importance.

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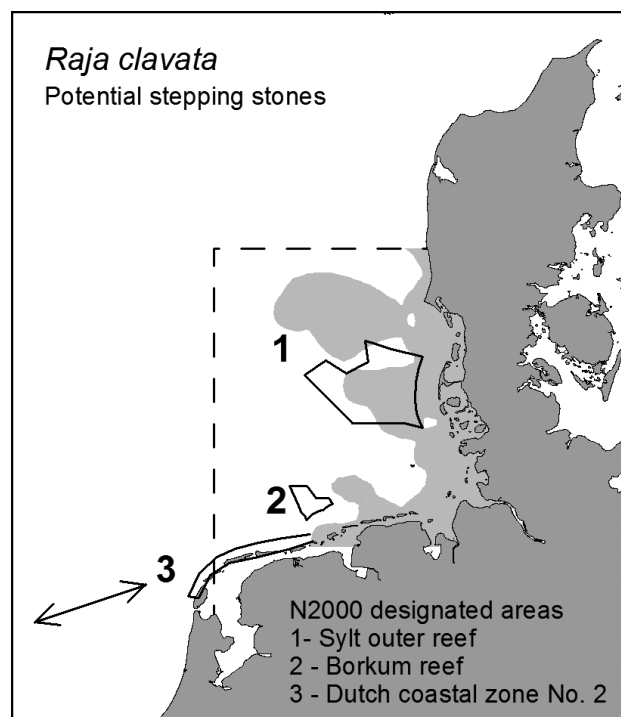


Fig. 5. Importance of marine protected areas (MPAs) to serve as habitat for recovery of thornback rays *Raja clavata*. Sylt outer reef (1) and Borkum reef (2) are part of the German Natura (N) 2000 network, whereas the Dutch coastal zone no. 2 (3) belongs to the Dutch Natura 2000 network and could serve as a stepping stone. The double-headed arrow indicates potential pathways for thornback rays to re-enter the German Bight from donor patches off the English east coast. Thin dashed line: area modelled 1930–32; bold black lines: designated MPAs; gray shading: distribution of thornback ray 1930–1932, see Fig. 4

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