Bom, R.A.; van de Water, M.; Camphuysen, C.J.; van der Veer, H.J. & van Leeuwen, A. (2020). The historical ecology and demise of the iconic Angelshark *Squatina squatina* in the southern North Sea. *Marine Biology*, 176, 91

Published version: https://dx.doi.org/10.1007/s00227-020-03702-0

NIOZ Repository: http://imis.nioz.nl/imis.php?module=ref&refid=325593

The historical ecology and demise of the iconic Angelshark *Squatina squatina* in the southern North Sea

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Abstract

There is a growing call to restore the natural richness of the North Sea, but it is often unclear what this natural richness actually was. Here we review the demise and the historical ecology of an iconic species, the critically endangered Angelshark *Squatina squatina* in the southern North Sea, using historical books and catch records of 104 individuals brought to the Dutch fish markets. These sources reveal that between 1600 and 1950, Angelsharks were annual visitors to the North Sea, and in some years were fairly commonly observed. The number of recorded individuals peaked in the early 20th century and between 1945-1955, and declining rapidly in the 1960s, with the last recorded observation in 1973. The decline coincides with the introduction of engine-powered fisheries, whereas the full extirpation followed the increased use of diesel-powered beam-trawlers. The recorded observations of

Angelsharks were most commonly from the summer season, in accordance with the prevailing notion of Angelsharks migrating to warmer waters in winter. Furthermore, most recorded catches were of newborns and adult females in shallow waters, showcasing the importance of the area for parturition and nursery. Our review exemplifies how a large predator disappeared from a marine food web and shows the importance of historical data to deduce the natural richness of the North Sea.

Key words: *Squatina squatina*, critically endangered, Dutch coastal waters, large marine predator, nursery ground, overfishing, parturition ground

1. Introduction

The North Sea used to be an incredibly rich ecosystem, hosting a large variety of marine fauna, and including large marine predators (Rogers and Ellis 2000; Bennema and Rijnsdorp 2015). Yet, as a result of a century-long intensive exploitation, North-Sea fish populations have either been reduced to low numbers or completely extirpated, with the species of large marine predators showing the most dramatic decreases (Pauly et al. 1998; Christensen et al. 2003; Sguotti et al. 2016). This has changed the ecosystem in a fundamental way (Christensen et al. 2003; Sguotti et al. 2016), potentially through trophic cascades (Baum and Worm 2009).

There is growing awareness of the adverse impact of humans on fish stocks and congruently there is an increasing demand to restore the North Sea ecosystem (ICES 2018). However, it is not always clear how to define the natural richness of an area. Often, fisheries-independent marine monitoring schemes are used as a baseline, but most of these surveys were established sometime after the 1950s (Jackson et al. 2001); well after the extirpation of numerous iconic species. Nevertheless, a range of data sources is available with information on the historical state of marine populations, such as books, reports, catch records, and newspapers. Collation of this information and a wider appreciation of such data can be used to give a long-term perspective on marine ecosystems and their historical state before the current levels of human intervention (Dalzell 1998; Jackson et al. 2001; Bennema and Rijnsdorp 2015).

One of the species that has disappeared from the North Sea is the critically endangered Angelshark *Squatina squatina* (Morey et al. 2019). This dorsal-ventrally flattened shark species once occurred throughout the Northeast Atlantic, Mediterranean and Black Sea, but nowadays its population persists in a few patches in the Northeast Atlantic, in the Mediterranean, and around the Canary Islands (Morey et al. 2019). In the North Sea, conservation measures for this species are hampered, in part due to the lack of information on its historical abundance and ecology, while temporary population dynamics are unknown (Heessen et al. 2015). It is generally thought that the species declined as a result of target-fisheries and incidental bycatch (Henderson 2014; Fortibuoni et al. 2016). The bottom-dwelling lifestyle and its low fecundity render the species particularly susceptible to demersal fisheries. Angelsharks are yolk–sac viviparous, with females having a two- or three year reproductive cycle with a gestation period of 6 to 10 months (Capapé et al. 1990; Miller 2016) and with litters up to 25 young (Quigley 2006), all characteristics of a 'slow life-history' and high sensitivity to (bycatch) mortality.

In this study, we use a variety of historical sources to set a historical baseline for the Angelshark and to reconstruct its decline from the southern part of the North Sea. We use these historical sources to deduce so-far unknown ecological characteristics of the species in the area.

