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Title: A long-term view on recent changes in abundance of common skate complex in the North Sea

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Abstract

Following decades of declines, populations of large fish recently started to increase in the North Sea, presumably due to reduced fishing pressure. However, population recovery may be too readily claimed, since standardised sampling of fish stocks commenced only in the 1970s, well after many species had already collapsed. A true recovery must be seen from a long-term perspective. The critically endangered common skate (*Dipturus batis*, Rajidae) species-complex is an example of a large-bodied fish that mostly disappeared before standardised monitoring took place. Here we put the recent increase in population size into a 120-year perspective, throughout three geographical divisions in the North Sea. We analysed a large range of mostly undisclosed historical data and contemporary sources. A reconstruction of Dutch commercial landings data confirms that the species used to be very abundant between 1902 – 1920, and shows how it steadily declined from 1920 onwards until it got extirpated around 1970. Based on a quantitative analysis of standardized catch numbers from fishery-independent surveys time we conclude that the current abundance of the species is still below historical baselines and represents a local recovery at most. We further demonstrate a prominent and consistent pattern in size-distribution, with larger (mature) individuals only occurring in the northern North Sea. A large dataset on historical stomach contents from the central North Sea confirmed the diet of young common skate, which consisted predominantly of shrimps. Our review exemplifies the importance of marine historical ecology to deduce the natural richness of the North Sea.

Keywords: *Dipturus batis*, *Dipturus intermedius*, Marine historical ecology, shifting baselines, number per swept area

Introduction

Centuries of overexploitation of marine and freshwater fish stocks has led to global population collapses in many species (Lotze *et al.*, 2006; Pitcher & Lam, 2015; Duarte *et al*., 2020). Large fish species, which typically have slow population growth rates, have been most vulnerable (Brander, 1981; Fernandez *et al.*, 2017). However, following stringent fisheries regulation and management, the North Sea seems to show local populations of some large-bodied fish species to be on the rise, inspiring the announcement of the 'age of recovery' (Engelhard *et al.*, 2015; van Gemert & Andersen, 2018; ICES, 2021). Yet, standardised fisheries-independent surveys started when populations of many species were already decimated and given that large fish occur at low abundance levels in the North Sea food web for over 50 years (e.g. Rice & Gislason 1996; Sguotti *et al.*, 2016), it can be questioned if these population increases represent true recoveries.

A true species recovery must be seen from a long-term perspective and would require assessment of both population trends and ecological functionality of a species (Akçakaya *et al.*, 2018). Marine historical ecology provides this viewpoint on marine ecosystems, by assembling various sources of information on the historical densities and ecology of marine species (Jackson *et al.*, 2001; Lotze & Worm, 2009; Engelhard *et al.*, 2016; Bom *et al.*, 2020). Historical fishery-independent surveys and catch data, despite their inconsistencies in methodology, are essential to set historical baselines, and to understand processes underlying potential change. Furthermore, multiple data sources such as size data, seasonal distribution patterns of catches and stomach analysis, provide important information that enable the identification of historical stock structures, seasonal migration, habitat use, and diet composition (Lotze & Worm, 2009). This understanding can be used to evaluate current changes in populations and identify potential windows for return (Lotze & Worm, 2009).

The critically endangered common skate (*Dipturus batis* species-complex, Rajidae) is an example of a large-bodied fish which population has recently increased in the northern North Sea (ICES, 2019). This increase seems to contrast with population developments in other parts of its historic distribution, i.e. marine waters throughout the northeast Atlantic from Morocco to northern Norway (Wheeler, 1978). For example, a long-term perspective by Sguotti *et al*. (2016) observed no recovery in the central and southern North Sea. A long-term quantitative evaluation of common skate throughout the North Sea is needed to assess the extent to which common skate has truly ‘recovered’ from its collapse. However, such an evaluation is complicated because the population collapsed in the 1960s-1970s (Dulvy & Reynolds, 2002; Sguotti *et al.*, 2016), i.e. before standardized fishery-independent surveys commenced throughout the North Sea. Furthermore, an evaluation of common skate is challenging given that it was recently split into two species, named common blue skate (*Dipturus batis*, Rajidae; previously described as *Dipturus* cf. *flossada* by Iglésias *et al.*, 2010) and flapper skate (*Dipturus intermedius*, Rajidae) (Iglésias *et al.*, 2010; Griffiths *et al.*, 2010; Last *et al.*, 2016). It is still unclear when and where each of these species used to occur, but it is likely that they occurred in mostly separate regions (Griffiths *et al.*, 2010). To start addressing the most glaring knowledge gap regarding the quantities of common skate complex, we create an overview of contemporary and historical data. With this we aim to deduce the potential for recovery, which is defined as a population increase with respect to historic levels, and considering the species' ecological functionality in the North Sea.

Here we give a long-term spatio-temporal perspective on the abundance and ecology of common skate in the North Sea, by analysing simultaneously a variety of historical and contemporary data. Firstly, we reconstruct abundance time series by analysing catches of fishery-independent surveys dating back to 1902 and by assembling fishery-dependent data from Dutch commercial landings data dating back to 1901. Secondly, we deduce part of the ecology of the species in the North Sea by using a range of undisclosed historical and contemporary data sources, including size and stomach data of over 400 individuals assembled by NIOZ Royal Netherlands Institute for Sea Research. Wherever possible we define common blue skate and flapper skate separately, with identification based on (i) a museum specimen, (ii) fish length of historical catch and landing data and (iii) separation of the two species in contemporary fishery-independent surveys.

Methods

Area definition & description

The historical analysis of this study focusses on the North Sea, a historical stronghold region of common skate (Heessen *et al.*, 2015). The North Sea is a shelf sea of the Atlantic Ocean, located on the European continental shelf between Norway, Sweden, Denmark, Germany, the Netherlands, Belgium, France and Great Britain. We follow the classification of the International Council for the Exploration of the Sea (ICES) and divide data into three divisions: northern North Sea (4.a), central North Sea (4.b) and southern North Sea (4.c)

(ICES, 2021). In the north, the northern North Sea reaches depths of 500 m and is influenced by oceanic inflow. The southern North Sea reaches a maximum depth of 50 m and receives large inputs of river waters. The sediments in the area consist mainly of mud and sand; boulders and gravel are found scattered throughout.

Abundance time series

We reconstructed long-term time series based on data collected from (i) fishery-independent surveys, and (ii) fisheries (Table 1). Here, data were treated at the *Dipturus batis* species-complex, with no abundance done by species.

Fishery-independent survey data

Fishery-independent surveys in the North Sea commenced in 1902 and continued, with some interruptions and modification of sampling design including gear and vessels, until now. Although these surveys were designed to monitor commercial teleost stocks, elasmobranch species were also recorded, and, with some precautions (see below), can be used to assess information on occurrence of elasmobranch species (Sguotti *et al.*, 2016). Especially the fishery-independent surveys between 1902 – 1965 were not standardized, mostly regarding sampling location and time, and these surveys are referred to as historical surveys. From 1965 onwards, the International Council for the Exploration of the Sea (ICES) coordinated fish stock surveys throughout the entire North Sea (data at https://www.ices.dk/marine-data). From 1977, the contemporary surveys were standardised with respect to sampling protocol, with hauls covering a regular grid (ICES, 2021). By 1992 all participating countries used the GOV as standard gear. We refer to these surveys as contemporary surveys. We refer to fishery-independent surveys as an overarching term of both historical and contemporary surveys.

The historical surveys were carried out with steam-trawlers. At selected stations these ships towed a beam trawl or otter trawl at a speed of approximately 2 knots, for various time durations. Historical surveys were almost exclusively spread over the central and southern North Sea (Fig. 1A). The contemporary surveys were carried out with diesel-powered vessels. At selected station these ships towed with a standardised speed of 4 knots and with a duration of 0.5 hours. In the standardised International Bottom Trawl Surveys (IBTS), a 'grande ouverture verticale' (GOV) otter trawl net was used (ICES, 2020a; Sguotti *et al.*, 2016).

From historical surveys we retained all records that refer to common skate, *Dipturus batis* or *Raja batis*. These records may include both flapper skate and common blue skate. In the contemporary surveys data on common skate may be confounded given identification issues of the newly described species, and species of the common skate species-complex were entered under several codes. We retained all records referring to *Dipturus batis*, *Dipturus flossada* and *Dipturus intermedia*.

Comparing the historical and contemporary surveys is problematic because of various methodological differences (Rijnsdorp *et al.*, 1996; Walker *et al.*, 2017; also see the discussion section). A major issue relates to the use of otter trawls versus beam trawls, the latter for instance sometimes use tickler chains, which may greatly affect the number of caught elasmobranches (Kynoch *et al.*, 2015). Therefore, to allow for comparison of fishing methodology, we retained surveys with otter trawls only. To compare the historical and contemporary surveys we used the same pragmatic approach as Rijnsdorp *et al.* (1996) and Walker *et al.* (2017) and calculated the number per swept area to quantitatively compare the survey data.

