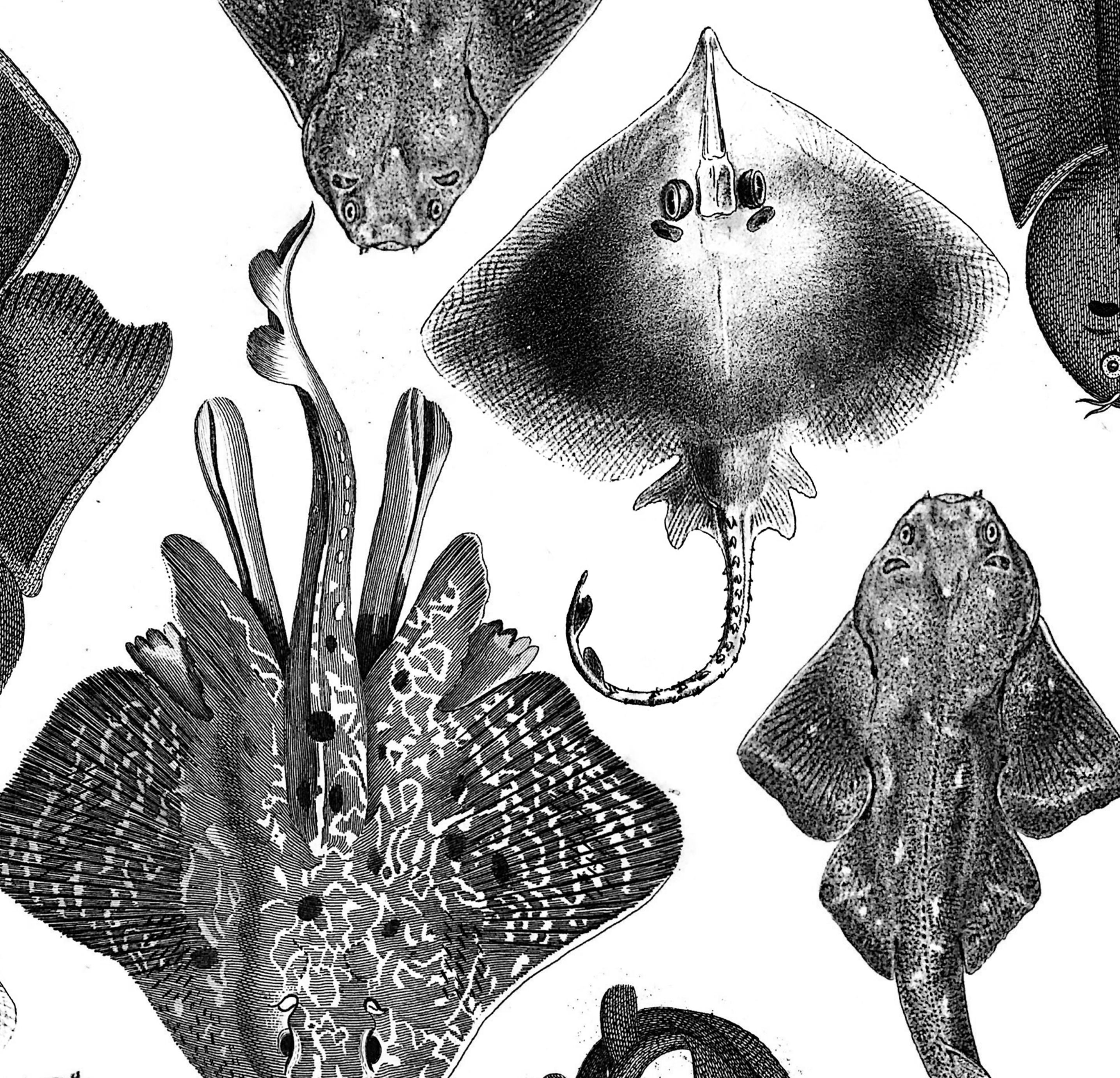

The historical occurrence of the angelshark *Squatina squatina* and common skate *Dipturus batis* in Dutch coastal waters

2019-01

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– Abstract

The North Sea is known for its natural richness. The area is also among the most intensively exploited seas in the world, and there is a rising concern of fisheries impact, as many fish species have disappeared or populations are marginalized. With the loss of fish biodiversity there is a growing call to restore the natural richness of the North Sea. However, it is often unclear what this natural richness is, because our baseline often dates back one or two human generations. Elasmobranchs (sharks, skates and rays) are an example of a group of species of which the populations in the North Sea have marginalized over the past century. Two Elasmobranch species, the angelshark *Squatina squatina* and common skate *Dipturus batis* are now locally extinct and are globally critically endangered. Here we review the historic abundance and some important life-history aspects of these species in the Dutch part of the area, and the adjacent Dutch inlet seas.
Palaeontological sources dating back to the origin of the North Sea (2.5 million year ago) suggest that angelshark and common skate have always been present in the North Sea. Written historical sources from the 16th to the 19th century suggest that the angelshark used to be fairly common and that the common skate was common or very common in the Dutch waters. Catch reports indicate that the angelshark started to decline at the onset of the 20th century and went locally extinct in the Dutch North Sea in the 1970s. Time series (landing data and fishery-independent data) of common skate show a similar picture. We see that the start of the decline of both species coincides with the onset of steam-powered fisheries whereas the demise follows on the intensification of diesel-powered beam-trawlers.
Historical reports and catch data indicate that the angelshark mainly occurred in the summer months in shallow waters close to the coast. Only adults, sometimes gravid females, and new-born individuals were caught, suggesting that the species used the area as a nursery ground. Common skates were mainly caught in winter months and these were mainly young individuals, below the maturation size. This suggest that this species used the area as a nursery ground, although catches of freshly laid eggs show that the species also used to reproduce in the area.
Our overview shows that species that are now lost from the Dutch waters were once an abundant part of the North-Sea food web. If we base our ideas of a North Sea ecosystem on a baseline view after 1900 we may have overly low expectations of its potential natural richness. That means that we may underestimate the value of restoration and reduction of exploitation.

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– Introduction

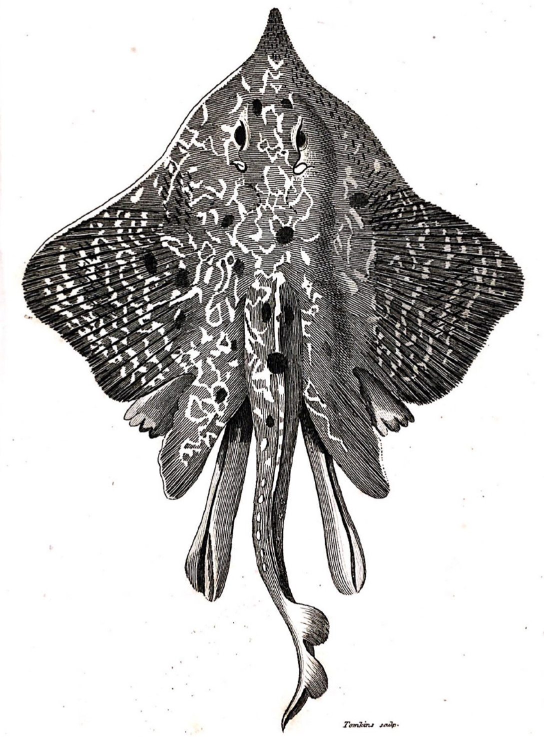
Overfishing has caused worldwide stock collapses and local extinctions, and although marine defaunation has lagged behind terrestrial species loss, the effects of anthropogenic impacts are catching up in the world's oceans (McCauley et al. 2015). The loss of ocean biodiversity has resulted in reductions of ecosystem services (Worm et al., 2006), and because the majority of these losses is seen in predatory species, they can result in wide-spread trophic cascades (Myers et al., 2007). Marine predatory fish biomass was in 2003 estimated to be at 10% of the biomass before industrial exploitation (Myers and Worm 2003). For the temperate Atlantic region, this estimate comes down to approximately 5% of predator biomass remaining (Myers and Worm 2003).

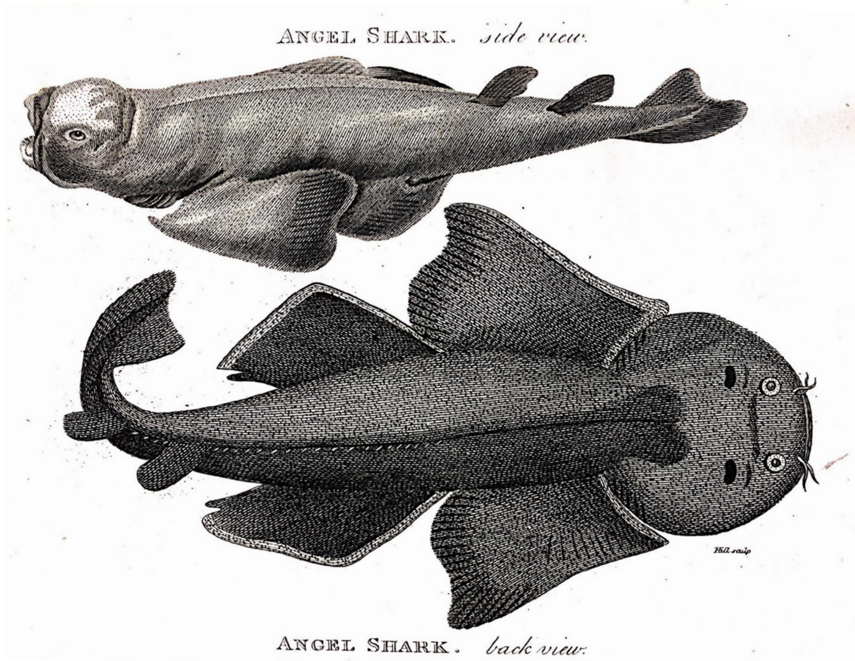
One system where the impact of anthropogenic forces has been seen over the course of multiple centuries is the North Sea. This area used to be extremely rich and arguably much of the sources of the Dutch and British golden ages are linked to the superfluous North Sea resources (Bennema and Rijnsdorp, 2015). Nowadays many fish populations are marginalized to low levels, and North Sea fisheries are not what they once used to be, although still, two million tonnes of fish are yearly taken from this ecosystem by 6600 fishing vessels (ICES, 2018a).

At the same time, the North Sea is an example of how reduction in fisheries can lead to the return of fish species: In the last decade, fisheries have reduced their impact and it is thought that many commercially fished populations are currently exploited at a sustainable level (ICES, 2018a). As a supposed result, standing stock densities of, for instance, plaice *Pleuronectes platessa* (ICES, 2017a) and thornback ray *Raja clavata* (ICES, 2017b) have increased.

A problem is that our knowledge of marine systems, including the North Sea, is predominantly based on data collected after humans started to exploit these systems, and often only since industrialized exploitation was well underway (Jackson et al., 2001). Such observations fail to encompass the life-spans of many ecologically important species as time series at best date back 30-50 years. To judge the status of an ecosystem on the basis of such time series, can lead to a 'shifting baseline' syndrome (Pauly, 1995). However, a wide range of different data sources is available to define or deduce historic marine population status, including 'traditional' written sources but also less conventional sources such as analysis of paleontological sources, archaeological remains, or simple anecdotal evidence (for instance deduced from newspapers). It has been argued that a wider appreciation of such data can clarify underlying causes and rates of ecological change (Dalzell, 1998; Jackson et al., 2001; Sáenz-Arroyo et al., 2006). Moreover, they set goals for restoration and management of coastal ecosystems that could not even be contemplated based on the limited perspective of recent observations alone (Jackson et al. 2001).