2. Methods

2.1 Area definition and description

We collected historical sources (sources older than 50 years), written in Dutch, and dealing with fisheries and fish fauna. These include books and records of individual Angelsharks brought to Dutch fish markets. Some of the books and individual records mention precise locations, which include the Dutch seas (Wadden Sea and the former Zuiderzee) and several estuaries (for fisheries the most prominent ones were the Eastern Scheldt, Western Scheldt, Grevelingen, and Haringvliet) and part of the southern North Sea, with a strong bias towards the Dutch coast (Fig. 1). We assume that catch records without a location and book records referencing terms such as ‘onze wateren’ (our waters), are indicative for the same area, to which we will collectively refer as the Dutch coastal waters.

The Dutch seas and estuaries are shallow areas that include large intertidal flats, consisting of muddy and sandy sediments. The southern North Sea that borders the Netherlands is a relatively shallow basin throughout, with a depth of less than 10 m within 12 nautical miles from the coast. In the north, areas with depths up to 70 m are found (IDON 2004, Fig. 1). The sea floor consists of fine to medium-coarse sand. Small gravelly areas occur in the northern part (Creutzberg et al. 1984; IDON 2004).

The Dutch coastal waters have been used for fisheries and other resources for centuries. Studies on excavated fishing villages show that exploitation of fish stocks dates back to the stone age (Brinkhuizen 2016). Exploitation increased in the 10th century (Barrett et al. 2011), in medieval times (Bennema and Rijnsdorp 2015), and especially in the wake of the industrial revolution (Engelhard 2008). Specifically impactful were the displacement of sailing vessels by steam-powered trawlers towards the end of the 19th century and the conversion from steam to diesel-powered beam trawlers, in the early 1960s (Rijnsdorp and Millner, 1996; Engelhard 2008).

The habitat characteristics of the Dutch coastal waters have changed in many ways over the last few centuries. Dike construction dates back to pre-medieval times but has accelerated in the 20^{th} century. Large construction works, with heavy impact on fish populations, include the (partial) closure of all estuaries, except for the Western Scheldt, which occurred between 1970-1986, and the closure of the former Zuiderzee in 1932 (Wolff 2000; Lotze et al. 2006). Other habitat changes with likely impact on fish populations, includes the removal of hard substrates in the 20th century (mainly oyster beds and large stones) and the introduction of artificial hard substrates (mainly oil- and gas platforms and wind turbines) in the 21th century (ICES 2018).

2.2 Data sources

2.2.1 Qualitative time series

We carried out an extensive search of historical books and reports to reconstruct a qualitative time series of Angelshark records in the Netherlands. Important data sources were the library of the NIOZ Royal Netherlands Institute for Sea Research, the online libraries www.books.google.com, http://beeld.teylersmuseum.nl/Digital_Library, and the

Royal Dutch library. We found 15 books mentioning the species, covering the period 1577-1966 (Table 1). We also checked Dutch newspapers and magazines using the online archive Delpher (www.delpher.nl), which contains known Dutch newspapers and magazines dating back to 1618 in a searchable digital format. We searched for records of Angelsharks using various Dutch names (*i.e.* Zee-engel, zee engel, zeeëngel, schoorhaai, schoerhaai, pakhaai, vioolvis, paddehaai, speelman, bergelote) and four scientific names (i.e. *Rhina squatina, Squatina squatina, Squatina angelis, Squalus squatina*) known to have been used (as synonyms) for the species.

2.2.2 Quantitative time series

Angelsharks were rarely caught in fishery-independent surveys and therefore it was not possible to reconstruct a fishery-independent time series for this species (see for instance Rijnsdorp et al. 1996; Rogers and Ellis 2000). Here we constructed a quantitative time series by assembling all reports of individual Angelsharks caught in the Dutch coastal waters. A major source was the archive of the NIOZ. This archive contained data of bycatch of commercial fishing vessels active in the southern North Sea between 1930-1990, that brought their fish to the Dutch markets of Den Helder, Texel, Wieringen, and Urk. This data contains 35 records of individual Angelsharks previously undisclosed in the literature. Also, the Delpher digital newspaper archive yielded several catch reports. Other sources were the Global Biodiversity Information Facility (www.gbif.org), a report of the first scientific fish survey in the Netherlands, carried out in 1877 (Anonymous 1878), the contemporary collection of the Dutch Natural History museum Naturalis, and the historical collection of the precursor of this museum (Popta 1924). We carefully checked all records for potential duplicates. See Table 2 for the number of individual Angelsharks found per source. We plotted the number of individual records per year between 1880 and 1990 to evaluate patterns over time. We fitted a LOESS with a smoothing parameter of 0.3 to better show patterns over time. Years with no records were treated as zeros.