The swept area can be calculated as the opening of the net multiplied by the distance towed (Rijnsdorp *et al.*, 1996; Walker *et al.*, 2017). The opening of an otter trawl is referred to as the 'wingspread' (for a complete, technical description of otter trawls we refer to Knijn *et al.*, 1993). This wingspread is a fraction of the length of the headline and depends on towing speed and depth. For the historical surveys the headline was known, but the availability of data in terms of the length of the headline and the wingspread was inconsistent in time. However, for the English research vessel RV 'Huxley', surveying between 1902-1909, the horizontal net opening was estimated at 2/3 of the length of the headline (Garstang, 1905) and for the Poseidon I surveys the horizontal net opening was assumed to be 70% of the length of the headline (Fock *et al.*, 2014). For consistency we assume that for historical surveys the wingspread is equal to the headline length multiplied by 2/3 (Table 2). For the early contemporary surveys, the wingspread is unknown, and also assumed to be equal to the length of the headline multiplied by 2/3 (Table 2). For the more recent contemporary surveys the distance between the wings is routinely measured, or wing spread can be calculated from information on door spread (see ICES 2020b for details on mathematical functions). For some of the early contemporary surveys were wingspread was not given or could not be calculated we use the gear-specific average wingspread (see Table 2). Nevertheless, the length of the headline and wingspread remained unknown for some gear used in the early contemporary surveys. These were omitted from the analysis (this excluded 2.32% of all contemporary surveys).

The distance towed was indicated for 66% of the contemporary surveys. Distance towed was not given for the historical surveys. For surveys with unknown distance towed, both historical and contemporary surveys, it was calculated as the tow duration multiplied by the speed (Table 2). For 19 stations visited by Poseidon I the tow duration was not given, thus, a tow duration of 60 minutes was assumed as the median duration of the remaining tows.

For each station we calculated the number per swept area by dividing the number of common skate caught per swept area. Next, we calculated the mean (±SE) number per swept area over a 5-year period (pentad) per division. To calculate standard errors, the number of stations sampled was taken as sample size. The pentad time interval was inspired by the approach of Sguotti *et al.* (2016) and was found to be a good compromise between having sufficient stations sampled per division to estimate number per swept area, and a sufficiently high temporal resolution (Fig. 1A).

The historical surveys were conducted randomly with respect to seasonal timing. The contemporary ICES-coordinated surveys were mainly conducted in the first and third quarters of the year (‘IBTS Q1’ and ‘IBTS Q3’), among which the surveys in Q1 (January till March) were most complete in space and time. In the main analysis, survey data from all seasons were retained (including Q2 and Q4). To account for a potential effect of season on the results, we also analysed the number per swept area over time only for data collected in Q1 and Q3 (Supplementary S2). All analyses were done using the R software version 3.6.3 (R Development Core Team, 2020).

Fishery-dependent data: Dutch commercial landings data

Between the years 1901 and 1983 (excluding the periods of the two World Wars), fish landings at all Dutch fish markets were registered by local authorities. For the period between 1930 and 1970 the total amount of landed common skate was reported in “Verslagen en mededelingen van de Directie van de Visserijen”, which translates as ‘Annals of the directorate of fisheries'. Prior to 1930, the landings of common skate were registered separately per fish market. For this period, we compile landings data for the periods 1901-1903, 1907-1910 and 1921-1929. After 1970, when common skate landings had dropped to virtually zero, these species were aggregated and reported as a generic category of skate species. Therefore, from this period onwards no reliable estimates are available. From 2009 onwards landing of common skate has been prohibited. All data are expressed in metric tonnes. The origin of the reported fish is categorised as 'Sea Fisheries', which is loosely specified as the waters in the North Sea, the Channel, the Irish Sea and sea around Iceland. It was impossible to deduce the amount of common skate caught in the North Sea from these data. In 1932 it was specified that 94 % of all fish brought to the Dutch fish markets were caught in the North Sea, 1% in the Channel and 5% near the Faroe Islands and Iceland, and we assume that these numbers are indicative for the origin of common skate landings in the Netherlands.

Ecological data

Size distribution

To evaluate potential spatial differences in size distribution, we used two datasets where size (total length) was measured of common skate with known catch location . The first data comprised 658 individual records from the historical and contemporary fishery-independent surveys (HL files from the DATRAS database; Table 2). The second dataset consisted of records from the NIOZ Royal Netherlands Institute for Sea Research bycatch programme (de Vooys & van der Meer, 1998). In this programme, NIOZ collected individuals from by-catches of commercial fishers and registered information such as catch date, location and depth , and individual size (total length) and sex. The programme ran between 1930 and 1990 and the data contains information on 633 common skate that were landed during 1938 – 1970 (Fig. 1B). Length was measured in 551 individuals (Table 1).

The size-distribution of common skate was evaluated in relation to size at birth, size at maturity, and maximum size. The length at 50% maturity ($L50$) is estimated to be 115.0/122.9 cm (males/females) and 185.5/197.5 cm (males/females) for blue skate and flapper skate, respectively (Iglésias *et al.*, 2010). The maximum length ($L\infty$) of flapper skate is 285 cm (Wheeler, 1978) and 143.2 for common blue skate is (Iglésias *et al.*, 2010). Common skate are oviparous and the length at birth (*L*birth) of common skate in the Irish Sea is 22 cm (Brander, 1981).

Differences in size-distributions between the northern, central and southern North Sea were explored using a linear model, with size and data origin (i.e. fishery-independent survey data or NIOZ-bycatch programme) as the dependent variable. Size was log-transformed in order to homogenize the variances. Contrasts were analysed in a post hoc comparison, where pairwise differences among divisions were tested in a two-sided t-test, with P values adjusted by Tukey's correction for multiple comparisons. It should be noted that size data from the central and southern North Sea were mainly from data collected prior to 1970 whereas data from the northern North Sea were mainly post 1970 (Fig. 1B). Post hoc analysis was done using the emmeans function from the emmeans package version 1.7.4-1 (Lenth *et al.*, 2018).

Seasonality in occurrence

Season trends in the occurrence of common skate by subdivision were evaluated (no data were available for the northern North Sea), through the use of NIOZ bycatch data of 755 individuals with associated catch date. We analysed the total number of common skate per month, separated for the central and southern North Sea.

Sex ratio

Potential habitat segregation amongst sexes was investigated through the use of NIOZ bycatch programme data, where the sex ratio by subdivision was evaluated using a Pearson's chi-squared test.

Diet

The diet of common skate was studied using prey composition in the stomach contents obtained during the NIOZ-bycatch programme from 1938 – 1970. The archived data contains information on 405 stomach contents from individual common skate. From these stomachs, prey remains were identified at the time of collection by biologists from the NIOZ. These data were also largely checked by renowned taxonomist L. B. Holthuis (1921–2008), from the natural history museum Naturalis in the Netherlands. Prey items were identified to species level, where possible, with others allocated to a higher taxonomic level. An index of vacuity was used to express the number of empty stomachs encountered as a percentage of the total stomachs examined. In addition, three numerical diet indices were calculated, given the lack of information on size of prey for most records (Brown *et al.*, 2012). (i) The average percentage of each prey species over all stomachs (%N) summarises relative importance. (ii) The prey-specific number by count (%PN) provides the relative abundance across stomachs with this prey species and thereby provides information on contribution when eaten (i.e. individual specialisation). (iii) The frequency of occurrence (%FO) reflects the proportion of analysed stomachs that contained the prey species and thereby gives another index of relative prey importance (Brown *et al.,* 2012).

Species identification

Further analysis was conducted to investigate the occurrence of the two different species in fisheries-independent surveys and samples from the NIOZ-bycatch programme. In the fishery-independent surveys species of the common skate species-complex are since 2012 identified as common blue skate or flapper skate, according to the identification guidelines of Iglésias *et al.* (2010). Note that only larger specimen can be identified reliably. Here, the incidence of each species was calculated. From the NIOZ-bycatch-programme we managed to identify a specimen caught on 14 April 1938, 35 miles north of the island of Terschelling (central North Sea). This individual was preserved on ethanol at the Naturalis Biodiversity Centre and registered under id RMNH.PISC.26860. It was identified based on keys provided by Iglésias *et al.* (2010). Each identified individual was plotted in terms of location recorded.

Results

Abundance time series

Fishery-independent survey data

The number per swept area for the three divisions are shown in Fig. 2A. We omitted seven pentads with less than 20 sampled stations from this figure as they may give a biased picture of the number of catches (supplementary material S1). The minimum number of surveys for any of the retained pentads was 39 and the mean number of retained surveys per pentad was

962 (SD ± 487) , 892 (SD ± 802) and 231 (SD ± 133) for the northern, central and southern North Sea respectively (all sample sizes shown in Fig 1A).