Sharks and rays (together grouped in the Elasmobranchii subclass) are among the large marine vertebrates that are now present in only a small fraction of their historical abundances, particularly in coastal ecosystems (Jackson 2001). According to the IUCN, currently 31% of shark and ray species are threatened with extinction [https://www.iucnredlist.org/]. Two elasmobranch species once occurring in the North Sea are now critically endangered at a global scale: the angelshark *Squatina squatina* and the common skate *Dibturus batis* (Dulvy et al., 2006; Ferretti et al., 2015). (Picture 1) Fishermen have largely forgotten these species, which may typically be a result of the shifting baseline syndrome (Pauly, 1995). Yet, conservation bodies are well aware that the species were once present in the North Sea food web but it remains largely unknown how abundant they once were, especially in case of the angelshark. Moreover their decline has been poorly reconstructed and their role in the historical North Sea food web is largely unknown, likewise it remains unknown how they used the area (Heessen et al., 2015). Here, using a wide range of paleontological, archaeological, historical and ecological sources, we aim to set a historical baseline for both species and at the same time aim to deduce their historic role in the food web in relation to changes in North Sea fisheries, climate and habitat.





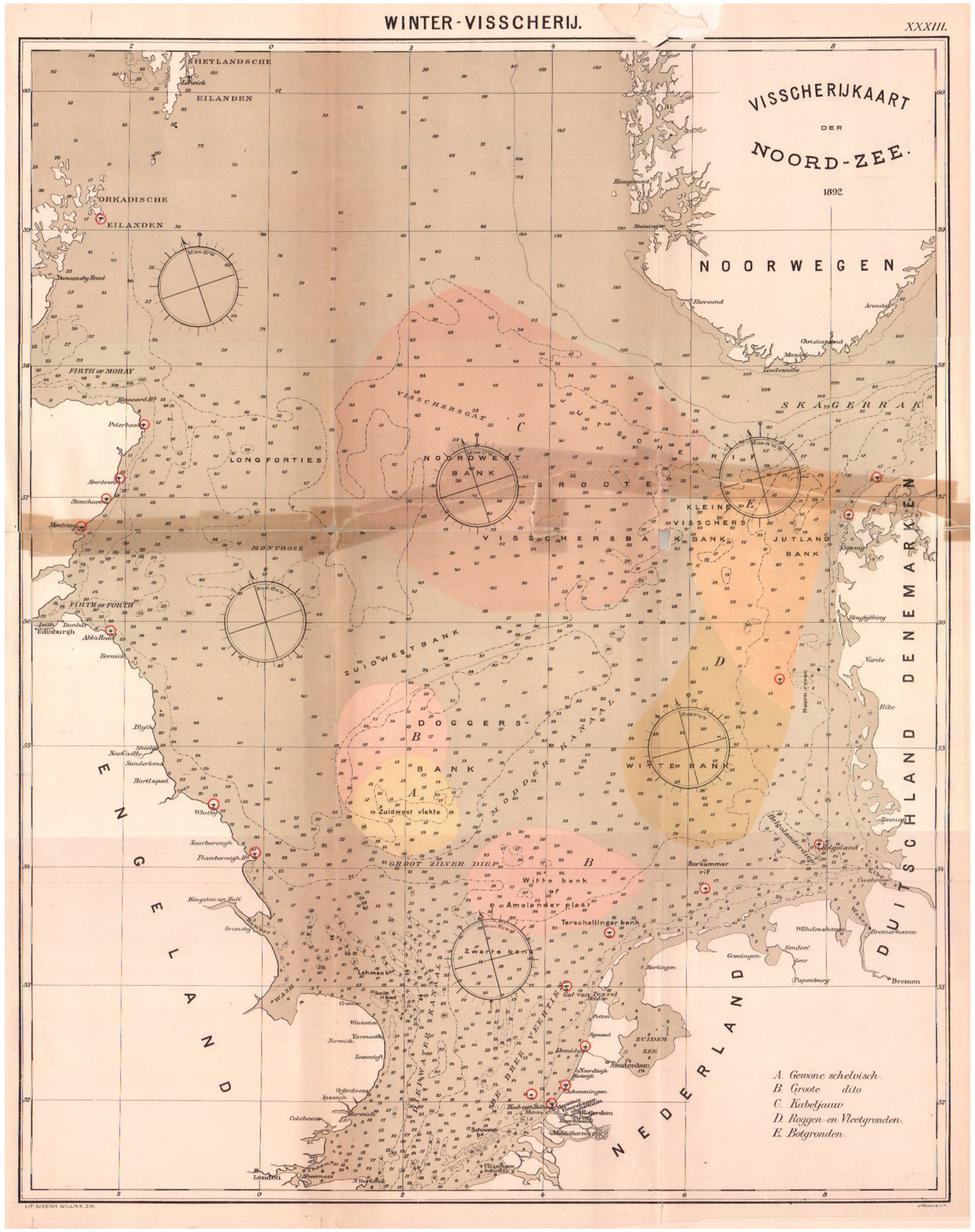
Picture 1. Angelshark and common skate according to Shaw (1804)

– Methods

To bring the historical occurrences of angelshark and common skate in the Southern North Sea into view, we focused on the Dutch part of the North Sea. This means we also focused our efforts in literature and data-base searches on material directly connected with the Netherlands or Dutch fisheries. The findings we present in this report differ between angelshark (mostly qualitative and anecdotal) and common skate (more quantitative and some time-series of longer duration). The background behind these data and the assumptions or conversions made to summarize them are detailed below.

Area definition

The North Sea is a marginal sea of the Atlantic Ocean, located on the European continental shelf between Norway, Sweden, Denmark, Germany, the Netherlands, Belgium, France and Great Britain. The North Sea occupies an area of 575.000 km². The Dutch part of the North Sea (Nederlandse Continentaal Plat, NCP) occupies an area of 57,000 km² and stretches north to a latitude of almost 56° NL and south to a latitude of about 51.5° NL.
The North Sea is a relatively shallow sea, with a depth of less than 30 m in the south to about 200 m in the north. Most of the North Sea consists of sandy sediments (IDON, 2004). The origin of the North Sea basin dates back to the onset of the Tertiary (66.0 to 2.58 million years), but most of the current geomorphology is related to Pleistocene and Holocene processes (2.58 million years to now (IDON, 2004).
The Dutch part of the North Sea is relatively shallow. Within 12 miles from the coast the depth is almost everywhere less than 10 m deep. Outside this area, in the southern part of the NCP the North Sea is hardly deeper than 20 m. In the northern part deeper areas up to 70 m are found (IDON, 2004). The sea floor of the NCP consists mainly of fine (125 - 250 µm) to medium sand (250 - 500 µm). Small gravelly areas occur in the northern part (Creutzberg et al., 1984; IDON, 2004). Scattered throughout the area some boulders, relicts from the last ice ages, can be found.
Besides the marine waters of the North Sea, the Netherlands consist of a number of inlet seas and estuaries that have been of great importance for fisheries (Picture 2). In this respect, the most important areas are the Wadden Sea, the Zuiderzee, the Eastern Scheldt (Oosterschelde), Western Scheldt (Westerschelde), Grevelingen and the Haringvliet. All these inlet seas are basins typically basins consisting of muddy and sandy sediments. The Wadden Sea covers Denmark, Germany and the Netherlands. The Dutch part is 2.500 km². The Zuiderzee was a large (5.900 km²) brackish inlet that has been closed off in 1932, after which it became a freshwater lake. The Eastern Scheldt is an estuary with a size of 350 km² that was partially closed by a storm surge barrier in 1986. The Western Scheldt is an estuary of 300 km² in the very south of the Netherlands. Grevelingen and the Haringvliet are inlet seas of 110 km² and 116 km² respectively that were completely closed off from the North Sea in 1971 and 1970 respectively.
In this study we mainly focus on fish catches in the Dutch inlet seas and the NCP. Collectively we refer to them as the Dutch waters. The motive for this focus is that many of the historical sources in Dutch language refer to the fish in these waters. We assume that historical sources that refer to 'onze wateren' (our waters) also cover this area.
To place the results in an ecologically more rel-



Picture 2. Map of Hoogendijk (1893) including the 'Vleetgronden' above the north-east of the Netherlands, Germany and stretching along the Danish coast (see letter D).

evant context we regularly refer to other studies in northern North Sea, central North Sea and southern North Sea. Following ICES standards, the border between the northern North Sea and the central North Sea is set at a latitude of 57.5° NL and the border between the central North Sea and the southern North Sea at a latitude of 53.5° NL. The southern North Sea stretches south to 51° NL. The NCP covers both parts of the southern North Sea and the northern North Sea.

Fisheries

Fish in the North Sea including the Dutch part has been exploited for centuries and fishing vessels and fishing gear have changed dramatically over time (Engelhard, 2008; Bennema and Rijnsdorp, 2015). In the 10th century fisheries shifted from inland to marine, whereas in medieval times demersal fish in shallow coastal waters were exploited from small sailing vessels (Bennema and Rijnsdorp, 2015). Arguably, one of the most dramatic changes in fisheries was the replacement of sailing vessels by steam-powered trawlers by the end of the 19th century and likewise the replacement of steam trawlers by diesel-powered motor trawlers in the early 1960s (Rijnsdorp and Millner, 1996; Rijnsdorp et al., 2008). Both changes in vessels and gear had enormous effects on fish populations. It is estimated that steam-trawlers were able to catch four times as much as contemporary sailing trawlers (Garstang, 1900). Diesel-powered motor trawlers probably had a similar effect (Daan et al., 1990).

Climate

Changes sea temperature can have profound influence on the distribution of species over time (Perry et al., 2005). Water temperature of the North Sea has changed dramatically over time, especially with the coming and going of the ice ages. After the last ice age (about 10.000 years ago) until now the North Sea has been relatively warm, though with still relevant fluctuation in sea temperature. From 1300 to 1850 the North Sea was affected by the so-called 'Little Ice Age' resulting in relatively colder temperatures (Mann et al., 2009). After 1850 temperatures rose until about 1900, after which it dropped little. In the 1980s temperatures rose again quite sudden (Perry et al., 2005). It is now thought that in that period, because of this sudden increase in temperatures, the ecosystem went through a regime shift (Beaugrand, 2004). At a local scale also large fluctuations in water temperature have been noted due to the influence of local atmospheric processes, leading to microclimates that varies between sites between years (MacKenzie and Schiedek, 2007).

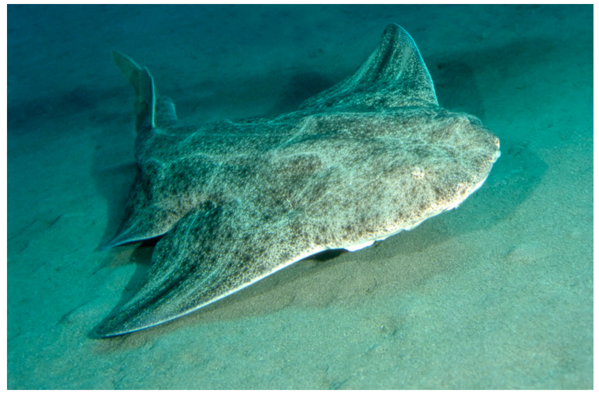
Habitat change

The North Sea habitat has gone through some recent changes, mainly after World War II. Many boulders have been removed by fishermen. On the other hand, structures have been introduced first in the form of oil and gas platforms and more recently in the form of windmill parks. These structures offer settlement and hiding opportunities for (prey of) fish, and they have large impact on fish populations because fishing is prohibited in their vicinity (ICES, 2018b).
The inlet seas in the Netherland changed under the influence of humans when dikes were constructed. Dike construction means that the gradual transition that existed between the sea and the land and freshwater became much more abrupt. In the last century artificial constructions propelled by the construction of dams sometimes completely closed off several inlet seas.