2.3 Historical ecology

We collated information on size, sex, catch timing, catch depth, catch location, and diet composition in order to reconstruct the ecology of Angelsharks in the Dutch coastal waters. First a quantitative ecological description was derived from the same written sources as mentioned in the *Qualitative time series*. Second, we performed a quantitative analysis based on parameters extracted from the individual records mentioned in the *Quantitative time series.* Not all individual records contained information on all parameters, and sample sizes are given in Table 2. Below we describe how the ecological information was extracted from the individual records.

2.4.1 Timing

We aggregated the number of reported individuals per month to evaluate a signature of seasonality in the records. We found three reports of females giving birth immediately after being hauled on board (to 4, 10, and 10 young), supposedly as the result of stress (Adams et al. 2018). The records of the newborns were excluded from the timing data.

2.4.2 Size and sex ratio

We evaluated the size of individuals caught in the area in relation to maximum size (180 cm for males and 244 cm for females; Ebert and Stehmann 2013; Miller 2016), size at maturity (for males 78 cm and females 80-132 cm; Capapé et al. 1990; data from the Mediterranean) and size at birth (25-28 cm in length in the Mediterranean; Capapé et al. 1990).

The individual records contain one occasion where a female gave birth on deck, and seven out of the ten newborns observed were measured. These young were probably about to be born, since they were reported to have no external yolk sac, and only one had a very small internal yolk sac. We have included these individuals in the size and sex data.

We used a Pearson's chi-squared test to evaluate if sex ratios differed from 1:1. This was done including and excluding the three cases where a (female) Angelshark gave birth on deck, because it is unclear if these animals were sexed on the basis of independent features. We assumed that variation in fishing effort had no effect on size and sex ratio.

2.4.3 Depth and location

Catch depth and location was used to study potential habitat preferences. Depth was tabulated in units of meters, with the conversion of 1 fathom = 1.8288 m. If the catch location was provided as a village or town, we assumed that the catch location was one nautical mile (1852 m) seawards from that village or town. This distance is realistic as the estuary was less than three nautical miles across at many of the mentioned locations (Fig. 1). When the location was given by buoy marker, the buoy location was used. When the location was mentioned to be a general area (e.g. Cleaver Bank, Brown Bank etc), the geographical centre of that area was used (obtained from a nautical map; Anonymous 1962).

3. Results

3.1 Time series

Most books published before 1900 described the Angelshark as a species native to the Dutch coastal waters, and two sources explicitly suggested that the species was fairly common (Table 1). Several sources post-1900 have suggested that the species was less abundant than before or even that it was 'rare'. Newspaper reports were contradictory, with some suggesting that the species was rare and others that it occurred regularly (Table 1). The numbers of individuals caught showed that the species was found at least annually between 1900-1970. There were two clusters in the individual catches: from the late 19th century to the early 20th century (mainly records from newspapers) and in the 1940-60s (mainly records from the NIOZ bycatch archive; Fig. 2). The last recorded observation was from 1973.

3.2 Historical ecology

The written historical sources indicated that Angelsharks were mainly caught in summer (Coenensz van Schilperoort 1577-1581; Muus and Dahlstrøm 1966). Individual catch data indeed showed a peak in summer, but these data also showed that the species was captured throughout the year. Gravid females were brought on board in summer (Fig. 3).

According to Coenensz van Schilperoort (1577-1581) and Bennet and Olivier (1825), the largest Angelsharks measured 6–8 feet (i.e. 1.8–2.4 m) in length. According to Schlegel

(1862), however, Angelsharks caught in the Dutch coastal waters were usually 2–3 feet (0.6–0.9 m) in length and only a few were double that size. Redeke (1941) reported a maximum length of ~1 m. In the individual records, we found clusters of size-classes: young animals (matching length at birth) and adults (Fig. 4).

Written sources did not mention sex ratios. In the individual records, sex ratios did not differ from 1:1, but there was a trend towards more females, both when testing including the three individuals that gave birth on deck ($N = 22$, $\chi 2 = 2.9091$, t1, $P = 0.088$) or excluding these ($N = 19$, $\chi 2 = 1.3158$, t1, $P = 0.2513$).

According to Muus and Dahlstrøm (1966), Angelsharks moved to shallow waters in summer. The collated individual records, which were mainly summer records, showed that all Angelsharks were caught in shallow waters, with a maximum depth of 50 m (Fig. 5). Most Angelsharks were caught close to the coast, usually in the North Sea, but also in estuaries and shallow seas including Grevelingen, the Eastern Scheldt, the Western Scheldt and in the Wadden Sea. There were no reports of Angelsharks from the (former) Zuiderzee, Haringvliet (Fig. 1).