In the central and southern North Sea number per swept area showed somewhat similar patterns: between 1902–1940, and again between 1950 and 1970, the number per swept area fluctuated around one individual per km^2 (Fig. 2A). After the 1970s, virtually no common skate were recorded in the central and southern divisions, despite a high number of stations sampled (Fig. 1A). Meanwhile, in the northern North Sea the number per swept area was close to zero around 1970, with the last three pentads suggesting and increase in trend. The contemporary catch rate for the northern North Sea is at the same level as the presented baseline levels (from around 1900) in the central and southern divisions.

Fishery-dependent data: Dutch commercial landings data

Landings data showed that the amount of common skate (expressed by weight) landed in the Netherlands steadily decreased from 1920 onwards. The last reported individuals were landed in 1970 (Fig. 2B).

Ecological data

Size distribution

In the fishery-independent surveys, the largest individuals were caught in the northern North Sea, with successively smaller-sized individuals in the central and southern North Sea (Fig. 3). The mean size of individuals in the northern North Sea was 79 cm (SD ± 44 cm, $n = 274$). Here, 13 individuals exceeded $L50$ for *D. batis* and 35 for *D. intermedius*. In the central North Sea, the size averaged 46 cm (SD ± 22 cm, $n = 207$) and almost all individuals were well below $L50$ of either species. In the southern North Sea, mean individual size was 39 cm (SD ± 17 cm, $n = 126$). Statistical modelling showed significant differences in size between divisions and sources. Pairwise contrasts of revealed significant differences in size between all divisions for fishery-independent data ($P < 0.0001$), but not for data collected in the NIOZ-bycatch programme ($P = 0.986$). Furthermore, there was a difference between data collected by the fishery-independent surveys and NIOZ-bycatch programme ($P < 001$).

Seasonality in occurrence

The NIOZ-bycatch programme contained catch data of 755 common skate, 501 from the central North Sea and 254 from the southern North Sea. In both divisions most individuals were caught in winter and early spring (Fig. 4). Data from fisheries-independent were not used as they were concentrated in Q1 and Q3.

Sex ratio

The NIOZ bycatch data contained 545 sexed individuals. Of these, 340 (196/171 male/female) were caught in the central North Sea and 205 (109/96 male/female) in the southern North Sea. Pearson's chi-squared test showed that sex ratios did not differ from 50:50 in the central North Sea (N = 340, $\chi 2$ = 0.012, p = 0.9136) and southern North Sea (N = 205, $\chi 2$ = 0.82439, t_1, p = 0.3639)

Diet

Stomach contents were checked in 405 individuals, of which 201 were identified as female and 196 as male (9 remained unsexed). Median total length of all individuals was 42 cm (range 20 – 177 cm), females had a median of 41 cm (range 23 - 177 cm) and males had a median of 43 cm (range 20 - 120 cm) . The index of vacuity was for all stomachs was 2.7%. The stomach contents of the inspected common skate (n = 405) were numerically dominated by shrimp, and further contained fish, crabs, and in two instances, cephalopods (Table 3). Frequency of occurrence (%FO) and average percentage number (%N) showed that the vast majority of prey were crustaceans, with shrimps of the families Crangonidae and Processidae occurring particularly frequently (Table 3). Fish were the second group of prey, with 10% FO and 6 %N on the basis of broad, non-taxonomic categories. Part of this general 'fish' category was identified down to Class level (6 % FO Actinopterygii). On the basis of these categories, crabs had 5% FO. Stomachs containing fish (N = 23) generally formed a moderate part of the diet as shown by the percentage of prey-specific number (%PN): e.g. *Clupea harengus* had 55% PN, *Merlangius merlangus* had 37% PN, and *Solea solea* had 100% PN, though these are based on low occurrences. Aside of higher occurrences, crustaceans also had higher contributions when eaten: *Crangon* spp 95% PN and *Liocarcinus* spp 75% PN (Table 3).

Other prey species recorded included cephalopods (N=2 stomachs) and polychaetes (N=1 stomach), though information was too limited to draw further conclusions.

Species identification

Contemporary surveys over the years 2012 – 2020, recorded 36 number of common blue skate and 127 number of flapper skate. Common blue skate were identified at a few single spots around the Orkney and Shetland Islands (Fig. 5). Flapper skate were identified in the same, but slightly larger area, including a few individuals in the central North Sea.

The single common skate from the NIOZ-bycatch programme preserved at the Naturalis museum was identified as flapper skate based on the iris colour and long interspace between dorsal fins (Fig. 5. and supplementary material S3)

Discussion

This study compiled a 120-year time series for common skate in the North Sea through the use of several complementary data sources. This time series shows unequivocally that in the central and southern North Sea, contemporary catch numbers are close to zero and far below historical catch numbers. Meanwhile, the numbers of common skate caught in contemporary surveys in the northern North Sea suggest an increase over the last 15 years, confirming a recent increase of a large fish with low reproduction rates in the North Sea (van Gemert & Andersen, 2018; ICES 2021). However, it is difficult to put this recent increase into perspective, given the lack of historical surveys in this division. The best information we have is from historical textbooks, stating that densities of common skate used to be highest in the northern part of the North Sea (Hoogendijk, 1893; Redeke, 1911). This suggests that contemporary catches in the northern North Sea are still well below historical levels, because current catch rates in the northern North Sea are ‘only’ at a similar level of historical catch rates in the central and southern North Sea. Thus, our study shows that any recovery of common skate is only of a localised nature and likely still limited.

The recovery of common skate in the North Sea over the last fifteen years, during which number per swept area of the species roughly doubled every five-year period, is unexpectedly fast for a species with low reproduction rates (Brander, 1981). It seems unlikely that new recruits played an important role in the observed increase, given that the species reaches reproductive maturity at an age of 11 years (Du Buit, 1977). Therefore, a possible explanation would be that individuals of a remnant population managed to successfully reproduce over multiple years. Furthermore, the increase in numbers observed in recent years could be due to an immigration of individuals from outside the North Sea (i.e. tracking studies suggest large-scale movements in large males; Wearmouth & Sims, 2009) and the fecundity estimates by Brander (1981) may have been an underestimate in the first place. Regardless of the cause of the recent increase, it shows that the species has the potential to recover.

Earlier reconstructed qualitative time series of common skate for the central and southern North Sea showed that the species was abundant in the early 20th century and was extirpated from the central and southern North Sea divisions around 1970 (Gmelig Meyling, 2009; Sguotti *et al.*, 2016). Our quantitative time series corroborates these earlier findings. However, the relative abundance for the period 1910 – 1940 was not assessed previously, nor was it clear when the species started to decline. By adding data of fishery-independent surveys from Poseidon I (1902 – 1932) and from commercial Dutch landings from 1901 – 1970 we were able to show that in the period of 1910 – 1940 common skate were still regularly caught in the central and southern North Sea, and landed in the Netherlands. However, the landing data also show that from 1920 onwards, the amount of landed common skate declined steadily. The decline from 1920 onwards was not well captured by the fishery-independent surveys, perhaps because of the still relatively low survey efforts between 1920-1950. Although landing data should always be interpreted carefully given that catch effort and location may be unknown (Froese *et al.*, 2012) we argue that the decline in landings from 1920 onwards may depict a genuine decline in the species, given that after 1918 fishing efficiency in the North Sea increased steadily through a series of innovations (Thursby-Pelham, 1939; Rijnsdorp & Millner, 1996). Furthermore, landing data of skates and rays (including common skates) in UK fisheries show a similar pattern, suggesting that our observations in the Netherlands' landing data is generic (Ellis *et al*., 2010). Also note the large sample size for this time series, confirming that the species used to be abundant, because we present data from the Netherlands only, which probably is just a fraction of the total landed common skates in the North Sea.

It is generally accepted that trawl catches made with the same gear reflect relative differences in abundance of demersal fish species (Rijnsdorp *et al*., 1996). Thus, although the analysed fishery-independent surveys were not specifically designed to sample elasmobranch fish, their relative abundance could be compared across a large time scale because we included surveys with otter trawls only. Nevertheless, fishing methods differed between historical and contemporary surveys, especially regarding tow speed, which could still lead to different catch results (Rijnsdorp *et al.*, 1996; Walker *et al.*, 2017). For instance, it might have been easier for common skate to escape from nets towed with low speed, especially for faster swimming, larger individuals (Heessen *et al.*, 2015). When tow speed is indeed positively correlated to catchability in common skate, the number per swept area in the historical surveys will be underestimated compared to contemporary surveys, given that historical surveys towed at a lower speed (2 knots) than contemporary surveys (4 knots). Another confounding factor could be that in the contemporary GOV trawls, the swept area is increased by an extension of the ground rope (sweep) between the wings of the net and the trawl doors (Knijn *et al.*, 1993). The sweeps may herd some species into the path of the net, thereby extending the effective trawl pathwidth beyond that of the wing spread (Ramm & Xiao, 1995). As far as we know no tickler chains were used in the selected surveys (e.g. Rijnsdorp *et al*., 1996). Methodological differences in our data sources may therefore result in an underestimate of historical catch rates, but not an overestimate, further validating our caution for overly optimistic interpretation of recent increases.