Species description

Angelshark

Historically, angelsharks (Picture 3) occurred around the European and North-African continental shelves, stretching from Scandinavia to Mauritania, and the Mediterranean Sea and the Black Sea (Ebert and Stehmann, 2013; Heessen et al., 2015). Angelsharks have declined dramatically over the last century and their distribution is now reduced to patches in the Mediterranean Sea and the European shelves. A presumed last stronghold population is located around the Canary Islands (Ferretti et al., 2015; Miller, 2016).
The angelshark is a dorsal-ventrally flattened species. The maximum 'authenticated' tail-length of angelsharks is 183 cm for males and 244 cm for females and the maximum weight is 80 kg (Quigley, 2006), but the source for these measurements remains unknown. The maximum length reported from the Mediterranean Sea is 130 cm for males and 169 cm for females (Capapé et al., 1990). The same study reports a length at maturity of 78 cm for males and 80-132 cm for females. Angelsharks are yolk–sac viviparous (Ebert and Stehmann, 2013). Females have a two- or three year reproductive cycle (Capapé et al., 1990) with a gestation period of 8 to 10 months. Young are born in December to February in the Mediterranean (Capapé et al., 1990) and in July in England waters (Compagno et al., 2005), although the source of this latter statement remains elusive. Angelsharks have litters of 8-18 young (Capapé et al., 1990), or perhaps up to 25 young (Quigley, 2006). Reported size at birth is 25-28 cm (Capapé et al., 1990). Growth parameters are unknown.
Angelsharks are sedentary bottom-dwelling species. They are ambush predators feeding upon flatfish and other fish, octopuses and crabs (Ellis et al., 1996; Rogers and Ellis, 2000).
There is a long-term, but unconfirmed suspect that the angelshark is a migratory species, at least in the northern range of its distribution (Quigley, 2006; Ebert and Stehmann, 2013).



Picture 3. Angelshark at an unknown location. Picture by Peter Verhoog.

Tagging of angelsharks in the Irish Sea confirmed that the species is capable of long migrations, but also showed that the species is highly site faithful, at least between years (Quigley, 2006). Tagging in the Mediterranean Sea suggested that the species is highly site faithful in this part of its distribution (Capapé et al., 1990). Angelsharks are found from inshore areas to the outer shelf, from 5 m to at least 150 m depth (Ebert and Stehmann, 2013). Apparently, shallow waters are generally more frequented by juveniles and pregnant females (Lipej et al., 2004; cited in Fortibuoni et al., 2016, data could not be checked).
The decline in angelsharks is poorly reconstructed, but is linked to the historical and current overfishing (Fortibuoni et al., 2016; Miller, 2016). The life-history traits of the species, such as living at the bottom and their low productivity renders the species particularly susceptible to non-targeted demersal fisheries.

Common skate

From the mid-19th century onwards two species of the common skate complex have become recognized: the flapper skate *Dipturus intermedia* and the blue skate *Dipturus flossada*. In 1926 these two species were synonymized into one species; the common skate *D. batis* (Clark,

1926). Only in 2010 genetic and morphological studies proved that there are indeed two species (Griffiths et al., 2010; Iglésias et al., 2010). Where possible this document refers to the species separately, the confounded data are referred to as common skate.
Historically the common skate (Picture 4) used to occur throughout the Eastern North Atlantic and the Mediterranean Sea. In the Atlantic its distribution ranged from East-Greenland and the Barents Sea in the north to Western North Africa in the south (Ebert and Stehmann, 2013; Heessen et al., 2015). The population is now marginalized to a few location in the European Atlantic. It is thought that the 'refugial' population of the flapper skate can be found in the northern North Sea and off northwest Scotland and the blue skates reside in the waters off the western coast of Ireland and the Celtic Sea (Heessen et al., 2015). It is thought that both species used to live sympatrically throughout most of their original distribution area, with the flapper skate having a more northwards oriented distribution (Ebert and Stehmann, 2013).

Picture 4. Common skate caught in 1965 by Dirk Hoek from Katwijk, vessel IJM 36 (from Heessen 2010).

The common skate is one of the largest benthic predators of the Atlantic Ocean (Wearmouth and Sims, 2009). The flapper skate is the largest of the two species. The maximum reported length of this species is 285 cm (Wheeler, 1978), and the length at 50% maturity was reported at 185 cm for males and 197.5 cm for females. The maximum length of the blue skate is 143.2 cm and the reported length at 50% maturity for this species is 115 cm for males and 122.9 cm for females (Iglésias et al., 2010). Common skates are oviparous. Their egg cases are very large compared to other oviparous fish, measuring up to 25 by 15 cm (Ebert and Stehmann, 2013). Egg cases are deposited in the spring and summer, with embryonic development taking several months to possibly years in colder waters at high latitudes (Ebert and Stehmann, 2013). The length at birth of common skate in the Irish Sea (i.e. probably blue skate) is 22 cm (Brander, 1981). Compared to other fish, including other Elasmobranches, the species is a relatively slow grower (Du Buit, 1977), resulting in a relatively high age at reproduction.
Stomachs of juvenile skates (< 50 cm) mainly contained crustaceans (*Crangon spp*. and *Pandalus spp*.) and some fish. Bigger specimens appeared to have fed principally on a wide variety of demersal fish, on several crustacean species, and on some cephalopods (Rae and Shelton, 1982). The species is reported to live in deep waters, around 200 m and down to 600 m (Ebert and Stehmann, 2013). There is little information on the migratory behaviour of common skates. Mark-recapture studies suggested that males move away from inshore fishing grounds (Little, 1997) whereas a recent tracking study suggested that (large) females off the west coast of Scotland refrain from large-scale migratory movements and in fact are highly site faithful throughout the year and only perform vertical movements (Wearmouth and Sims, 2009).
The species is thought to have declined at many parts of its distribution since the early years of the twentieth century, including the Irish Sea (Brander, 1981) from which it was extirpated in the 1970s (Dulvy and Reynolds, 2002). Its decline is linked to fishing as it is thought that the relatively slow growth, late maturation and low fecundity renders common skate populations particularly susceptible to high mortality rates (Brander, 1981). Historically (at the end of the 19th century) the species was targeted by fisheries, at least in the North Sea near Helgoland (Hoogendijk, 1893), but probably most of the recent mortality is linked to non-targeted fisheries.
Currently, the IUCN lists the common skate as critically endangered (Dulvy, et al., 2006). It is thought that the flapper skate is the more endangered of the two (Griffiths et al., 2010), but the IUCN assessment has not been updated for the two species.

Data sources

Paleontological and archaeological records

Paleontological surveys often reveal teeth of sharks, rays and skates, which in many cases can be identified at the species level. When fossils are found in sediment layers of known age, they can be linked to a specific time period. We searched the online peer-reviewed archive (https://scholar-google-nl) and the online portal for Dutch nature magazines (http://natuurtijdschriften.nl) for paleontological surveys in the Netherlands to report angelshark and common skate. Selected articles were restricted to time periods in the Pleistocene (i.e. when the current North Sea was formed). These same sources were used for records of angelshark or common skate based on archaeological excavations.

Qualitative time series

We carried out an extensive survey using historical books and reports to reconstruct a qualitative occurrence of angelshark and common skate in the Netherlands in the last 4 centuries. For this, the prime source was the library of the NIOZ which has extensive access to historical books. Other books were consulted via the online library www.books.google.com and via the Royal Dutch library https://www.kb.nl/galerij. In total we checked 16 books and reports in the time period 1577-1987.

Quantitative time series

We reconstructed quantitative time series for angelshark and common skate on the basis of available data, which differed for the two species.
Angelsharks were rarely caught in fishery-independent surveys (see below), and therefore it is impossible to reconstruct a fishery-independent time series for this species. For the angelshark a time series was made by assembling all specimen caught in the Dutch waters. For this collection, an important source was the archive of Royal NIOZ-of landed fish. This archive contains data of bycatch of commercial fishing vessels from the Southern North Sea between 1930-1990 (de Vooys and van der Meer, 1998). Another source for catch data was the Dutch newspaper and magazine archive (www.delpher.nl), which has archived most of the Dutch newspapers and many magazines dating back to 1618. In this archive we searched for the various Dutch names (i.e. Zee-engel, zee engel, zeeëngel, schoorhaai, schoerhaai, pakhaai, vioolvis, paddehaai, speelman, bergelote) and the four Latin names (i.e. *Rhina squatina*, *Squatina squatina*, *Squatina angelis*, *Squalus squatina*) that have been used as synonyms for the species. Other sources were the Global Biodiversity Information Facility (https://www.gbif.org), the contemporary collection of the Dutch Natural History

	angelshark	time period	common skate	time period
NIOZ landing Archive	33	1933-1972	633	1934-1974
RIVO survey data	0		37	1904-1911
Newspaper	29	1882-1967	2	1947
Museum	27	1848-1977	15	1862-1864
other	11	1882-1973	1	

Table 1. Total number of records for angelshark and common skate in the Dutch waters

museum Naturalis and the historical collection of the precursor of this museum (Popta, 1924). See Table 1 for the number of angelsharks found per source and Pictures 5, 6, 7 and 8 for some examples of newspaper reports.

For common skate two time-series could be constructed.
1. Between 1901 and 1983 (except for the period of the First and Second World War) landing data from Dutch fish markets was registered by local authorities. Between 1930 and 1970 the common skate was registered separately from other rays and skates and reported for the entire country in "Verslagen en mededelingen van de Directie van de Visserijen" (Anonymous). Prior to 1930 landings of skates were registered per fish market. We could reliable compile landing data for the entire Netherlands for the period 1901-1903, 1907-1910 and 1921-1929. All data is expressed in metric tonnes. The catch location of the landed fish is not registered else than 'sea fisheries', and assumingly covers the entire North Sea.
2. Fishery-independent surveys could be used to compile a quantitative time series on the standing stock densities of common skates. First and foremost this includes the ICES coordinated surveys for fish stocks in the North Sea from 1965 onwards (ICES, 2017c). These surveys mainly took place in the first and third quarter of the year. Transects sampled during the first quarter of the year (IBTS Q1) give most valuable data (i.e. others surveys were less extensive) and were used for this analysis. Sampling was done with diesel-powered vessels, at a standardized speed of 4 knots and with a tow duration of 0.5 hours (Sguotti et al., 2016). As a historical baseline we used surveys carried out between 1902-1911 and 1903-1909 by the institutes RIVO (Netherlands) and CEFAS (United Kingdom) respectively. These surveys were carried out with steam-trawlers, which towed the trawl at a speed of approximately 2 knots, and used different gear compared to the contemporary ICES-coordinated surveys. However, it is argued that these methodological differences does not affect the catch rate for slow-swimming species such as the common skate (Sguotti et al., 2016). Here we constructed different time series for the northern, central and southern North Sea.

Historical ecology

To reconstruct ecological aspects of the angelshark and the common skate in the Dutch waters we collected information on time of occurrence, size, habitat preference and diet composition both from written sources and from specimen caught in the Dutch waters. The written sources that we checked were similar to those used to reconstruct a long-term quantitative time series (see above). Details on the sources of specimen caught in the Dutch waters were already given for angelshark. Similar data sources were checked for common skate (Table 1). Yet, for this species the newspaper archive did not show any information because the common skate is known under two names (Vleet or Fleet), which however have 15 other meanings (https://www.encyclo.nl/begrip/Vleet). These words are widely used in the Dutch language and any search on these words yields 1000s of positive cases, which we did not further checked. In addition to the already mentioned data sources, another data source for the common skate was the surveys of the RIVO in the Dutch waters between 1903 and 1912 with the research vessel Wodan (introduced above). Below we describe how we extracted ecological information from the specimen caught in the Dutch waters.

Timing

We plotted the number of reported individuals per month to evaluate potential seasonality in the occurrence of either species. The numbers of individuals for which catch date was reported are listed in Table 2. In case of the angelshark, we found three reports of females giving birth (to 4, 10 and 10 young, Picture 7), immediately after being hauled upon board (probably due to stress). We have indicated the month at which these females were caught (and do not include the newborn individuals separately).

Size

We checked the distribution of the reported sizes to evaluate the size of the species caught in the area in relation to the known size at birth, size at maturity and maximum size (see under species description). The number of individuals per species for which size was reported are listed in Table 2. This includes 17 individuals of common skate for which the disc width, instead of the more commonly reported head-tail length, was reported. For these specimen we calculated the head-tail length using non-linear function *x=1.327457 * y^0.9142347*, where x is the head-tail length in meters and y is disc width in meters (see appendix ı for derivation). In one of the occasions in which the angelshark gave birth at the deck, seven out of the ten young were measured. These young were probably about to be born as they were reported to have no external yolk sac, and only one had a very small internal yolk sac. Therefore we have included them in the plot and indicated them with a different colour. The same was done for the females that gave birth.