4. Discussion

Ecological data obtained from historical books and fish statistics should always be carefully considered, since both correct and incorrect information can propagate between books, and 'hard' data sources are generally lacking (Bennema and Rijnsdorp 2015). Here we collated both historical books spanning the years from 1600 to 1950 and independent individual catch records of Angelsharks in the Dutch coastal waters, and we found that the insights from both sources match in many aspects. The books each reported different observations and gave precise density estimates and information on the ecology of the species, suggesting that these sources used independent material. Our conclusions are therefore based on the combination of non-confounded sources and we conclude that the Angelshark was most likely at least an annual visitor of the Dutch coastal waters. In some years the species might even have been fairly common, as claimed by some authors in the 19th century (Schlegel 1862; van Bemmelen 1866).

This characterization is in agreement with reports from nearby countries. For instance, the Angelshark used to be a common species in Britain in the 19th century and 'most numerous on its southern coast' (Yarrell 1836). Halfway the 20th century the Angelshark was listed as a common species for Belgium (Poll 1947). Rappé (2008), analysing historical catches by Belgian fleets as found in interviews with fishermen, lists catches of Angelsharks as very occasionally between 1945 and 1965, but very rarely ever since.

Justification of a more quantitative estimate of Angelshark abundance in Dutch coastal waters, and in fact in the entire North Sea, suffers from the lack of fishery-independent density estimates. During the first scientific fishing survey in the Netherlands, carried out in 1877 (Anonymous 1878), one Angelshark was caught in 110 hours of fishing. However, this record cannot be compared to contemporary fish-abundance estimates because of differences in fishing gear and vessels. In fishery-independent surveys performed by MS Huxley between 1902-1909, one Angelshark was caught during 1550 fishing hours in the southern North Sea (6×10^{-4} hr^{-1}) (www.cefas.com; and see Sguotti et al. 2016). For comparison, during these same surveys, species of the common skate complex *Dipturus batis*, were captured at a rate of 0.065 hr^{-1} and plaice *Pleuronectus platessa* was captured at a rate of 4.5871 hr^{-1}. Because these observations pertain to a single individual, it is difficult to evaluate this record, but it suggests that Angelsharks, although present, were far less common than other species in the area. In later fishery-independent surveys, which became widespread and standardized only after the 1950s (Sguotti et al. 2016), no Angelsharks were caught in the North Sea.

4.1 The demise of the Angelshark in Dutch coastal waters

Interpreting trends in opportunistic, fishery-dependent catches is challenging because of the difficulty to separate true population trends from changes in fishing effort (Hiddink et al. 2019). Given the lack of good data on fishing effort for the 110 years included here, we could not standardize our data in any meaningful way. Yet, it is well known that fishing intensity increased over the period of time reported (Rijnsdorp and Millner 1998), which implies that the species' decline over time is probably more dramatic than shown by the individual records. Furthermore it was argued that data collected by NIOZ between 1933—1990 lends itself for interpretation of species' trends over this time period, as trends derived from this data have been shown to be comparable to long-term series from independent sources (de Vooys and van der Meer 1998; note that Angelsharks were not included in this analysis). The NIOZ data is an important source in our analysis and we argue that the decline of individual records after 1970 most likely represents a genuine decline and the lack of records after 1973 marks the local extinction of the species. Likewise, the increased number of recorded individuals between 1940—1950 may be genuine.

It is more difficult to interpret the increased number of recorded individuals around 1900. Most records from this period originated from newspapers, so it could mean that the species became newsworthy around 1890 (i.e. became rare). Yet, this interpretation is not supported by the newspaper records themselves, which present varying views on the species' abundance and do not mention any trends. Thus, the simplest explanation is that the species was more abundant at the beginning of the 20th century and declined afterwards. Redeke (1941) also mentions that the species was less abundant than before.

The disappearance of the Angelshark from the North Sea has not been rigorously evaluated; our study is the first attempt to do so. To reconstruct the species' disappearance, we emphasize that it was important to thoroughly check a large variety of sources in the local language; previous attempts to unravel the historical ecology of the Angelshark were based on museum collections alone (Zidowitz et al. 2017; Lawson et al. 2020), and thus our study unveiled far more data, which had previously gone unrecognized. The reconstruction we present here is more or less congruent with anecdotal information on the species' decline that commenced in the late 19th century (Miller 2016), and with a report from southern England where the Angelshark was described as relatively abundant around 1900 and absent in the 1990s (Rogers and Ellis 2000; Henderson 2014). Likewise, in most parts of the North Sea, the last reports of Angelshark catches stem from the 1970s (Lawson et al. 2020). Also, in the Mediterranean the species is shown to have declined rapidly after 1960 (Fortibuoni et al. 2016; Giovios et al. 2019), while in the waters of Ireland and Wales, the species declined sharply in the 1990s (Hiddink et al. 2019; Shephard et al. 2019).