Ecology of common skate in the North Sea

In data of ecological traits and characteristics, the differences in size-distributions in the three divisions revealed the most prominent pattern. Strikingly, individuals larger than *L*50 for either species were almost exclusively caught in the northern North Sea, suggesting that reproduction takes place in this division. This corresponds to reports by Phillips *et al.* (2021), where reproduction continues to occur in the northern North Sea, with eggs deposited in boulder reefs and on rocky substrates. On the contrary, the smaller immature individuals caught in the central and southern parts suggest that these divisions were of particular importance for immature life-history stages in common skate. Again, due to size-dependent catchability , these data may not give a perfectly representative picture of the size distributions within the population. However, given that the same gear was used in the central and southern North Sea, the size differences for these divisions are genuine. This observation is also confirmed by historical textbooks, indicating that in the southern North Sea mainly individuals smaller than 50 cm were caught (Anslijn, 1828). Yet, historical textbooks also indicate that larger individuals, up to 2 m in size, have been found along the Dutch coast (Coenensz van Schilperoort, 1577–1581; Bennet & Olivier, 1825) and English coast (Shaw, 1804). Furthermore, the presence of fresh egg cases in the central North Sea in the early 20th century (Tesch, 1911) shows that the species used to reproduce in this division.

Following our conclusion that reproduction mainly took place in the north, we hypothesise that the smaller individuals in the central and southern North Sea moved south from their birthplace in the north. We further postulate that small individuals may migrate south because of favourable climate conditions, resource availability, or because of intraspecific resource competition in the north. None of these (non-mutually exclusive) scenarios are conclusive, yet we found that small individuals were caught more frequently in winter and early spring (further discussed below). This seasonality could be a result of timing of reproduction, but may also indicate that environmental conditions, such as bottom temperature, can affect the distribution of common skate. We further note the equal sex-ratios found for the individuals caught in the central and southern North Sea, indicating that if small individuals indeed migrate, this happened at the population level. This may contrast with large individuals, of which females have high site fidelity throughout the year, while large males are thought to migrate (Wearmouth & Sims, 2009).

Fishery-dependent data showed a peak in records in late winter/ early spring. These data originate from around the 1950s, a time period when fisheries in the North Sea were most active in summer (Rijnsdorp *et al.*, 2008). Thus, the dip in summer and the peak in spring are probably genuine, whereas the numbers in winter were probably higher than depicted. Historical assessments do not report any seasonality in the species (Schlegel, 1862), although Hoogendijk (1893) mentions that Dutch fisheries targeted common skate in winter/early spring. If the species has any seasonality in the central and southern North Sea it is peaking in winter/early spring. With contemporary surveys mainly done in the first quarter of the year (January – March), it can be expected that the lack of common skate in the central and southern North Sea are not a result of seasonal movements.

Common skate is a bottom feeder and stomachs of juvenile skate (< 50 cm) contained mainly crustaceans (*Crangon* spp. and *Pandalus* spp.) and some fish (Du Buit, 1968; Brown-Vuilmin *et. al.*, 2020). We analysed a large dataset of stomach contents for relatively small juveniles from the central North Sea, which confirmed that the diet of this size class consisted predominantly of crustaceans. Moreover, the low index of vacuity suggests an opportunistic feeding mode in terms of prey choice (Brown *et al.*, 2012). Note that most fish species show substantial ontogenetic changes in feeding behaviour, so our study captures part of this species' historical diet only (Scharf *et al.*, 2000). Indeed, the diet of larger specimens appears to have been a wide variety of demersal fish (Rae and Shelton, 1982), including other elasmobranchs (Steven, 1932).

Species identification

In recent fishery-independent surveys, common blue skate and flapper skate have been recorded in the North Sea, with the larger species *D. intermedius* being the most abundant common skate encountered. A museum specimen obtained from the NIOZ-bycatch programme was unequivocally identified as flapper skate based on long interspace between dorsal fins and iris colour. Although it is not certain how the years and preservation technique may have influenced the iris colouration, identification of Museum specimen seems to be a promising approach to further identify historical species occurrence. Historical accounts of common skate also, unintentionally, refer to flapper skate in the North Sea; the maximum size reported in historical documents signifies that flapper skate occurred in the southern part of the North Sea; the maximum size of common skate in the coastal water of the Netherlands was 6 feet (1.8 m) (Coenensz van Schilperoort, 1577–1581) or larger (Schlegel, 1862). Thus, flapper skate might have been the most abundant species throughout the North Sea, although it remains difficult to fully deduce the relative abundance of the two species.

Potential for further population increase

The recent increase in common skate in the northern North Sea raises the question as to whether there is potential for the species to expand into all its endemic regions. This question is not easy to answer because the area has changed in many ways since the disappearance of the species in the 1970s; human activities, habitat, food web, and temperature all changed since then. Changes in habitat should have little effect on the species distribution, as it was argued that common skate have no specific habitat preference (Sguotti *et al.*, 2016). Yet it remains unknown how the species responds to, for instance, disturbance through the building and running of offshore wind farms and gas and oil installations. Furthermore, the species is currently known to place eggs in rocky structures (Phillips *et al.*, 2021), which have largely disappeared from the central North Sea (Callaway *et al.*, 2002; Heessen *et al.* 2015). Present food availability is not expected to pose limits on the species' return to southern regions, since all of the important prey types as found in this study are still present in both the southern and northern North Sea (Callaway *et al.*, 2002), and in comparable densities to historical time periods (Reiss & Kröncke, 2004; Callaway *et al.*, 2007). However, whether food availability may hamper large adult individuals, which were reported to feed on elasmobranch species (Steven, 1932), remains an open question. Changes in water temperature could potentially prevent the species' return to the south, as its stronghold is, and has been, in the colder northern waters (this study and Redeke, 1911). Rather, a northward shift is seen in many species in response to current climate change (Rogers & Millner, 1996; Perry *et al.*, 2005; Dulvy *et al.*, 2008). All these factors notwithstanding, fishing and bycatch pressure seem to be the ultimate factors affecting the species expansion (Brander, 1981; Walker & Hislop, 1998).

Conclusion

By assembling multiple independent historical and contemporary data sources we reconstructed a 120-years perspective on the abundance and ecology of two critically endangered species of common skate in the North Sea (Ellis *et al.* 2021a,b). This information is important for current management and future conservation strategies for both species. Based on our long-term view, we argue that any recovery of common skate is only localised and likely still limited. Our reconstruction of the historical ecology of common skate strongly suggests that the species used to reproduce predominantly in the northern part of the North Sea. Furthermore, we show that it is most likely flapper skate that used to be abundant in the North Sea, whereas the abundance of common blue skate remains unknown. Future disclosure of historical data, especially from museum collections, could further elucidate aspects of the life and fate of common skate and the relative occurrence of flapper skate and common blue skate.

Compliance with Ethical Standards

Conflict of interest: The authors declare that they have no conflicts of interest.

Human and animal rights statement: This article does not contain any studies with animals performed by any of the authors.

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Author contributions RB: Conceptualization, data collection, data analysis, writing. AB: Conceptualization. JJP: Conceptualization. JB: Conceptualization, HvdV: Conceptualization, writing. AvL: Conceptualization, data collection, data analysis, writing.

Data Availability Statement: All data presented in this manuscript will be uploaded to the NIOZ Data Archiving System (https://www.nioz.nl/en/research/dataportal/das).

References

Akçakaya HR, Bennett EL, Brooks TM, Grace MK, Heath A, Hedges S, Hilton-Tayler C, (...) Young RP (2018) Quantifying species recovery and conservation success to develop an IUCN Green List of Species. Cons Biol, 32(5), 1128-1138.