Depth

The frequency distribution of catch depth was plotted to study potential habitat preference. The number of individuals per species for which catch depth was reported are listed in Table 2. For several records catch depth was reported in Fathom or Feet, and here conversed to meter by multiplying with 1.8288 and 0.3048 respectively.

Sex ratio

For some of the angelshark and most of the common skates sex was determined. We used a Pearson's chi-squared test to evaluate if sex ratios differed from 50:50.

Location

Catch location was plotted to further deduce habitat preference. The number of individuals per species for which catch location was reported are listed in Table 2. In case the location was mentioned as being near a village or town we assumed that this was one Nautical mile seawards from that village or town. In case the location was mentioned as close to a buoy, the location of that buoy was used. In case the location was mentioned as being in a larger area (e.g. Cleaver bank, Brown bank etc), the centre of that area was used (obtained from a nautical map).

Diet composition

The diet of angelshark and common skate could be studied as the stomach of many of the landed fish that were brought to the NIOZ were checked for prey remains (Table 2). Prey remains were identified by biologists from the NIOZ, and a large part was checked as well by L. Holthuys from the natural history museum Naturalis. The majority of prey items could be identified to the species level. Prey that could not be identified to the species level were identified to the genus level (i.e. shrimp, fish). In some cases the size of the prey was mentioned, but because the vast majority was not, the diet is shown on a numerical basis. To account for individual diet specialization we first calculated for each individual its diet as the percentage of each prey species. Ultimately, for both angelshark and common skate the diet was calculated by averaging individual values.

	angelshark	common skate
Total N	100	775
catch date	72	701
size	47	514
catch depth	17	621
catch location	62	591
stomach content	4	411
sex	20	545

Table 2. Number of records from which life-history information could be derived.

Picture 5. Newspaper report on angelshark caught in the Eastern Scheldt: Provenciaalse Zeeuwse Courant 1955-06-24

Picture 6. Newspaper report on angelshark caught in the North Sea: Godsdienstig-staatkundig dagblad 13-08-1932.

Picture 7. Newspaper report on angelshark that gave birth to 10 young: Provenciaalse Zeeuwse Courant, 1967-07-28.

Picture 8. Newspaper report on an exceptionally large common skate caught at an unknown location (and therefore not included in this analysis). Dagblad de Gooi en Eemlander 1947-05-21

Zeldzame vis in de Oosterschelde

Haaiachtige „zee-engel"

Vrijdag 24 Juni werd door de heer L. v. d. Vliet uit Yerseke in de Oosterschelde, het Z.O. deel dat te boek staat als Koeiengat, een vreemde vis gevangen. Bij nader onderzoek bleek deze vis, die er rogachtig uitzag, te behoren tot de haaien en wel tot de z.g. schoorhaaien, een overgangsvorm tussen haai en rog.

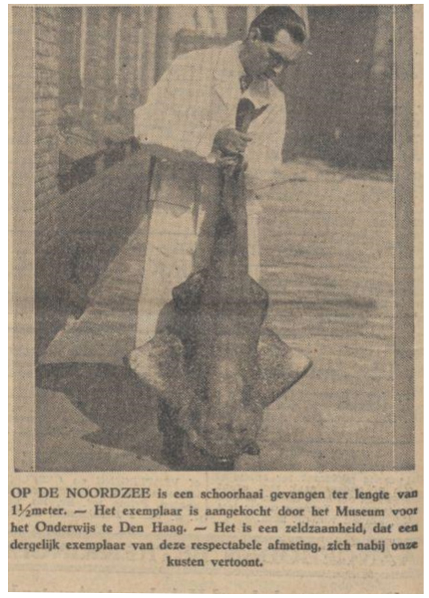
Het dier draagt de naam zee-engel, hoewel het er niet bepaald engelachtig uitziet. In de oudere uitgaven van Brehm (Ned. bewerking) wordt ook de volksnaam zeeduivel opgegeven. Dit brengt echter maar verwarring, daar de Nederlandse naam zeeduivel is gereserveerd voor een vis van heel andere aard en klasse-indeling.

De zeeëngel onderscheidt zich bij oppervlakkige beschouwing direct van de roggen, doordat de sterk verbrede borstvinnen niet met de kop zijn vergroeid en de minder brede buikvinnen wat overdekken. Hij vertoont zich dus als een viervinnige rog.

Redeke vermeldt voor de Zeeuwse wateren enkel voorkomen in de Ooster-Schelde uit de mededelingen van Bottemanne ,zodat tussen dit stuk 1883—'84 en 1941 (Redeke) geen zeeëngel in de Zeeuwse stromen schijnt te zijn vermeld.

Het in Yerseke bewaarde dier meet 22 cm, de soort kan ongeveer een meter lang worden.

Picture 5.



OP DE NOORDZEE is een schoorhaai gevangen ter lengte van 1½meter. — Het exemplaar is aangekocht door het Museum voor het Onderwijs te Den Haag. — Het is een zeldzaamheid, dat een dergelijk exemplaar van deze respectabele afmeting, zich nabij onze kusten vertoont.

Picture 6.

ZEE-ENGEL MET TIEN JONGEN IN YERSEKE....

YERSEKE — In de monding van de Oosterschelde, in de Roompot, heeft de ,Yerseke 78' van schipper Pekaar vrijdagmorgen vroeg een opmerkelijke vangst in de netten gekregen: een zee-engel van bijna anderhalve meter. De vis, die nog leefde, werd meegenomen naar Yerseke, eerst naar het mosselkantoor en later naar het hydrobiologisch instituut (af-

De zee-engel, die door de ,Yerseke 78' bij het garnalenvissen werd gevangen, meet om precies te zijn 1,42 meter. De vis heeft iets van een grote rog en behoort tot de laagste categorie van de haai-achtigen. Ze zijn ,kosmopolitisch' ingesteld, worden wel gesignaleerd in de Noordzee, maar minder vaak gevangen in de Oosterschelde.

Picture 7.

Een vleet van 80 kilo

HILVERSUM. — In de nacht van Maandag op Dinsdag deed de Nederlandse stoomtrawler „Gloria", die in IJmuiden thuis hoort, een wel zeer uitzonderlijke vangst. De netten bevatten namelijk twee vissen van buitengewoon formaat, welke naderhand onderscheidenlijk tachtig en acht en zestig kilogram bleken te wegen.

Het binnenhalen van de netten ging hierdoor niet zonder moeilijkheden gepaard en zelfs werd daarbij een net verspeeld.

Een dezer vissen, de grootste, is thans te zien in een vishal aan de Oude Doelen, alhier.

Het is een vleet, welke behoort tot de rogvissen. De vleet — ook wel gespeld fleet — waarvan de Latijnse naam is Raja Batis, wordt in de Noordeuropese wateren tamelijk veel gevangen.

Doorgaans wegen de exemplaren ongeveer tien kilogram. Een vleet van twintig kilogram is reeds een bijzonderheid en vangsten als de „Gloria" deed zijn hoogst zeldzaam. Met recht kan men zeggen; vleet van dergelijk formaat geeft het niet bij de vleet.

Begrijpelijkerwijs trok het ontzagelijke exemplaar vandaag reeds grote belangstelling.

Het grote gevaarte, dat de typische vierkante vorm heeft, die men bij de roggen aantreft en 2,53 meter lang is bij een breedte van 2.04 meter, zal nog wel enige dagen te kijk hangen.

Het kleinere exemplaar van 68 kg zal bestemd worden voor de export naar België.

Picture 8.

– Results

Angelshark

Paleontological records

One fosselized tooth was found in a borehole in Ouwerkerk on the isle of Schouwen Duiveland in Early Pleistocene sediments (2,400,000 – 1,800,000 MA). (Bosch, 1978). The online collection of Naturalis yielded two fossilized teeth from the North Sea near Scheveningen with an unknown age (appendix II).

Archaeological records

Comprehensive overviews of archaeological records of fish fauna in the Netherlands do not report remains of angelshark (Prummel, 1987; Brinkhuizen, 2016). These overviews cover 15 settlements and a time period ranging from 3500 BC to 1700 AD.

Historical documents Dutch waters

The first comprehensive book to mention fish fauna in the Netherlands is the handwritten 'Visboek' (Fish book) by Adriaen Coenen (Bennema & Rijnsdorp, 2015; Coenen, Egmond, & Mason, 2003; Coenensz van Schiperoort, 1577-1581). In this book, the angelshark is mentioned to be well known to the fishers of Scheveningen and to be caught 5-6 times per year (Bennema and Rijnsdorp, 2015).
No references for angelshark could be found from the 17th century.
We found two books written in the 18th century that mentioned angelsharks (Gronovius, 1754; Houttuyn, 1764). Both sources note that the species occurs in the Dutch waters without providing further information.
We could find six handwritten sources from the 19th century to mention the species: Bennet and Olivier (1825) note that the species was caught in the North Sea and along the Dutch coast. Anslijn (1828) mentions that the species was sometimes caught along the Dutch coast. Van den Ende (1847) mentions that the angelshark is sometimes caught along the coast of Katwijk. Schlegel (1862) reports that along our coast the species is not rare, but that it is never caught in great abundance. Van Bemmelen (1866) mentions that the species is not rare along our coast. Bottemane, (1883-1884) notes that the species is very rare in the Eastern Scheldt. According to Bellen en Kerbert (1888, cited in Redeke 1941) the species is not rare at all.
In the 20th century many more handwritten sources list the species. An important document is the book by Redeke (1941), mentioning that the species is less abundant in our waters than it used to be. According to Muus and Dahlstrøm (1966) the species is rather rare at our coast. A similar abundance estimate is given by Nijssen and Groot (1987), although at that time the species was already extinct from the Dutch waters for 10 years (see below). The species was not in the list of fish species occurring in the Zuiderzee before its enclosure (Redeke 1922). In the Wadden Sea the species was listed as extremely rare (Witte and Zijlstra, 1978).

Time series

Records of individual catches show two peaks: one in the early 20th century, containing mainly records from newspapers and one halfway the 20th century containing mainly records from the Royal NIOZ by-catch archive (fig.1).

Ecology of the angelshark in the Dutch waters

Catch month

Angelsharks were caught throughout the year, with a clear peak in the summer months June-August. These were also the months that gravid females were brought on board (fig. 2).

Size distribution

The frequency distribution of angelshark caught in the Dutch waters showed two clear peaks: one at a length matching with the length at birth and one at the length matching mature adults (fig. 3).

Catch depth

Most angelsharks were caught in relatively shallow waters, with a maximum depth of 40 meter (fig. 4).

Catch location

Matching the catch depth, most of the angelsharks reported in the Dutch waters were caught close to the shore. Most individuals were reported from the North Sea and some were

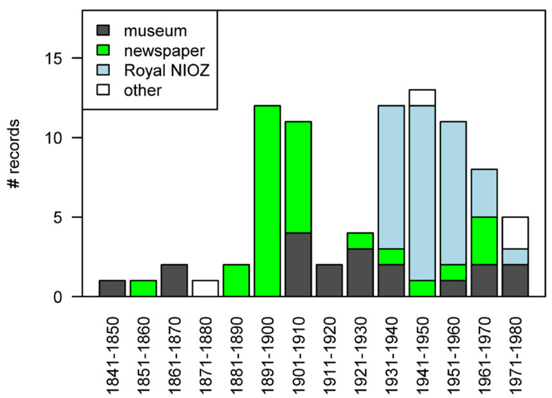


Figure 1. Catch reports of angelsharks in the Dutch waters per decade.

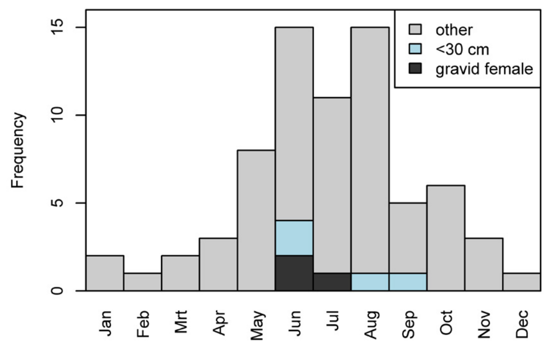


Figure 2. Frequency distribution of the catch month of angelsharks in the Dutch waters. Females with young are indicated in dark grey. Data for the years 1859 – 1977, excluding newborn individuals.