4.2 Causes of extinction

The disappearance of Angelsharks from the North Sea is often linked to mortality imposed by fisheries (Fortibuoni et al. 2016; Miller 2016; Hiddink et al. 2019). Our data may not lend itself for in-depth analysis of extinction causes, but some interpretation is warranted. We argue that overfishing may explain the demise of Angelsharks also in Dutch coastal waters; most powerfully, the demise of the species in the 1970s follows the introduction of beam-trawling to the region (Rijnsdorp et al. 2008). Additionally, the decline early in the 20th century could have been a result of overfishing, because this period marks the onset of steam trawling (Rijnsdorp and Millner 1996). Another indication that the species suffered from overfishing is derived from reports on size-distributions. Historical books (<1900) mention a maximum size of 2.4 m in length (Coenensz van Schilperoort 1577-1581; Bennet and Olivier 1825), considerably larger than the 2.0 m in more recently collected catch data. It is impossible to check the reliability of historical reports, yet a reduction in maximum size is seen in many marine species (Genner et al. 2010), and is one of the most commonly observed effects of overfishing due to size-selection in demersal fisheries (Froese 2004) and recreational fisheries (Francis et al. 2019; Jiménez-Alvarado et al. 2019).

If the species indeed suffered from fisheries, this is because of bycatch mortality and not the result of targeted fisheries, i.e. none of the historical books and newspapers mentioned targeted fisheries on Angelsharks. It is important to mention that, despite a lack of targeted fisheries, the species was probably not discarded once caught, i.e. Coenensz van Schilperoort (1577-1581) mentions that the species was only eaten by the poor, because of the bad quality of the meat. This might have accelerated the extirpation of the species from the area, but perhaps at a different rate than in areas such as the Mediterranean Sea and parts of the Northeast Atlantic (Spain and France), where it is thought that targeted fisheries did wipe out the species (Fortibuoni et al. 2016; Giovos et al. 2019, Lawson et al. 2020).

Other factors that should be considered as drivers of population change in Angelsharks are climate change and habitat loss. The Angelshark is a warm-water species (Rogers and Ellis 2000), and the species might have been more abundant at the end of the 19th and beginning of the 20th century in the waters south of England because this was a warmer period (Garstang 1900; Rogers and Ellis 2000). Indeed, we found clusters of individual records around 1900 and between 1945-1955 that roughly fall within two warmer periods (www.aoml.noaa.gov), so climate could potentially be a driver of the species' distribution at its northern range. Nevertheless, the North Sea is currently warmer again (Perry et al. 2005), and Angelsharks have not returned so far, suggesting that climate is not the ultimate cause of the species' disappearance from the North Sea. Also, prior to 1900 and in the 20th century the North Sea went through several temperature oscillations, including a cooling phase (the 'Little Ice Age' (1300-1850); Mann et al. 2009), a period during which the species was (perhaps even commonly) found in the North Sea (Coenensz van Schilperoort 1577-1581).

Reduction in fish populations is sometimes linked to habitat loss (Ward-Paige et al. 2010). The (partial) closure of Dutch estuaries is the most obvious change in habitat with reported impacts on fish populations (Wolff 2000; Lotze et al. 2006). Nine of the 104 individual Angelsharks in our dataset were caught in such an estuary, the now partially closed Eastern Scheldt. Although this closure negatively affected marine fish populations (Nienhuis and Smaal 2012), we argue that it did not contribute to the local extirpation of the Angelshark, because this estuary was partially closed well after Angelsharks disappeared from the area. It could, however, affect the opportunities for the species to return.

4.3 Ecological inferences

The historical books together with the data of individual Angelshark catches disclose some aspects of the ecology of the species in the Dutch coastal waters. First of all, we show that Angelsharks were mainly caught in the summer months. Whether this is the result of the species' ecology or of seasonally higher fishing intensity cannot be known, because we lack precise information on fishing intensity for the reported period. Prior to the 1970s, fishing intensity peaked in the summer, but fisheries did continue in the winter months; in 1967–1969 it was estimated that fishing intensity was twice as high in summer as in winter (Rijnsdorp et al. 2008). This is not sufficient to explain the seasonal patterns that we observed, suggesting that Angelsharks indeed were more abundant in summer. A summer peak is also in line with the written knowledge from historical books, which indicate that the species was mainly caught in summer (Coenensz van Schilperoort 1577-1581; Muus and Dahlstrøm 1966). Furthermore, it is generally thought that Angelsharks used to be migratory at the northern part of their distribution (Ebert and Stehmann 2013) and visited the northern regions only in warm seasons.