Anslijn N (1828) *Systematische beschrijving der voor ons meest belangijke visschen*. Leyden NL, D. du Mortier en Zoon

Bennet IA, van Olivier G (1825) Naamlijst van Nederlandsche Visschen. de Wed. A. Loosjes, Pz., Haarlem. 122 pp

Bom RA, van de Water M, Camphuysen CJ, van der Veer HW, van Leeuwen A (2020) The historical ecology and demise of the iconic Angelshark *Squatina squatina* in the southern North Sea. Mar Biol 167: 1–10

Brander K (1981) Disappearance of common skate *Raia batis* from Irish Sea. Nature 290: 48–49

Brown SC, Bizzarro JJ, Cailliet GM, Ebert DA (2012) Breaking with tradition: redefining measures for diet description with a case study of the Aleutian skate *Bathyraja aleutica* (Gilbert 1896). Environ Biol Fishes 95: 3–20

Brown-Vuillemin S, Barreau T, Caraguel JM, Iglésias SP (2020) Trophic ecology and ontogenetic diet shift of the blue skate *Dipturus* cf. *flossada*. J Fish Biol 97: 515–526

Callaway R, Alsvåg J, de Boois II, Cotter J, Ford A, Hinz H, Jennings S, Kröncke I, Lancaster J, Piet G, Prince P, Ehrich S (2002) Diversity and community structure of epibenthic invertebrates and fish in the North Sea. ICES J Mar Sci 59: 1199–1214

Callaway R, Engelhard GH, Dann J, Cotter J, Rumohr H (2007) A century of North Sea epibenthos and trawling: comparison between 1902–1912, 1982–1985 and 2000. Mar Ecol Prog Ser 346: 27–43

Coenensz van Schilperoort A (1577–1581) Visboeck. Scheveningen, NL

de Vooys CGN, van der Meer J (1998) Changes between 1931 and 1990 in by-catches of 27 animal species from the southern North Sea. J Sea Res 39: 291–298

Duarte CM, Agusti S, Barbier E, Britten GL, Castilla JC, Gattuso JP, Fulweiler RW, (...) Worm B (2020) Rebuilding marine life. Nature, 580, 39–51.

Du Buit MH (1968) Alimentation de quelques Rajides. Bull Soc sci Bretagne 43: 305–314

Du Buit MH (1977) Age et croissance de *Raja batis* et de *Raja naevus* en Mer Celtique. J Cons Int Explor Mer 37: 261–265

Dulvy NK, Reynolds JD (2002) Predicting extinction vulnerability in skates. Conserv Biol 16: 440–450

Dulvy NK, Rogers SI, Jennings S, Stelzenmüller V, Dye SR, Skjoldal HR (2008) Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. J Appl Ecol 45: 1029–1039

Ellis JR, Silva JF, McCully SR, Evans M, Catchpole T (2010) UK fisheries for skates (Rajidae): History and development of the fishery, recent management actions and survivorship of discards." ICES CM 1–38

Ellis J, McCully-Philipps SR, Sims D, Derrick D, Cheok J, Dulvy NK (2021a) *Dipturus batis*. *The IUCN Red List of Threatened Species* 2021: e.T203364219A203375487. https://dx.doi.org/10.2305/IUCN.UK.2021-2.RLTS.T203364219A203375487.en. Accessed on 17 June 2022

Ellis JR, McCully-Philipps SR, Sims D, Walls RHL, Cheok J, Derrick D, Dulvy NK (2021b) *Dipturus intermedius*. *The IUCN Red List of Threatened Species* 2021: e.T18903491A68783461. https://dx.doi.org/10.2305/IUCN.UK.2021-2.RLTS.T18903491A68783461.en. Accessed on 17 June 2022

Engelhard GH, Lynam CP, Garcia-Carreras B, Dolder PJ, Mackinson S (2015) Effort reduction and the large fish indicator: spatial trends reveal positive impacts of recent European fleet reduction schemes. Environ Conserv 42: 227–236

Engelhard GH, Thurstan RH, MacKenzie BR, Alleway HK, Bannister RCA, Cardinale M, Clarke MW, (…) Lescrauwaet A-K (2016) ICES meets marine historical ecology: placing the history of fish and fisheries in current policy context. ICES J Mar Sci 73: 1386–1403

Fernandes PG, Ralph GM, Nieto A, Criado MG, Vasilakopoulos P, Maravelias CD, Cook RM (…) Carpenter KE (2017) Coherent assessments of Europe’s marine fishes show regional divergence and megafauna loss. Nat Ecol Evol 1: 0170Fock HO, Kloppmann MHF, Probst WN (2014) An early footprint of fisheries: changes for a demersal fish assemblage in the German Bight from 1902–1932 to 1991–2009. J Sea Res 85: 325–335

Froese R, Zeller D, Kleisner K, Pauly D (2012) What catch data can tell us about the status of global fisheries. Mar Biol 159: 1283–1292

Garstang W (1905) Report on the trawling investigations, 1902–3, with especial reference to the distribution of the plaice. First Report on Fishery and hydrographic investigations in the North Sea and adjacent waters (southern area), International Fisheries Investigations, Marine Biological Association, UK: 67–198

Gmelig Meylin A (2009) Eikapsels van roggen, zeldzamer dan ooit. De Levende Natuur 110: 261–262

Griffiths AM, Sims DW, Stephen P, Nagar A El, Ellis JR, Lynghammar A, Mchugh M, (…) Genner MJ (2010) Molecular markers reveal spatially segregated cryptic species in a critically endangered fish , the common skate *Dipturus batis*. Proc R Soc B: Biol Sci 277: 1497–1503

Heessen HJL, Daan N, Ellis JR (2015) Fish Atlas of the Celtic Sea, North Sea and Baltic Sea: Based on International Research-vessel Surveys. Wageningen, NL, Wageningen Academic Publishers

Hoogendijk A (1893) De grootvisscherij op de Noordzee. HD Tjeenk Willink, Haarlem. 349 pp

ICES. (2020a) Manual for the North Sea International Bottom Trawl Surveys. Series of ICES Survey Protocols SISP 10-IBTS 10, Revision 11. 102 pp. http://doi.org/10.17895/ices.pub.7562

ICES. (2020b) SweptArea-based calculations – 2020. 15 pp. https://www.ices.dk/data/Documents/DATRAS/NS-IBTS_swept_area_km2_algorithms.pdf

ICES. (2021) ICES Advice 2021, Book 6.1.1 Greater North Sea Ecoregion - Ecosystem overview. 21 pp

ICES. (2019) Working Group on Elasmobranch Fishes (WGEF). ICES Scientific Reports. 1:25. 964 pp

Iglésias SP, Toulhoat L, Sellos DY (2010) Taxonomic confusion and market mislabelling of threatened skates: important consequences for their conservation status. Aquat Conserv: Mar Freshw Ecosyst 333: 319–333

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, (…) Warnder RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293: 629–637

Knijn RJ, Boon TW, Heessen HJL, Hislop JRG (1993) Atlas of North Sea fishes. ICES cooperative research report, 194 pp

Kynoch RJ, Fryer RJ, Neat FC (2015) A simple technical measure to reduce bycatch and discard of skates and sharks in mixed-species bottom-trawl fisheries, ICES J Mar Sci 72: 1861–1868

Last PR, White WT, de Carvalho MR, Séret B, Stehmann MFW, Naylor GJP (2016) Rays of the World. Melbourne: CSIRO Publishing & Cornell University Press. 790 pp

Lenth R, Singmann H, Love J, Buerkner P, Herve M (2018) Emmeans: Estimated marginal means, aka least-squares means. R package version, 1: 3

Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH, Cooke RG, Kay MC, Kidwell SM, Kirby MX, Peterson CH, Jackson JB (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312: 1806–1809

Lotze HK, Worm B (2009) Historical baselines for large marine animals. Trends Ecol Evol 24: 254–262

Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. Science 308: 1912–1915

Phillips ND, Garbett A, Wise D, Loca SL, Daly O, Eagling LE, Houghton JDR Verhoog P, Thorburn J, Collins PC (2021) Evidence of egg laying grounds for critically endangered flapper skate *Dipturus intermedius* off Orkney, UK. J Fish Biol 4: 1492–1496

Pitcher TJ, Lam ME (2015) Fish commoditization and the historical origins of catching fish for profit. Marit Stud 14: 1–19

R Development Core Team (2020) R: A language and environment for statistical computing. R foundation for statistical computing. Version 3.6.3. Vienna, Austria

Rae BB, Shelton RGJ (1982) Notes on the food of nine species of elasmobranch (part I) and nine species of demersal teleost (part II) fishes from Scottish waters. (Mimeo) ICES CM 1982/G:56

Ramm DC, Xiao Y (1995) Herding in groundfish and effective pathwidth of trawls. Fish Res 24: 243–259

Redeke HC (1911) Visschen verzameld op de tochten van de Wodan 1902-1911. *In* Jaarboek Rijksinstituut Onderzoek der Zee 1911, pp. 63–85

Reiss H, Kröncke I (2004). Seasonal variability of epibenthic communities in different areas of the southern North Sea. ICES J Mar Sci 61: 882–905.