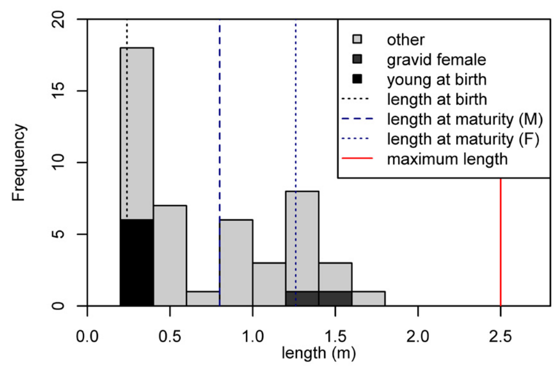


Figure 3. Size frequency distribution of angelsharks caught in the Dutch waters. Lines refer to length at birth (Miller, 2016), length at maturity for males and females and maximum length (see legend) (Roux et al., cited in Heessen et al 2015).

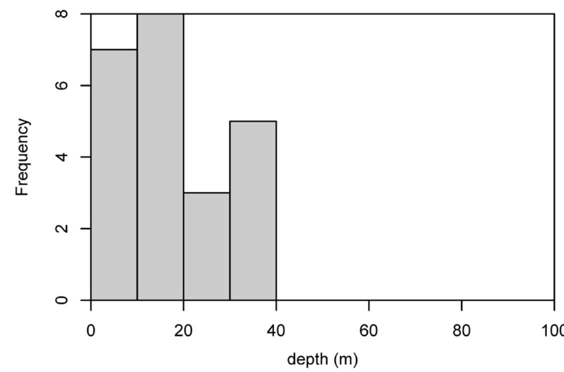


Figure 4. Frequency distribution of angelshark caught in the Dutch waters showing a skew towards shallower depths. The general areas of occurrence went to a maximum depth of 60 m.

caught in the Eastern Scheldt, Western Scheldt and in the Wadden Sea. None were found the in the former Zuiderzee (fig.5).

Sex ratio

Sex ratio did not differ from and equal distribution (N = 20, $\chi 2 = 3.2$, t_1, P = 0.07), although there was a trend towards more females

Diet

Stomach analysis of 4 individuals showed fish, shrimp and squid.

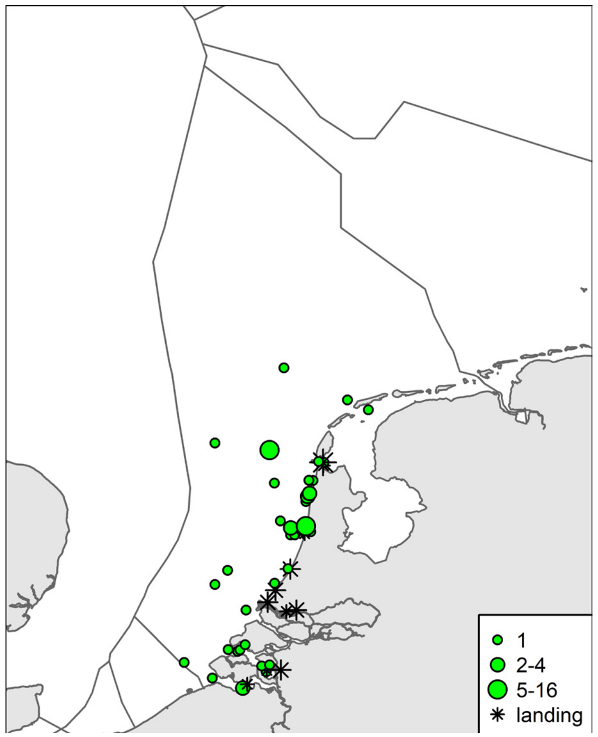


Figure 5. Catch location of angelshark in the Dutch waters. For some individuals the landing location was reported (and no catch location). These cases are indicated with a star. Dot sizes reflect the number of individuals caught.

Common skate

Paleontological records

Several fossils of common skate have been found throughout the Netherlands. One was found in early Pleistocene sediments (2,300,000 - 800,000 MA) in a borehole in the south-west of the Netherlands (Gaemers, 1988). Another was found in a borehole in Ouwerkerk (in the province of Zeeland, south of Zuid-Holland), also in Early Pleistocene sediments (2,400,000 – 1,800,000 MA). (Bosch, 1978). The Naturalis collection stores a tooth found in Renesse (in the province of Zeeland, south of Zuid-Holland) dating from the Eemiaan (0,126 - 0,116 Ma); two from Zierikzee (in the province of Zeeland, south of Zuid-Holland, unspecified age), one from Scharendijke (in the province of Zeeland, south of Zuid-Holland, unspecified age); and three from an unknown location in the North Sea (unspecified age) (for references see appendix II).

Archaeological records

Comprehensive overviews of archaeological records of fish fauna in the Netherlands do not list remains of common skate (Prummel, 1987; Brinkhuizen, 2016). These overviews cover 15 settlements and a time period ranging from 3500 BC to 1700 AD.

Historical records

The 'Visboek' by Adriaen Coenen (Coenensz van Schilperoort,1577-1581.; Coenen et al., 2003; Bennema and Rijnsdorp, 2015) mentions that the common skate is well known to the fishermen of Scheveningen and that it is often caught along the coast.
No references for common skate could be found for the 17th century.
We have found two books from the 18th century that mention the species. Gronovius (1754) mentions the presence of the species and according to Houttuyn (1764) the species is plentiful in the North Sea.
In the 19th century common skate is mentioned in several books. According to Bennet and Olivier (1825) the species is plentiful in the North Sea, sometimes weighing 200 pounds (≈ 91 kg; according to length-weight conversion given by Froese et al., (2014) this corresponds with 217 cm), Anslijn (1828) notes that the species mainly occurs in the North Sea, further mentioning that the species usually is 0.2 to 0.5 long, but sometimes reaches 3 (units are not given, but earlier in the book units are in Dutch El. 1 el is about 69.4 cm, so 3 el = 208.2 cm). Van den Ende (1847) mentions that the common skate is among the species caught along the coast of Katwijk. According to Schlegel (1862) the species is common at our coast. Van Bemmelen (1866) noted that the common skate is very abundant along our coast. Bottemane, (1883-1884) notes that the species is very rare in the Eastern Scheldt. Hoogendijk (1893) mentioned that Dutch fishermen would fish for common skate in the 'skate and ray ground' stretching

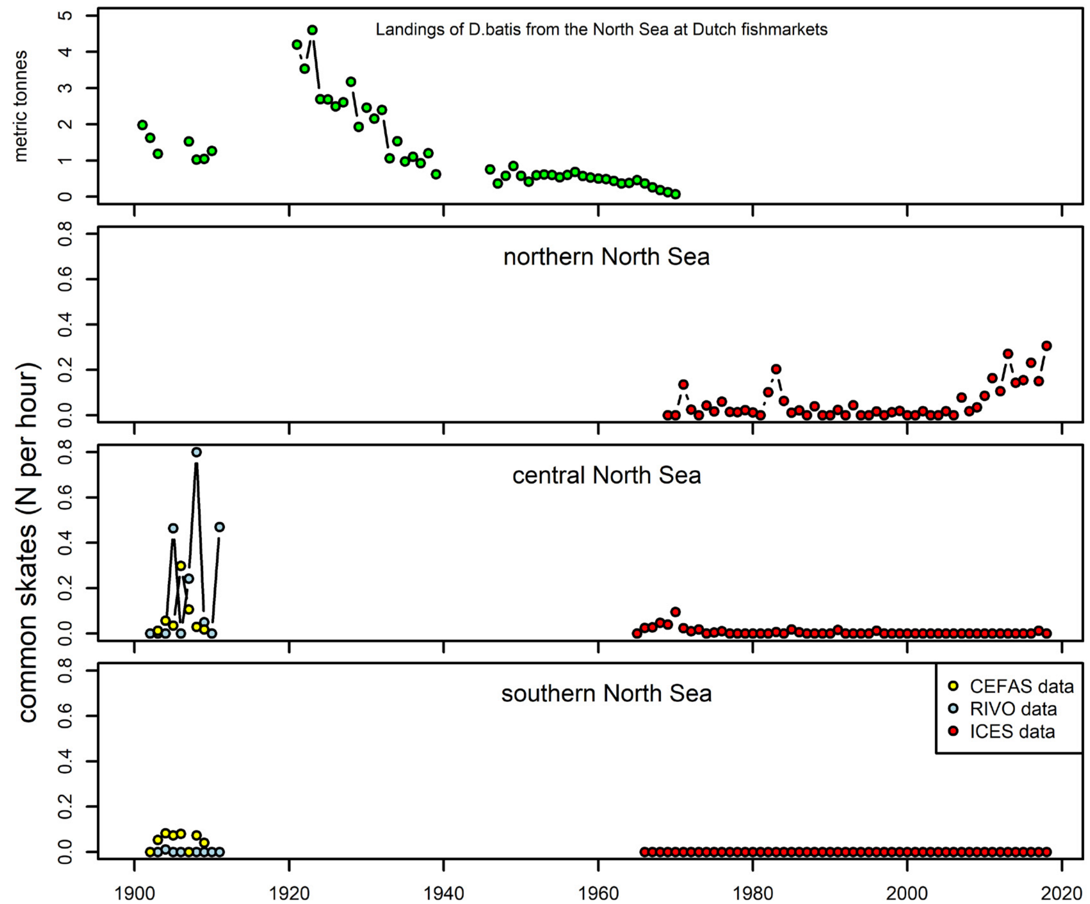


Figure 6. Time series of common skate. The upper graph shows landings in the Netherlands originating from the entire North Sea. The lower three graphs show data from fishery-independent surveys in the northern, central and southern North Sea. Note the different units on the y-axes.

from Ameland to Denmark (Picture 2). Fishermen would go there in winter (January-March). In the early 20th century, Redeke (1911) wrote that the common skate is found in many places, although never close to the coast. He further notes that most often, individuals of intermediate size were caught, with a width of 20-60 cm and that the largest individuals were found close to the Dogger Bank. The same author (Redeke, 1935) reported that the common skate was found in cold water at 100-200 m depth, and was only found in more shallow areas in spring and summer. He further mentioned that the species was rare in the southern part of the North Sea. Individuals with a size of around 1 m total length are not rare, sometimes up to 2.5 m (Redeke, 1935). In the 1940s Redeke, (1941) mentioned that the species is less abundant than it used to be. According to Muus and Dahlstrøm (1966) the species was rare at our coast. Nijssen and Groot (1987) mention that the species was not very abundant at our coast (although at that time the species was already extinct from the Dutch waters for over 10 years, see below) and that it occurred mainly in the summer. According to Redeke (1922) the species was never found in the Zuiderzee before the enclosure. The common skate is also absent from the list of species occurring in the Wadden Sea (Witte and Zijlstra, 1978).

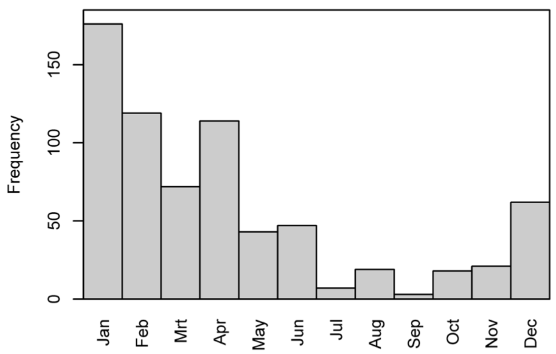


Figure 7. Frequency distribution of catch month of common skate in the Dutch waters.