The two clusters in the size data, one matching young individuals and the other mature individuals, indicate that adult Angelsharks moved into the Dutch coastal waters to reproduce, and that young individuals used the area as nursery grounds. The designation of this region as parturition ground is further supported by three reports of gravid females and a trend in the records towards a female-biased distribution (the fact that also mature males were caught suggests that the area was also used as mating ground). All reported gravid females and young individuals are from summer, which matches reports of birth events happening in July in European waters (Compagno et al. 2005).

Together with the observation that most individuals were caught in shallow waters close to shore, our data suggests that Angelsharks used to move to shallow waters for parturition in the summer months (*cf.* Muus and Dahlstrøm 1966). This behaviour has also been documented for two other species of angelsharks, *Squatina oculata* in the Mediterranean Sea (Capapé et al. 1990) and *S. guggenheim* in Argentinean waters (Vooren and Da Silva 1991).

4.4 Concluding remarks

The North Sea has been described as a strikingly rich sea with a diversity of species and fish density that is difficult to imagine nowadays (Bennema and Rijnsdorp 2015). This review shows that the iconic Angelshark used to be part of the North Sea ecosystem, where it moved to the coastal waters in summer for mating and parturition, and where newborn individuals had their nursery grounds. Our review is a case study in how a large predator disappeared from a marine ecosystem; such losses can lead to wide-spread trophic cascades and thereby change the ecosystem in fundamental ways (Baum and Worm 2009; Hammerschlag et al. 2019). Although the results of effects are present in the current day, we are only be able to see them when we view the system in the context of its historical state. Records dating back further than fifty years are essential to disclose the potential of the natural richness of the North Sea ecosystem.

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.

The supplementary material accompanying this publication is registered under DOI:10.25850/nioz/7b.b.0 and available at https://doi.org/10.25850/nioz/7b.b.0

Acknowledgements

We are grateful to a large number of people who helped us to create this overview. Leonne van Weegen and Marlies Bruining from the NIOZ library were of great support in finding historical documents. Suzanne Poiesz and Vincent van Ernich helped with digitizing the bycatch data from the NIOZ archives. Hans Witte provided a large variety of data sources and advice and helped reconstructing catch locations. Jan Jaap Poos, Jurgen Batsleer, Adriaan Rijnsdorp, and Henk Heessen all gave constructive comments on our interpretation of the data and Henk Heessen gave excellent comments on an earlier version of this manuscript. Jaap Quak, Floris Bennema, Adrie Vonk, Judith van Bleijswijk, Guido Leurs and Jan van de Voort helped with finding data in more or less unexpected locations. We thank Ronald de Ruiter from Naturalis for providing us with the data in the museum's catalogues and Georg Engelhard for advice on how to interpret our data. We thank Gardner Creech for his thorough text-editing of a late manuscript version. We further thank two anonymous reviewers for constructive comments on earlier versions of the manuscript. We acknowledge a research fund from WWF for the work by RB in this project

Author contributions

	RB	MvdW	KC	HvdV	AvL
conceptualization	x	x	x	x	x
data collection	x		x		
data analysis	x				
writing	x		x	x	x

Tables

Table 1. Historical sources (books and newspapers > 50 years old) reporting on the abundance of Angelsharks in the Dutch coastal waters.