Rice J, Gislason H (1996) Patterns of change in the size spectra of numbers and diversity of the North Sea fish assemblage, as reflected in surveys and models. ICES J Mar Sci 53: 1214–1225

Rijnsdorp AD, van Leeuwen PI, Daan N, Heessen HJL (1996) Changes in abundance of demersal fish species in the North Sea between 1906–1909 and 1990–1995. ICES J Mar Sci 53: 1054–1062

Rijnsdorp AD, Millner RS (1996) Trends in population dynamics and exploitation of North Sea plaice *Pleuronectes platessa* L. since the late 1800s. ICES J Mar Sci 53: 1170–1184

Rijnsdorp AD, Poos JJ, Quirijns FJ, HilleRisLambers R, De Wilde JW, Den Heijer WM (2008) The arms race between fishers. J Sea Res 60: 126–138

Rogers SI, Millner RS (1996) Factors affecting the annual abundance and regional distribution of English inshore demersal fish populations: 1973 to 1995. ICES J Mar Sci 53: 1094–1112

Scharf FS, Juanes F, Rountree RA (2000) Predator size-prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. Mar Ecol Prog Ser 20: 229–248

Schlegel H (1862) Natuurlijke Historie van Nederland. De Dieren van Nederland: Kruipende Dieren. Haarlem, NL, AC Kruseman

Sguotti C, Lynam CP, García-Carreras B, Ellis JR, Engelhard GH (2016) Distribution of skates and sharks in the North Sea: 112 years of change. Glob Change Biol 22: 2729–2743

Shaw G (1804) General Zoology, or systematic Natural History. London, UK, G. Kearsley Fleet Street

Steven GA (1932) Rays and skates of Devon and Cornwall. II. A study of the fishery; with notes on the occurrence, migrations and habits of the species. J Mar Biol Ass UK 18: 1–33

Tesch JJ (1911) Over grootte rogeieren uit de Noordzee. Mededeelingen over visscherij; maandblad in overleg met het College voor de Zeevisscherijen, 18: 38–40

Thursby-Pelham DE (1939) The effect of fishing on the stock of plaice in the North Sea. Conseil Perm. Int. pour L'Exploration de la Mer. Rapp, et Proc-verb Réun, 110: 40–63

van Gemert R, Andersen KH (2018) Challenges to fisheries advice and management due to stock recovery. ICES J Mar Sci 75: 1864–1870

Walker ND, Maxwell DL, Le Quesne WJF, Jennings S (2017) Estimating efficiency of survey and commercial trawl gears from comparisons of catch-ratios. ICES J Mar Sci 74: 1448–1457

Walker PA, Hislop JRG (1998) Sensitive skates or resilient rays? Spatial and temporal shifts in ray species composition in the central and north-western North Sea between 1930 and the present day. ICES J Mar Sci 55: 392–402

Wearmouth VJ, Sims DW (2009) Movement and behaviour patterns of the critically endangered common skate *Dipturus batis* revealed by electronic tagging. J Exp Mar Biol Ecol 380: 77–87

Wheeler A (1978) Key to the fishes of Northern Europe. London, UK. Warne Ltd

Wimpenny RS (1953) The plaice: Being the Buckland lectures for 1949. E. Arnold. London

Tables & Figures

Table 1. Data sources used for this study, including details of the data

Type of data	Analysis	Sample size	Classification	Period	Source	North Sea division	Origin
fishery-independent surveys	number per swept area	252 surveys	Historical	1902−1911	RIVO Dutch governmental fishing agency	central and southern	Redeke (1911)
fishery-independent surveys	number per swept area	3227 surveys	Historical	1902−1964	CEFAS The Centre for Environment, Fisheries & Aquaculture Science	central and southern	downloads from https://data.cefas.co.uk/
	size	308 individuals					
fishery-independent surveys	number per swept area	685 surveys	Historical	1902−1932	Research Vessel FRV "Poseidon I"	northern and central	Heino Fock personal information
	size	71 individuals					
fishery-independent surveys	number per swept area	28409 surveys	Contemporary	1965−2020	ICES International Council for the Exploration of the Sea	northern, central and southern	https://datras.ices.dk/Data_products/Downlo d/ Download_Data_public.aspx haul information (HH,) and length information (HL) downloaded
	size	299 individuals					
	species identification	163 individuals					
Fishery-dependent	Dutch commercial landings data		Historical and Contemporary	1901−1970	local Dutch authorities	greater	reported in "Verslagen en mededelingen van d Directie van de Visserijen"
Fishery-dependent	size	658 individuals	Historical and Contemporary	1930−1990	NIOZ-bycatch programme	central and southern	NIOZ archive
	seasonal occurrence	755 individuals					
	sex ratio	491 individuals					

	stomach contents	405 individuals					
	species identification	1 individual					

Table 2.

Fishery-independent surveys summary in terms of vessel, gear, period, number of sampled stations, , surface of swept area, towing speed (knots), headline (m), wingspread (m) and wing distance (m) between 1902–2020. Note: Wing distance recorded or calculated from the headline and assumed wingspread. Towing speed and wing distance used to estimate abundance (number per swept area).

Classification	Vessel	Nation	Gear	Period	# Stations	Surface of swept area (km^2)	Towing speed (knots)	Headline (m)	Wing spread	Wing distance measured (%)	Average wing distance (m)	comm skate record (#)
Historical	Wodan	the Netherlands	otter trawl	1902-1911	252	29	2	26.5[1]	2/3 of headline			29
Historical	Huxley	United Kingdom	otter trawl	1902-1909	350	97	2	26.5[1]	2/3 of headline			69
Historical	Poseidon I	Germany	otter trawl	1902-1906	91	16	2	27[2]	2/3 of headline			34
Historical	Poseidon I	Germany	otter trawl	1904-1932	623	61	2	29[2]	2/3 of headline			87
Historical	George Bligh	United Kingdom	otter trawls	1922-1939	205	29	2	18.92[3]	2/3 of headline			2
Historical	Sir Lancelot	United Kingdom	otter trawls	1947-1960	1,382	141	2	24.383[4]	2/3 of headline			99
Historical	Platessa	United Kingdom	otter trawl	1946-1959	757	60	2	18.93[3]	2/3 of headline			89
Historical	Platessa	United Kingdom	Dutch Herring Trawl	1951-1959	159	11	2	23.74[4]	2/3 of headline			4
Historical	Clione	United Kingdom	otter trawls	1961-1964	210	17	2	26.5[5]	2/3 of headline			4
Historical	Clione	United Kingdom	Dutch Herring Trawl	1961-1964	164	13	2	23.74[5]	2/3 of headline			3
Contemporary	ICES	all*	Dutch Herring Trawl	1965-1979	1182	121	4	23.76[6]	2/3 of headline			12
Contemporary	ICES	all*	Herring Bottom Trawl 180 feet	1966-1984	931	191	4	54.84[5]	2/3 of headline			20
Contemporary	ICES	all*	Aberdeen 18 ft trawl	1992-1997	529	74	4		measured	61%	20.44	0

Contemporary	ICES	all*	GOV trawl	1967-2020	29,588	1887	4		measured	28%	19.2	288

*United Kingdom, Norway, Denmark, Sweden, Germany, the Netherlands, France

1) Rijnsdorp *et al.* (1996); 2) Fock *et al*. (2014); 3) assumed from Wimpenny (1953); 4) Wimpenny (1953); 5) ICES 2020; 6) assumption present study; 7) Knijn *et al.* (1993)

Table 3. Diet composition of common skate in the North Sea (N = 405, median = 42 cm, 20 – 177 cm LT) caught during 1946 – 1969 in the NIOZ-bycatch programme, analysed in the early 20th century, showing number of stomachs with prey (n_i), percentage of prey-specific number (%PN), percentage of numbers (%N), and the percentage of occurrence (%FO)

Class	**Order**	**Family**	**Species**	**n_i**	**%PN**	**%N**	**%FO**
Actinopterygii				23	54.77	3.11	5.68
	Clupeiformes	Clupeidae		3	37.10	0.27	0.74
			Clupea harengus	2	54.55	0.27	0.49
			Clupea spp	1	2.22	0.01	0.25
	Gadiformes			5	37.00	0.46	1.23
		Gadidae		5	37.00	0.46	1.23
			Merlangius merlangus	3	36.67	0.27	0.74
			Trisopterus minutus	2	37.50	0.19	0.49
	Perciformes	Ammodytidae		4	42.99	0.42	0.99
			Ammodytes marinus	1	50.00	0.12	0.25
			Hyperoplus lanceolatus	3	40.66	0.30	0.74
	Pleuronectiformes			13	53.19	1.71	3.21
		Bothidae		1	25.00	0.06	0.25
			Arnoglossus spp	1	25.00	0.06	0.25
		Pleuronectidae		3	69.44	0.51	0.74
			Limanda limanda	2	70.83	0.35	0.49
			Pleuronectes platessa	1	66.67	0.16	0.25
		Soleidae	*Solea solea*	1	100.00	0.25	0.25
	Scorpaeniformes	Agonidae	*Agonus* spp	1	100.00	0.25	0.25
Cephalopoda				2	22.50	0.11	0.49
	Sepiida	Sepiolidae	*Sepiola* spp	1	25.00	0.06	0.25
Malacostraca	Decapoda			377	97.72	90.97	93.09
		Corystidae	*Corystes cassivelaunus*	1	100.00	0.25	0.25
		Crangonidae		332	78.46	64.32	81.98
			Crangon allmanni	206	50.50	25.69	50.86
			Crangon crangon	145	53.03	18.99	35.80
			Crangon spp	63	94.83	14.75	15.56
			Philocheras trispinosus	47	28.90	3.35	11.60
			Pontophilus spp	1	38.46	0.09	0.25
			Pontophilus spinosus	18	32.49	1.44	4.44
		Polybiidae		13	69.60	2.23	3.21
			Liocarcinus spp	12	74.80	2.22	2.96
			Macropipus spp	1	7.14	0.02	0.25
		Portunidae	*Portunus holsatus*	2	41.67	0.21	0.49
		Processidae		161	58.10	23.10	39.75
			Processa canaliculata	9	32.61	0.72	2.22
			Processa spp	151	59.08	22.03	37.28
			Processa parva	4	34.66	0.34	0.99
	Isopoda			1	0.90	0.00	0.25
	Mysida			1	16.67	0.04	0.25
Polychaeta				1	50.00	0.12	0.25