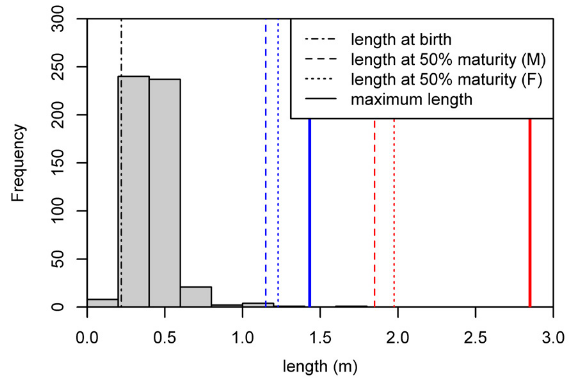


Figure 8. Frequency distribution of length of common skate caught in the Dutch waters. The vertical black line depicts length at birth (Brander, 1981). Vertical blue lines show for blue skate the length at which 50% of the individuals reached maturity for males (M) and females (F) and maximum length (Iglésias et al., 2010). Red lines show for flapper skate length at which 50% of the individuals reach maturity for males (M) and females (F) (Iglésias et al., 2010) and maximum length (Wheeler, 1978).

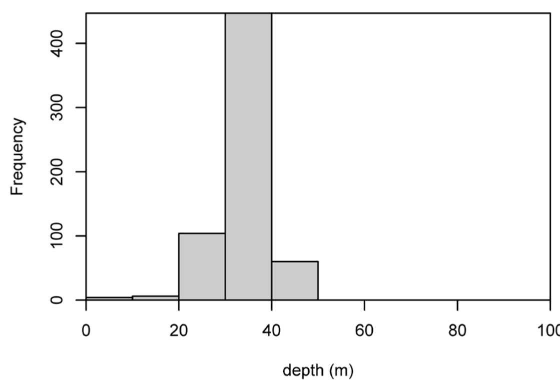


Figure 9. Frequency distribution of catch depth for common skate in the Dutch waters.

Time series

Time series of landing data show that the number of common skate landed at the Dutch markets steadily decrease from 1920 onwards, and reach zero around 1970 (fig. 6). In the 1920s most common skates were brought to the Dutch marked, with a maximum up to almost 500,000 kg. Given that a common skate weighs between 0.1 (10 cm) and 100 kg (2.5 m) (Ebert and Stehmann, 2013; ICES, 2017), 500.000 kg of common skates corresponds with between 5 million and 5000 individual common skates. Fishery-independent time series coordinated by ICES suggest that between 1965 until now the species is absent from the southern and central North Sea. In the northern North Sea the species abundance steadily increased during the last decade. Survey data from the beginning of the 20th century suggest that the species used to be more abundant in the central North Sea than it is nowadays in the northern North Sea.

Ecology of the common skate in the Dutch coastal waters

Catch month

Most common skates were caught in the winter months and early spring, with most of catches between January and April (fig. 7).

Size distribution

Most common skates caught in the Dutch waters were relatively small, i.e. the vast majority was below the size at which either of the two species is mature and close to the size that is the length at birth (fig. 8).

Catch depth

Most common skates were caught at intermediate depths, ranging from 20 to 50 meters (fig. 9).

Catch location

Corresponding with the catch depth, most individuals were mainly caught away from the coast (fig. 10).

Sex ratio

Sex ratio in common skate did not differ from and equal distribution (N = 545, $\chi 2 = 0.2202$, t_1, P = 0.64)

Diet

Stomach analyses showed that the diet of the inspected common skates mainly consisted of shrimp (appendix III). Also fish species, cephalopods and crabs were found.

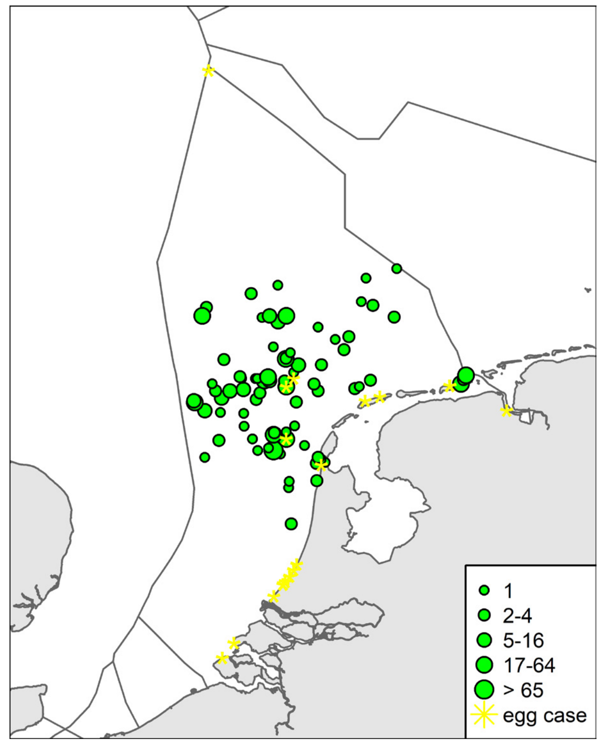


Figure 10. Catch locations of common skate in the Dutch waters. The size of the dots refers to the number of individuals caught at that location (see legend). Most of the reported locations are from fisherman that landed their fish in Den Helder, which may explain the rather northern distribution of the species.

– Discussion

Our review confirms that the North Sea used to be a strikingly rich sea with a diversity of species and encompassing densities we cannot imagine nowadays. Species such as the angelshark and common skate, now locally extinct and perhaps almost forgotten by fishermen, were part of this food web either because they were yearly visitors to the area or because they were common or even very common.

Angelshark

Long-term perspective on population dynamics

Fossilized teeth of about 2.5 Ma old found in excavations show that the angelshark at least sometimes occurred in the ancient Dutch waters web. Based on these paleontological records it is not possible to conclude anything about the relative abundance of the species. Yet, given that the species is a warm water species (Rogers and Ellis, 2000) it is conceivable that it was more abundant during warmer periods and less abundant during colder times.
Archaeological excavations of fishing villages in the Netherlands do not report any remains of angelsharks. In a large excavation in the 15th century fishermen villages of Raverzijde (Belgium) just south of the Netherlands, remains of angelsharks have been reported (Pieters et al., 2013), but compared to other species the species was of probably of negligeble importance for consumption.
Historical documents are in agreement that roughly between 1600 – 1950 the angelshark was at least a yearly visitor of the Dutch waters. Whether the species ever has been fairly common, as some textbooks claim (Schlegel, 1862; van Bemmelen, 1866), remains unknown, largely because the sources on which these statements are based are not reported, nor is there any quantitative data given. Perhaps the species has been fairly common in some years, which would corroborate the large variation we found in the number of records per year in the period 1848-1973 (fig. 1). When landed, the species was sold for consumption, but because of the meat was of poor quality it was not very popular (Coenensz van Schilperoort, 1577-1581).
A good estimate of angelshark abundance is also lacking because of the lack of fishery-independent density estimates. During the first scientific fishing survey in the Netherlands in 1877 (Anonymous, 1877, see Picture 9), an angelshark was caught during a maximum of 110 fishing hours. However, because the fishing gear and vessel differed substantially from the more contemporary fish-abundance estimates, these values cannot directly be compared, and unfortunately precise numbers of catches of other more abundant species were not specified. Perhaps the only fishery-independent estimate that can be made for the North Sea originates from the MS. Huxley which, between 1902-1909, caught one angelshark during 1568 fishing hours in the Southern North Sea (0.0006 N/hour). During these same surveys, common skates were caught with a rate of about 0.01 N/hour and another bottom-dwelling species, the plaice was caught with a rate of 4 per hour. Thus at that time the species was caught 17 times less often than the common skate and about 10.000 times less often than the plaice. However, given that only one individual was caught also this record is of limited use for a precise abundance estimate.
The individual records give the best picture of the demise of the angelshark from the Dutch waters. They show that after 1960 the number of recorded angelsharks rapidly declines, and the last specimen caught in Dutch waters known to us was hauled upon board on 23 May 1977, almost four years after the second last reported catch. The Royal NIOZ kept on recording and rewarding by-catch data of commercial fishing vessels from until 1990 (de Vooys and van der Meer, 1998), so arguably the lack of records in the 1970s marks the local extinction. Likely, the species already declined at the end of the 19th century or at the beginning of the 20th century. In this period the species was newsworthy (i.e. we found 20 records), after which the number of reports in the newspaper quickly went down (fig. 1). The decrease of reports of the species in the newspapers around 1920 also corroborates with a written account of Redeke (1941) were it was mention that the species was less abundant than it used to be.
The disappearance of the angelshark from the North Sea has never been thoroughly reconstructed. The here reconstructed decline is congruent with the believe that the species decline started at the end of 19th century (Miller, 2016) and is in line with a report from the South of England where angelsharks were relatively abundant around 1900 and were absent in the 1990s (Rogers and Ellis, 2000). It also corroborates with a report in the Northern Adriatic Sea (Mediterranean Sea) where the species is shown to have declined rapidly after 1960 (Fortibuoni et al., 2016).
The disappearance of the species from the North Sea is often linked to fisheries (Fortibuoni et al., 2016; Miller, 2016). Indeed, the presumed start of the decline at the end of the 19the century coincides with the onset of steam trawling (Rijnsdorp and Millner, 1996) and the demise of the species in the 1970s follows on the intensification of beam-trawling fisheries (Rijnsdorp et al., 2008). The angelshark is a warm water species, and Rogers and Ellis (2000) discussed the possibility that the species was more abundant at the beginning of the 1900 century because this marks a warmer period that coincided with an increase in common octopus *Octopus*