reference	year	source	area and abundance description
Coenensz van Schilperoort (1577-1581)	1577-1581	book	well known to the fishermen of Scheveningen, caught 5-6 times per year
Gronovius (1754)	1754	book	caught at our coast
Houttuyn (1764)	1764	book	present at our coast
Bennet and Olivier (1825)	1825	book	home in the North Sea and along the Dutch coast
Anslijn (1828)	1828	book	sometimes caught along the Dutch coast
van den Ende (1847)	1847	book	caught along the coast of Katwijk
Schlegel (1862)	1862	book	not rare at our coast, but never caught in great abundance
van Bemmelen (1866)	1866	book	not rare at our coast
Bottemane (1883-1884)	1882	book	very rare in the Eastern Scheldt
Bellen en Kerbert (1888, cited in (Redeke, 1941)	1888	book	not rare at all at our coast
Haagsche courant	1889	newspaper	rarely caught at Scheveningen
De Telegraaf	1898	newspaper	caught in the Eastern Scheldt where it is rarely caught, although the species is common near our coasts
De Telegraaf	1898	newspaper	common at our coast, but rarely caught
Rotterdamsch nieuwsblad	1899	newspaper	caught in North Sea where it is a rare species
Het nieuws van den dag	1906	newspaper	caught in the Eastern Scheldt where it is rare
Haagsche courant	1907	newspaper	This fish is caught every now and then in the North Sea, but never in great abundance
Redeke (1922)	1922	book	not in the list of fish species occurring in the Zuiderzee
Redeke (1941)	1941	book	is less abundant in our waters than it used to be
Het vrije volk	1961	newspaper	caught in the North Sea where it is very rare
Muus and Dahlstrøm (1966)	1966	book	rare at our coast

Table 2. Summary of the sample sizes used in this study and their origin. The numbers refer to the number of individual Angelshark records for which the associated variable is available. See the supplementary material for the full data.

	total N	*year of catch*	*month of catch*	*size*	*catch depth*	*catch location*	*sex*	*time-range*
museum	30	20	11	7	0	6	0	1840-1973
newspaper	29	29	27	15	0	10	2	1859-1967
other	10	5	5	3	0	8	0	1877-1973
NIOZ archive	35	35	35	26	18	32	20	1933-1972
total	*104*	*89*	*78*	*51*	*18*	*56*	*22*	*1840-1973*