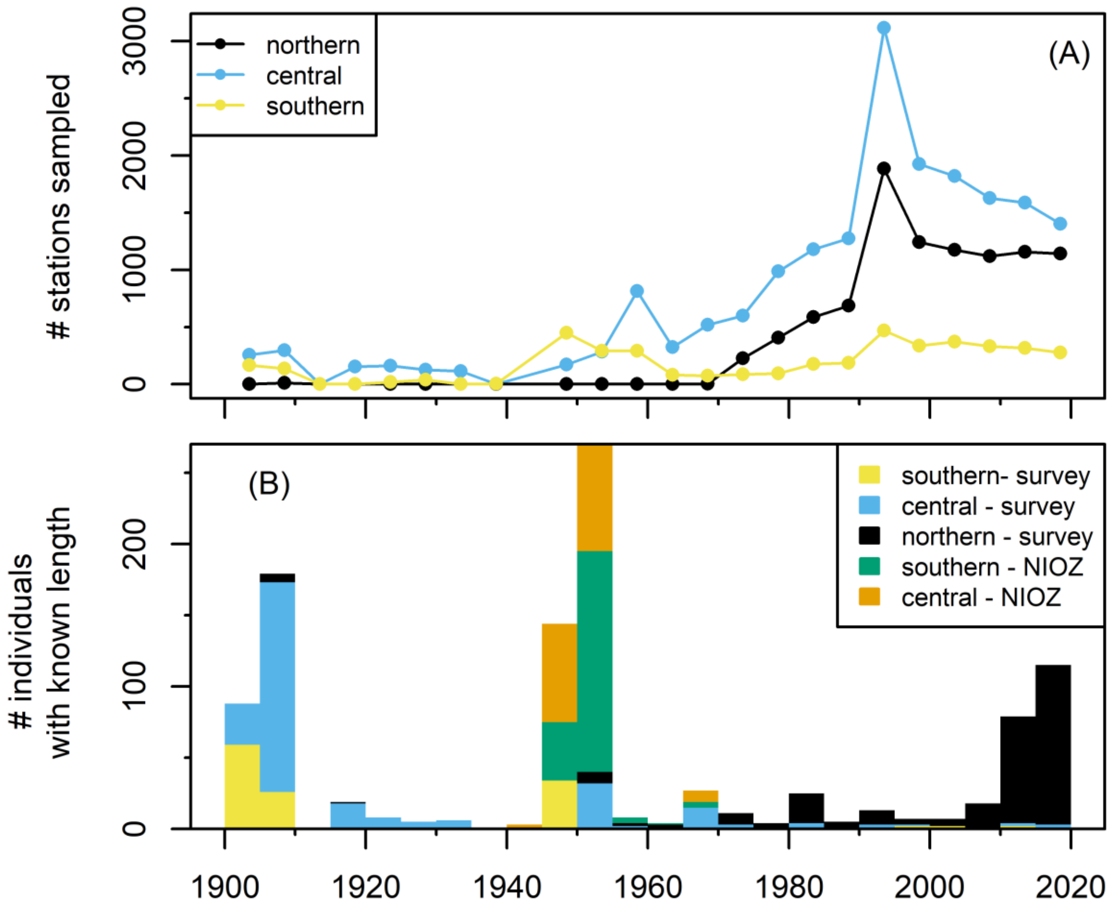

Figure 1. (A) Number of stations sampled during fishery-independent surveys in the North Sea by ICES Division over a 120-year time period, aggregated across pentad. (B) Number of common skate with available length information used in the analysis by ICES Division and data source (fishery-independent surveys or NIOZ-bycatch programme), aggregated across pentad.

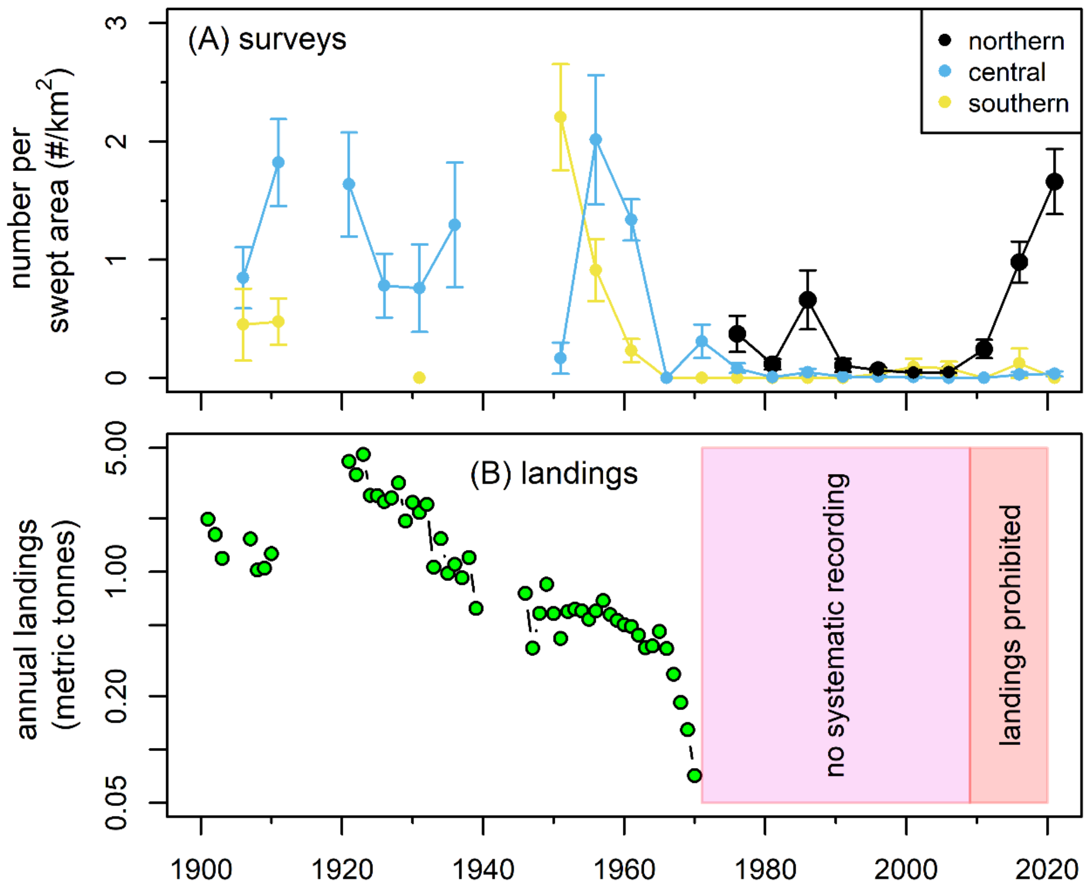

Figure 2. Time series of common skate abundances: (A) Number per swept area per pentad calculated from fishery-independent surveys in the northern, central, and southern ICES divisions in the North Sea. Error bars represent standard errors calculated by taking the number of stations sampled per pentad as sample size. Data included from Q1 to Q4. (B) Annual landings of common skate in the Netherlands. Data from other nations not considered. Note the log scale on the y-axis of figure B.