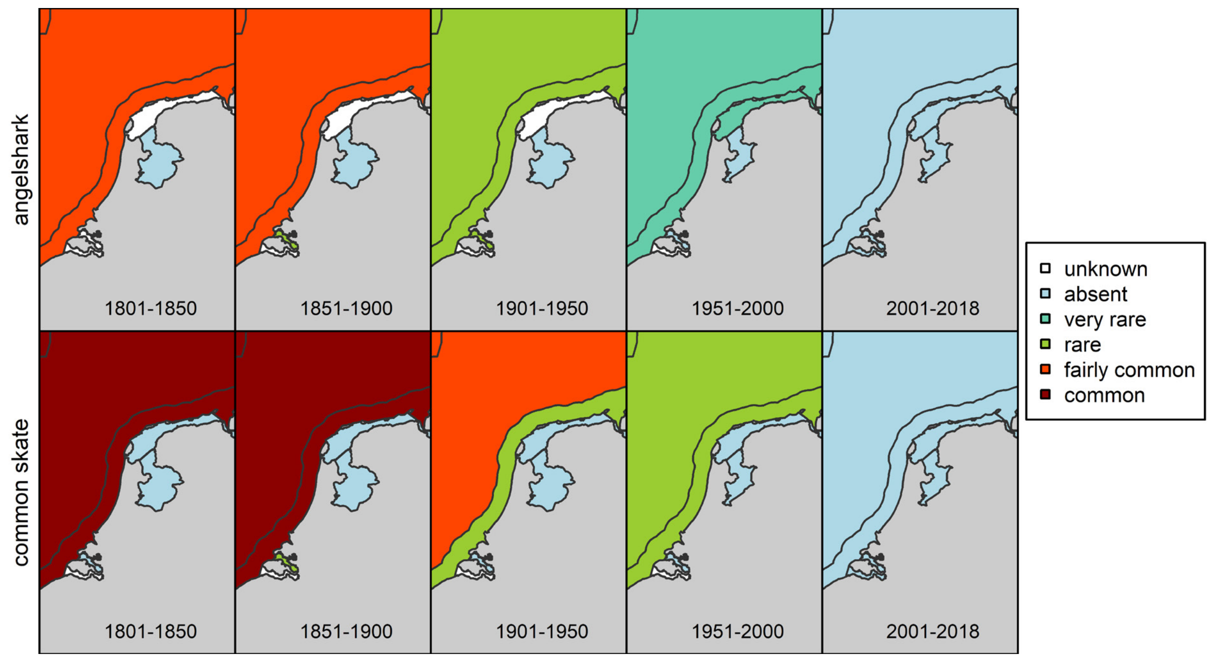
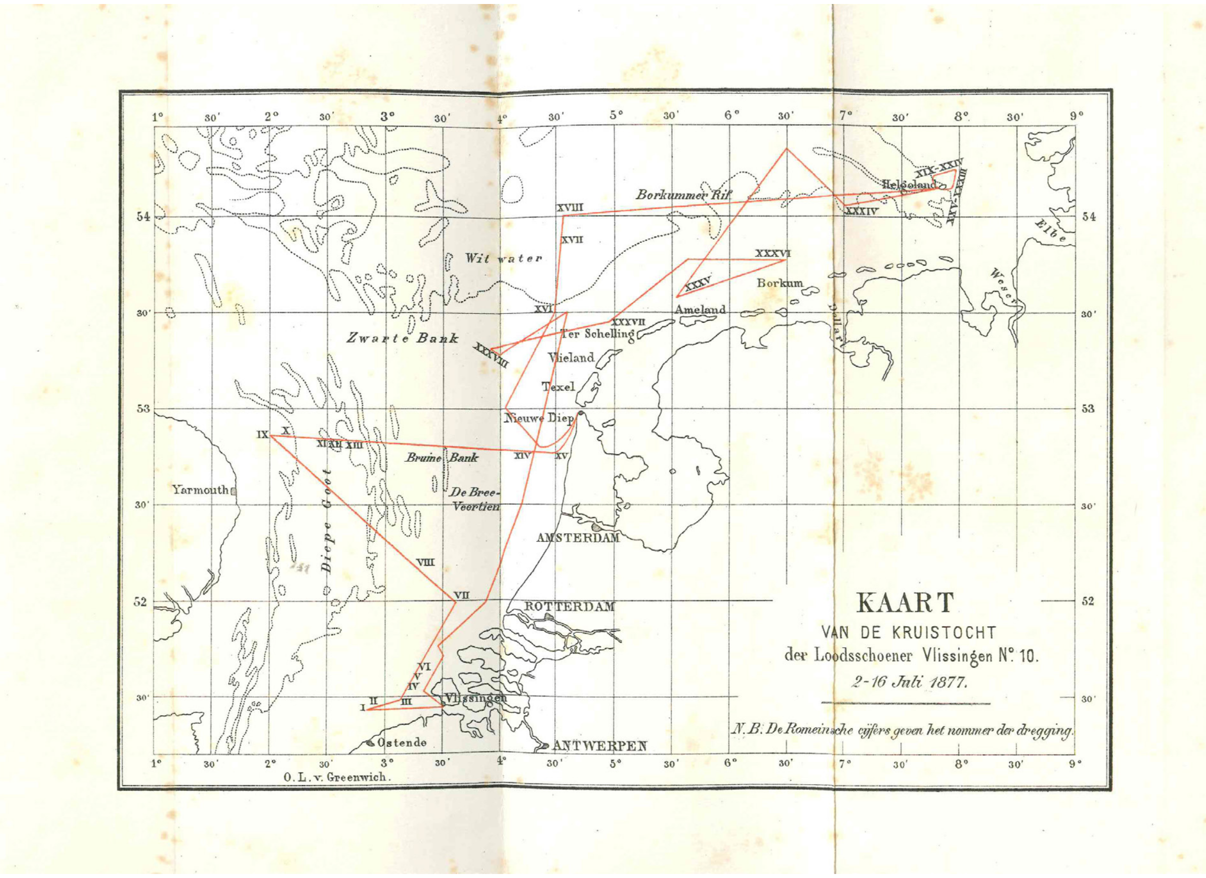


Figure 11. Interpretation of the abundance of the angelshark and common skate in the Netherlands over the last 218 years.



Picture 9. Map of the first scientific fish survey, carried out in 1877 by the schooner 'Vlissingen No. 10' (Anonymous 1978). At this survey an angelshark was caught near Vlissingen.

vulgaris, a presumably preferred prey item of angelsharks. Whereas we cannot exclude that climate has an (indirect) effect on the distribution of the species, climate change is unlikely the ultimate cause of the extirpation of the species, because prior to 1900 the North Sea also went through several temperature oscillations (e.g. the 'Little Ice Age' [1300-1850]), a period during which the species was found in the North Sea (this study). Likewise, nowadays the North Sea is a warmer sea again, and the species has not returned.

With again a warmer North Sea nowadays and a reduced impact of the fisheries (ICES, 2018b), there might be opportunities for angelsharks to return to the North Sea especially because its main prey, octopuses and small fish, are still abundant in the area (Allcock et al. 2018). However, a reason for concern is the fact that angelshark occurred in the shallow coastal region and estuaries specifically (fig. 5), whereas several of such areas in the Netherlands are now (partly) closed off by construction works.

Ecology of the angelshark in the Dutch waters

The data of individual catches on angelshark give hints regarding the ecology of the species and how it used to use the Dutch waters. Our data show that the vast majority of angelsharks were caught in the summer months (fig. 2) and most were caught near the shore at shallow depths (figs 4 and 5). At that time, fishery intensity peaked in the summer (Rijnsdorp et al., 2008), but fisheries continued in the winter months, also at deeper waters (de Vooys and van der Meer, 1998; and see results of common skate), so it unlikely that the lack of records of angelshark in the winter months and from deeper waters reflects spatio-temporal patterns in fishery intensity. This suggests that the species used to migrate between the shallow coastal waters of the Netherlands and other, unknown places outside the Dutch waters. Given that the Dutch waters are at the northern range of the historical distribution of the species (Ebert and Stehmann, 2013), it is plausible that the species moved southwards in winter. Our summer-peaking records are in agreement with the notion of Coenen that the species was found in the summer in Scheveningen (Coenensz van Schilperoort, 1577-1581). The records also support the long-term suspect that the angelshark is a migratory species, at least to some extent. These results partly contrast with the notion that the angelshark is a highly site faithful (at least not year round) (Capapé et al., 1990; Quigley, 2006), and they fully contrast with the notion that the species is not likely to migrate or disperse (ICES, 2017c), and so does not support the remark that angelsharks "should be managed on the smallest possible spatial scale" (STECF, 2003).

The individual catches suggest that the reason to migrate into the North Sea is linked to reproduction. First of all, most of the angelsharks caught in the Dutch waters were adult individuals, which have a length exceeding the size at which the species becomes mature. The catches included three gravid females, which gave birth just after they were hauled on board. Aside of the adult catches, also a number of smaller individuals were caught, the sizes of which matched those of newborns (fig. 3). Species of intermediate size have been recorded only in one occasion. Thus, these observations suggest that the Dutch waters used to have a parturition and nursery function for angelsharks. These are probably the first records underpinning the long-term believe that the angelshark migrates in summer to shallow waters for reproduction, a behaviour that is convincingly showed for two other species of angelsharks, *Squatina oculata* in the Mediterian Sea (Capapé et al., 1990) and *Squatina guggenheim* in Argentinean waters (Vooren and Da Silva, 1991).

Common skate

Long-term perspective on population dynamics

Paleontological data of a relatively large number of fossilised teeth found in the Netherlands and dating back 2.5 million years ago suggest that common skates has occurred in the area as long as the basin has been there. Archaeological excavations of fishing villages in the Netherlands covering a more recent period (3500 BC – 1700 AD) do not report any remains of common skate, suggesting that the species was never of major important for local fisheries. Remains of common skates in a large excavation in the 15th century villages of Raverzijde (Belgium) just south of the Netherlands (Pieters et al., 2013) does not conflict this statement, as at this site relatively commons skate remains where found compared to other species.

That commons skates were never of great commercial importance was not because the species was not found in the area, i.e. all historical sources that we could find indicate that the species prior to 1900 was common, or even very common in the Dutch waters. In fact, Hoogendijk (1983) argues that it is a shame that not many Dutch people know the fine taste of the common skate. Together with its large size the species could have been a valuable source for fisheries. Indeed, this was the case in the United Kingdom, where, for example, it was reported that one common skate could feed a whole society of 120 men (Shaw, 1804).

In the beginning of the 20th century common skates were still regularly caught in the Dutch waters (Redeke, 1911). Yet, it could well be that at that time the species was already declining as the species was only found in deeper parts of the North Sea (Redeke, 1911), whereas historical documents suggest that the species used to be common close to the shore before 1900 (Schlegel, 1862; van Bemmelen, 1866). In 1941 the decline of the species was apparent to Redeke (1941). This is congruent with time series from landings brought to the Dutch markets, which shows a steep decline after 1920. Although these time-series data are not independent from fisheries and should therefore be carefully considered, a decline in landed fish often represents a genuine decline (Pauly et al., 2013). Given that fishery intensity in the North Sea between 1920-1940 were in the same order of magnitude (Rijnsdorp and Millner, 1996), it is conceivable that indeed the reported decline in common skates reflects a population decline. After the Second World War the species probably got quickly extirpated from the Dutch waters. The number of landings of common skate brought to the Dutch market continued to decline and approached 0 around 1970. According to our information, on 27 March 1974 the last common skate was caught in the Dutch waters. There are unconfirmed rumours that the species are nowadays again sometimes caught in the Dutch waters, but we could not deduce any of these records. For instance, the exact catching location of a large common skate in caught 2008 'north of (the Dutch island of) Vlieland' (Heessen and Ellis, 2010) was not reported and could not be traced back and is therefore not included.
The here reconstructed decline of the common skate in the Dutch waters is by and large congruent with the index-based time series of Sguotti et al. (2016) who used fisheries-independent data to construct a time series for the common skate in the southern North Sea. The reconstructed decrease of common skate landings after 1950 is also in line with the decreasing trend in eggs of common skate found at the Dutch beaches (Gmelig Meyling, 2009).
Overfishing is thought to be the prime reason of the disappearance of common skates from the North Sea and adjacent waters (Brander, 1981). Being a large species with slow maturation at large sizes, the common skate has a low reproduction rate and fecundity. Populations with these characteristics are particularly sensitive to fishing pressure (Brander, 1981).
Congruent with reduced fishing efforts the common skate recently increased in the Northern part of the North Sea (ICES, 2017, fig. 6a). An increase in the central and southern part of the North Sea is, however, not observed (fig. 6 b and c). Whether the species may be expected to expand again towards more southern areas, if fishing intensity remains at the current level or decreases even further, remains to be seen. Much of the preferred prey food (Callaway et al., 2002) is still abundant and is probably not preventing the species' return to the southern North Sea. Yet, climate change may do so as the common skate had and have its stronghold in the northerly waters (Redeke, 1911) and a northward shift is seen in many species in response to climate change (Perry et al., 2005).

Ecology of the common skate in the Dutch waters

Analyses of individual catches on common skates suggest that the species could be mainly found in the area in winter and spring months (December-May). The winter catch peak is not a result of increased fisheries as, until the 1960s fishing effort showed a clear seasonal pattern with a low in the winter months (Rijnsdorp et al., 2008). It should be noted that the vast majority of the reported records are from the 1950s, when the species was already close to local extinction, and it is questionable if the reported data is representative for a longer time-scale.