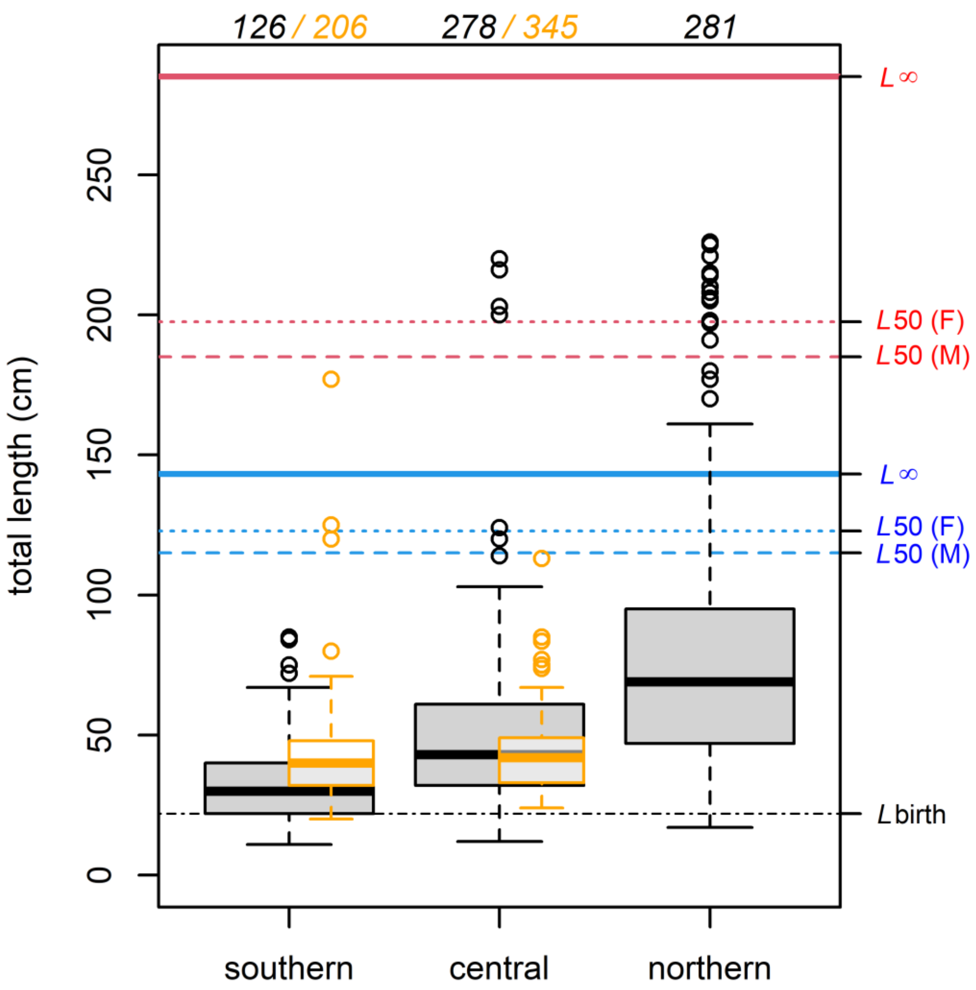

Figure 3. Total length of common skate in catches from northern, central, and southern ICES divisions in the North Sea. Thick horizontal black and orange lines show medians, top and bottom lines of boxes show the 25th and 75th percentiles, whiskers show 1.5 times the interquartile range. Black boxplots show data from fishery-independent surveys and orange transparent boxplots show data from the NIOZ-bycatch programme. Numbers at the top refer to sample sizes. See the main text for referred sources to justify size thresholds connected with life-history events in common blue skate and flapper skate, as indicated on the right.

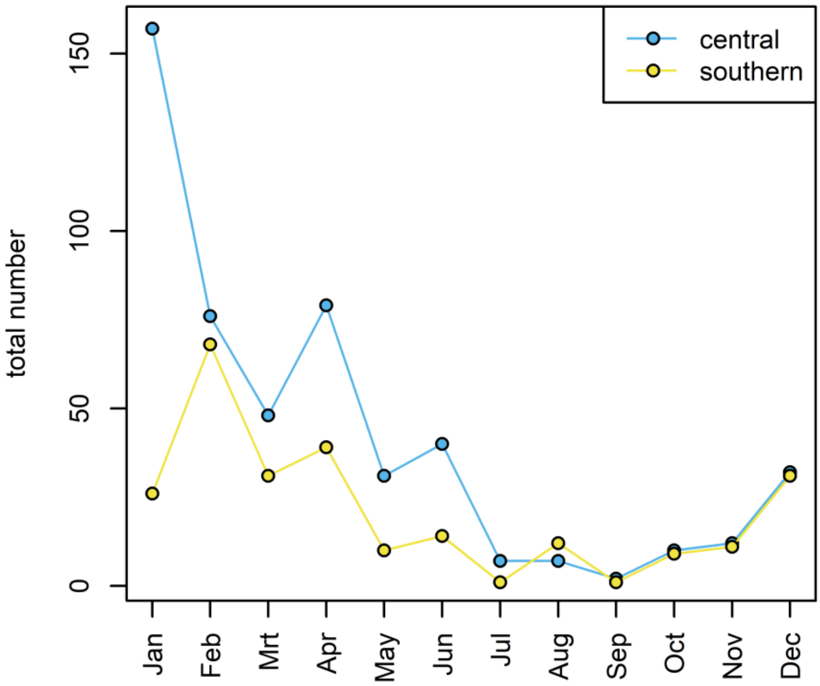

Figure 4. Total number of common skate caught monthly in the central and southern ICES divisions in the North Sea reported in the NIOZ-bycatch programme during 1938 – 1970.

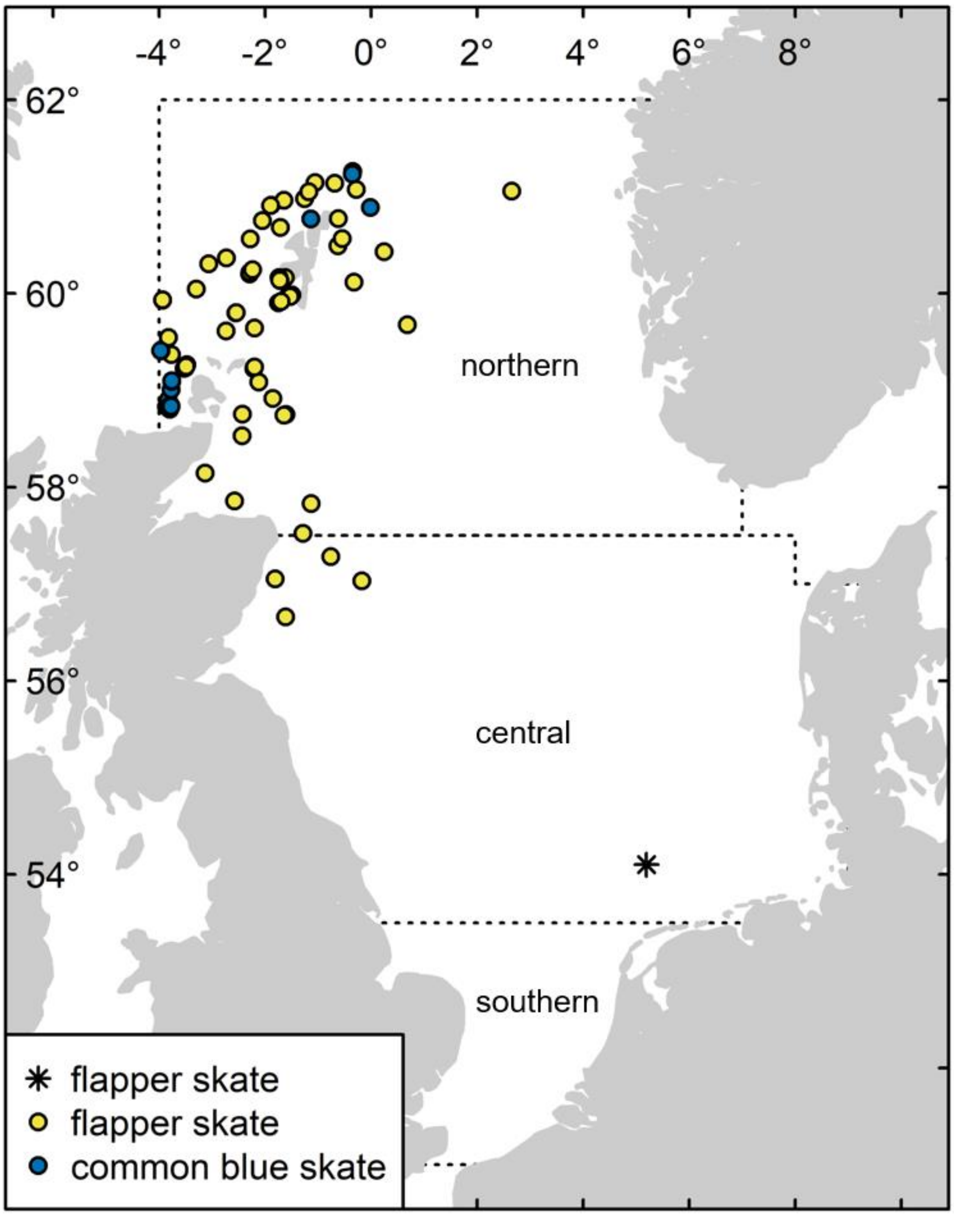

Figure 5. Location records of common blue skate and flapper skate in the North Sea fishery-independent surveys from 2012 – 2020 (circles) and record of a single specimen of flapper skate encountered in 1938 from the NIOZ-bycatch programme (Asterix). Note: Different colours and symbols to represent species and sources. Dashed lines show the boundaries of the ICES divisions in the North Sea.