Indeed, none of the historical assessments report any seasonality in the species, although Hoogendijk (1893) mentions that fisheries targeted on common skates in winter. Yet systematic, fishery independent data from the beginning of the 20th century do not show such a pattern (unpublished data Ms Huxley).
It remains unknown if the common skate has indeed been migratory or if it was a year-round resident. Accordingly, there is still no consensus on the migratory behaviour of the species (Wearmouth and Sims, 2009). Given that sex ratios were equal in our records, our data are not in favour of the male-biased migration hypothesis (Wearmouth and Sims, 2009). Rather, they suggests migration at the population level. Our data also do not support the hypothesis that the common skate migrates to shallow water in summer (Nijssen and Groot, 1987).
The vast majority of reported specimen were individuals smaller than 50 cm. The here reported data mainly concern specimen collected in the 1950s, but a historical report of Anslijn, (1828) suggests that catches always contained mainly small individuals. Also about 70% of the catches of ms Huxley at the start of the 20th century contained common skates smaller than 50 cm (data from http://data.cefas.co.uk). Individuals smaller than 50 cm are well below the size of maturity (Brander, 1981). According to growth rates given by Du Buit (1977) a size of 50 cm matches with an age of about 2 years. According to the slightly faster growth rates presented by www.gishbase.org 50 cm correlates with an age of 1 year. This suggests that the Dutch waters and/or the southern North Sea were predominantly used as a nursery grounds for relatively young commons skates. It cannot be excluded that larger individuals were present but better able to escape the fishing nets as suggested by Heessen et al. (2015).
Larger individuals certainly have occurred in the area throughout the last centuries. First of all this is indicated by a large number of historical sources, mentioning that also larger individuals up to 2 meters have been found in the Netherlands (Bennet & Olivier, 1825; Coenensz van Schiperoort, 1577-1581). Also the fact that fresh egg cases used to be found, and perhaps were even common (Tesch, 1911), shows that larger (mature) individuals were present in the area. The extend of this and the importance of the area as a breeding ground remains unknown. Our data give a good idea of the species' diet around the 50s, although we cannot exclude that some easy to digest prey was missed (e.g. shells etc). Many, if not all of the important prey species around that time are still present in (both the southern and northern) North Sea (Callaway et al., 2002). Furthermore, the most important prey, the shrimp *Crangon allmanni* did not change over the last 100 years (Callaway et al., 2007). Also the Processa shrimp, another important prey item, is still abundant (Reiss and Kröncke, 2004).

Blue skate Dipturus flossada or flapper skate Dipturus intermedia

Our data do not give a conclusive answer with regard to the species identification issues of the common skate in the Dutch waters. Yet, based on size, a few flapper skates could be positively distinguished in our data (fig. 8). Also the sizes reported in historical documents show that the flapper skate did occur in the Netherlands. However, most of the reported sizes are within the range of both the blue skate and the flapper skate. We could find only a few pictures of common skates (e.g. Picture 4) and they are all of too poor quality for identification.
Based on size and distribution we can further speculate that flapper skate was indeed the species that used to occur in the Dutch waters. Currently the refugial population of the flapper skate can be found in the northern North Sea around the Shetland Isles and the Orkney Islands in Scotland and the blue skates still reside in the Irish sea (Heessen et al., 2015). Given that

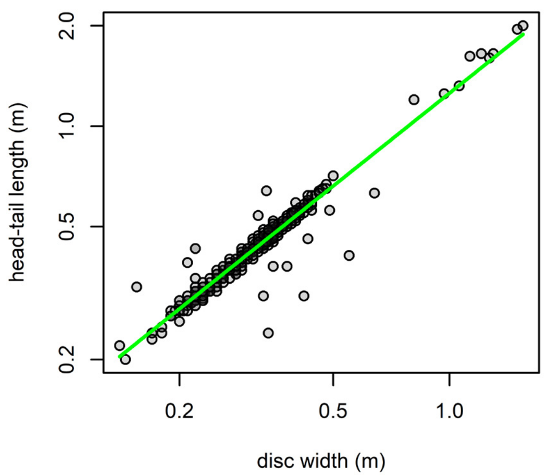
our records mainly come from the northern part of the Dutch waters and that they were peaking in winter, it is conceivable that these individuals originate from the northern population of flapper skates from which (small) individuals migrated southwards to the Dutch waters in winter.

General discussion

Industrial fisheries have changed marine ecosystems in fundamental ways. Large marine predators, representing the top of the food web, have been reduced by at least one order of magnitude (Myers and Worm, 2005) with reverberating impact on the multitude of ecosystem functions these species provide (Hammerschlag et al., 2019). The data we have aggregated picture the demise of both the angelshark and common skate throughout the southern North Sea that started at the onset of the 20th century or perhaps at the end of the 19th century. Our study shows how our baseline of the natural richness of the North Sea has shifted since the early 20th century. Large predators, including the angelshark and common skate, were once an integral part of the North Sea food web and our understanding of this ecosystem is incomplete without these species.
The cause of the declines in both these species was not directly studied, yet we see that the start of the decline coincides with the period during which steam trawlers started to be used in fisheries and we further notice that the actual disappearance if the species from the Dutch waters in the 1970s follows the introduction of diesel-powered fishing trawlers (Rijnsdorp and Millner, 1996). Typically, large fish such as angelshark and common skate, with concomitant low maturation rate and fecundity, are particularly sensitive to increased mortality, including bycatch from fisheries. (Fernandes et al., 2017) and we reason that also the extirpation of the angelshark and common skate from the Dutch waters is directly linked to overfishing.

We argue that insight in the historical developments leading to the demise of marine species in highly exploited regions such as the North Sea, can and should be used for our understanding of the ongoing processes in systems that currently deal with increasing exploitation. A commonly described pattern in the exploitation of fish communities is the phenomenon of ‘fishing down the food web’, where large species at high trophic levels initially receive the highest impact from exploitation practices (Pauly et al., 1998). Once large predators are extirpated, commercial interest shifts towards species at lower trophic levels, often with higher population production and resilience against the increasing impact of exploitation. In the North Sea ecosystem, management of commercial fisheries relies on baselines from recent periods, well after fisheries have been moving down the food web. Awareness of the ongoing changes in patterns as they take place, could prevent the depletion of crucial ecosystem functions in regions where large predators are currently exploited and are becoming more commercially interesting.
The insights we present here on the history of the North Sea ecosystem species can be used as a warning for less exploited regions, not to wait with establishing monitoring schemes and exploitation management until after iconic species have disappeared. This study may also function as a reminder of how fast our collective memory may forget the occurrence of iconic species and their role in the ecosystems we interact with. At the same time, we may be able to use our understanding of more pristine systems in our views on what represents the ‘natural state’ of the North Sea, and on the baselines we rely on for managing this system.
The realization that angelsharks and common skates used to be an integral part of the North Sea food web does not guarantee that once the impact of fishing is reduced sufficiently, populations of these species will be able to recover and return to this region. Even if fisheries have played a major role in the demise of these species, other aspects of the ecosystem have also changed in the past decades and it is possible that some of these changes, such as structural protection of the coast, removal of hard substrate in deeper areas, sea water temperature fluctuations, as well as compositional changes in the food web, present biotic and abiotic conditions that are unfavourable to the return of the angelshark and common skate. For example, the last stronghold of the common skate (flapper skate) is in northern, colder waters (Dulvy et al., 2006) and it may well be that the southern extreme of its occurrence range has shifted northward with increasing temperatures.
These considerations notwithstanding, we present a piece of the puzzle of what a more pristine North Sea ecosystem is like. This perspective is crucial if we want to comprehend how severely depleted the current system is, and if we want to hold on to a more appropriate baseline.
These insights are necessary for a complete ecological perspective of the system and for our expectations of the potential of this ecosystem.
These insights may even affect the goals set for conservation and restoration efforts in the North Sea ecosystem.

– Appendix



Appendix I. Allometric relation between disk-width and head-tail length in common skate. The regression line was fitted with non-linear regression models using R software (R Development Core Team 2019), with the package 'nlme' (Pinheiro et al., 2011). The VarPower function was used to correct for variance in head-tail length that increased with size. The relationship was fitted on 476 points. The source of the eight largest points is Wearmouth and Sims (2009), the source of all other points is the landing data of the Royal NIOZ.

species	location	link
angelshark	Scheveningen	http://data.biodiversitydata.nl/naturalis/specimen/RGM.405805.A
angelshark	Scheveningen	http://data.biodiversitydata.nl/naturalis/specimen/RGM.405879.A
common skate	Renesse	http://data.biodiversitydata.nl/naturalis/specimen/RGM.1311377
common skate	Zierikzee	http://data.biodiversitydata.nl/naturalis/specimen/RGM.1311487
common skate	Scharendijke	http://data.biodiversitydata.nl/naturalis/specimen/RGM.1311488
common skate	North Sea	http://data.biodiversitydata.nl/naturalis/specimen/RGM.405866
common skate	North Sea	http://data.biodiversitydata.nl/naturalis/specimen/RGM.94176
common skate	North Sea	http://data.biodiversitydata.nl/naturalis/specimen/RGM.94177

Appendix II. References to the fossilized teeth of angelshark and common skate that are in the collection of Dutch natural history museum Naturalis

species	diet (%)	present in southern North Sea
Crangon allmanni	26.29	++
Processa sp.	22.43	?
Crangon crangon	19.50	++
Crangon sp.	15.13	
Philoceras trispinosus	3.46	++
Pisces	2.94	
Liocarcinus	2.26	
Philoceras bispinosus	1.47	
Pleuronectiformes	0.90	++
Brachyura	0.89	
Processa canaliculata	0.74	
Processa sp.	0.50	
Limanda limanda	0.36	++
Processa parva	0.35	
Hyperoplus lanceolatus	0.31	
Merlangius merlangus	0.28	++
Clupeiformes	0.27	
Solea solea	0.25	
Corystes cassivelaunus	0.25	
Agonus	0.25	
Portunus holsatus	0.21	
Trisopterus minutus	0.19	
Pleuronectes platessa	0.17	
Polychaete	0.13	
Ammodytis lanceolatus	0.13	
Pontophilus	0.10	
Sepiida	0.06	
Arnoglossus	0.06	
Cephalopoda	0.05	
Mysidacea	0.04	
Macropipus	0.02	
Clupea	0.01	

Appendix III. Diet composition of common skate (based on 411 individuals). The last column indicates whether the prey species are still present in the North Sea food web according to Callaway et al. (2002)

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Colophon

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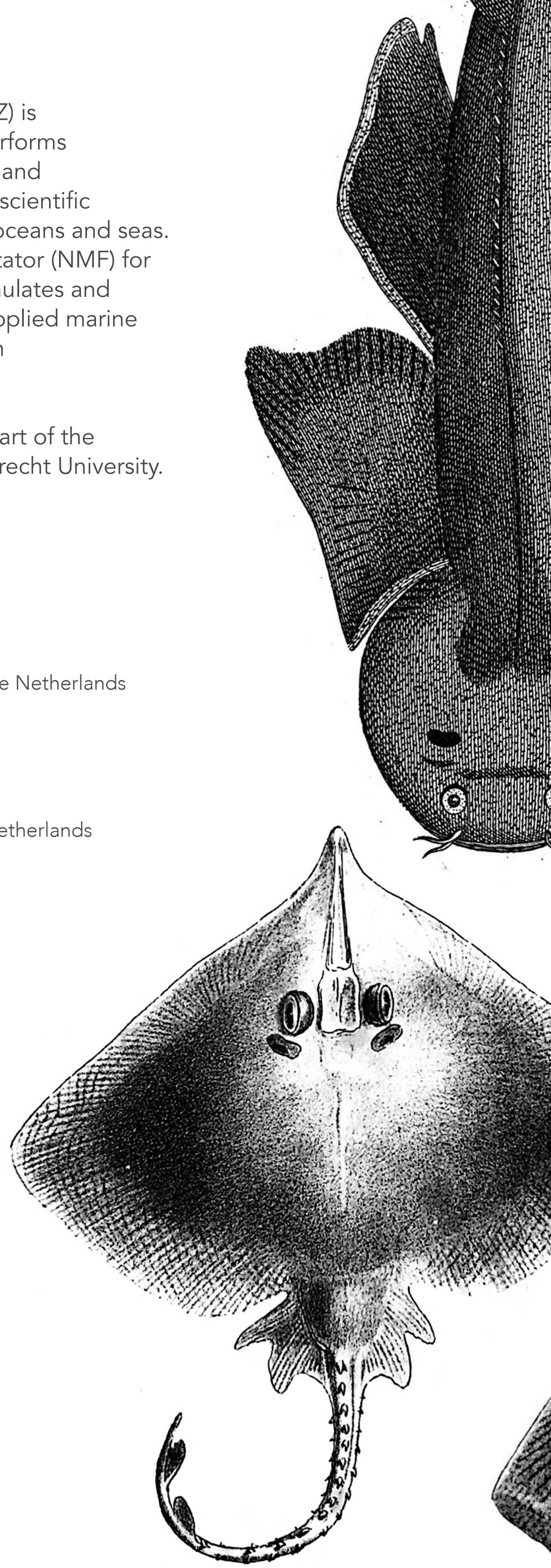

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