Figures

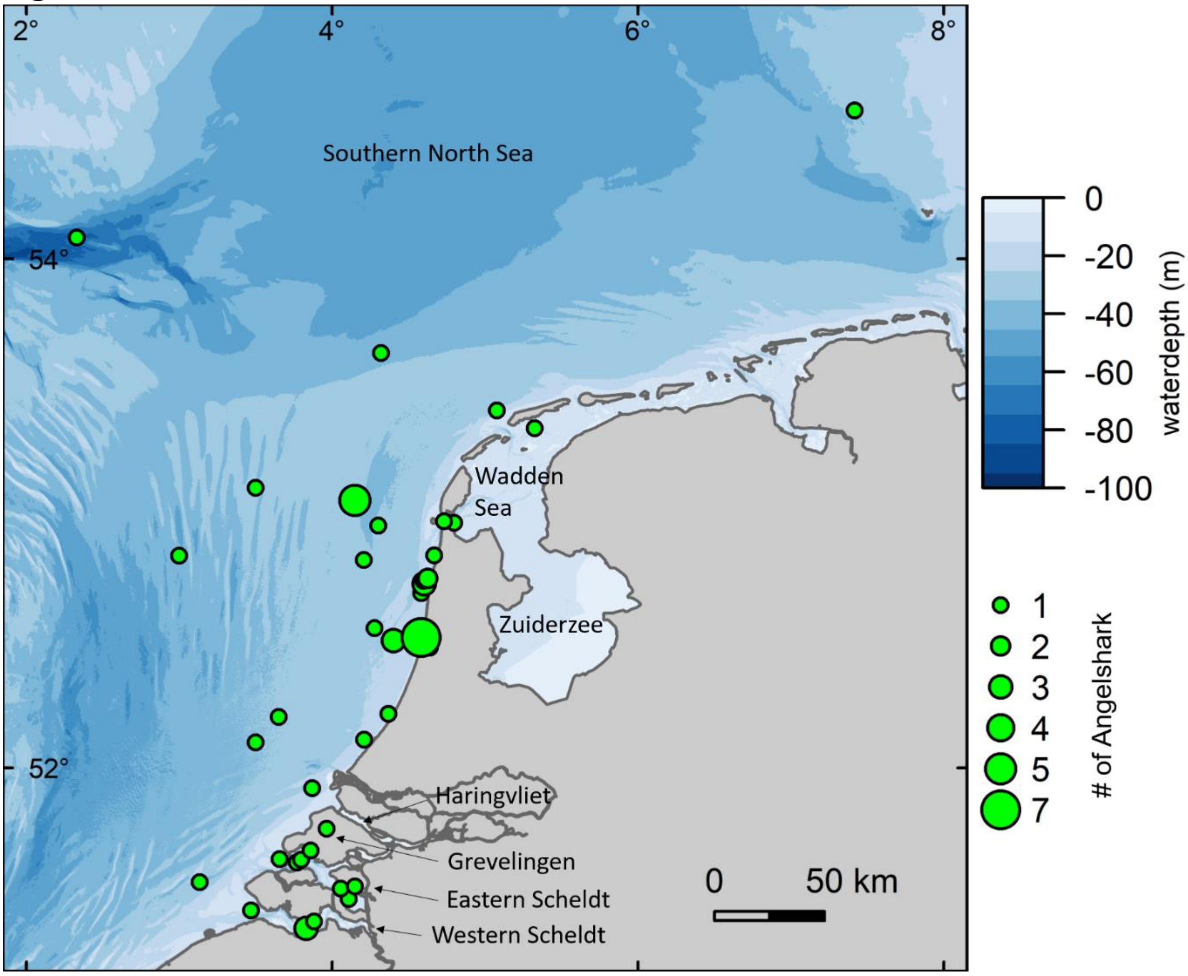

Figure 1. Map of the Netherlands before 1932 with known catch locations of Angelsharks. The size of the dots reflects the number of individuals caught. The water depth is taken from the EMODnet Bathymetry Consortium (2018). The water depth of the now reclaimed polders in the former Zuiderzee was assumed to be between 0-5 m. Sources and numbers are listed in Table 2.

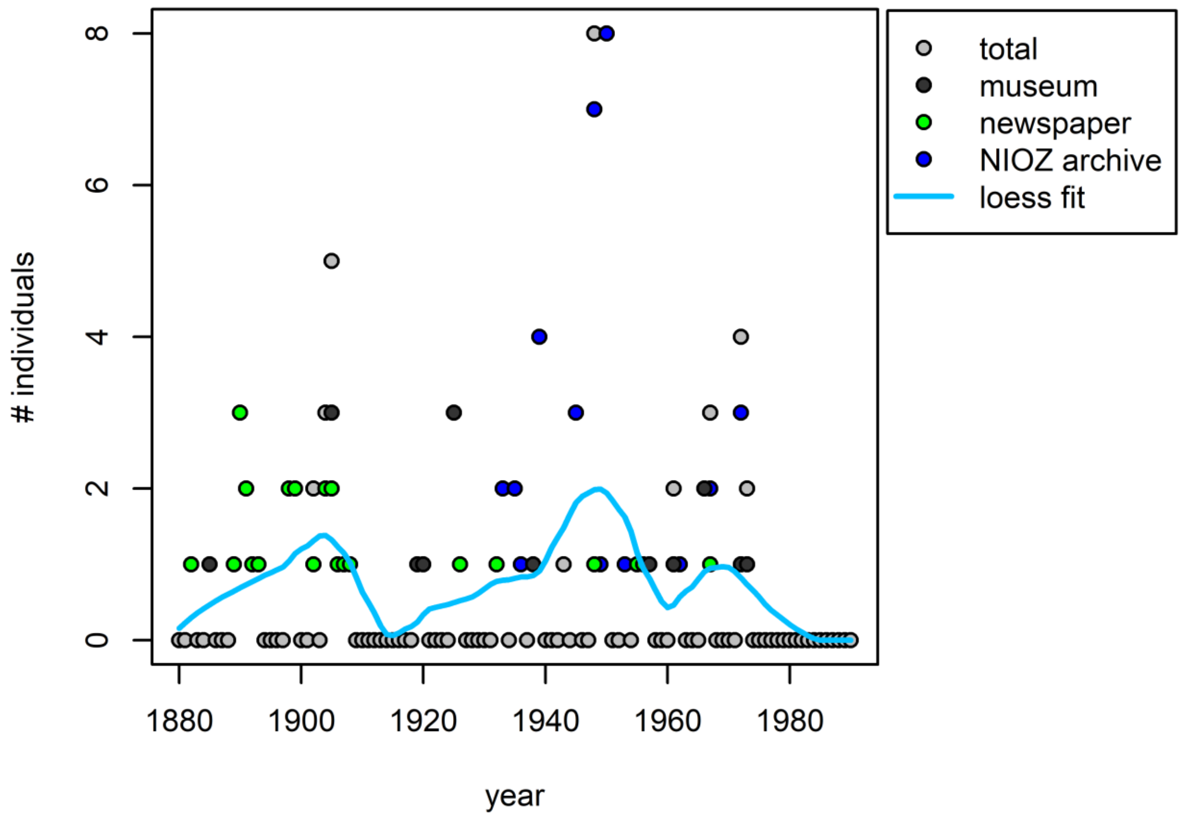

Figure 2. Number of catch records of Angelsharks in the Dutch coastal waters per year. Sources and numbers are listed in Table 2. Note if the total was comprised of a single source, the symbol colour corresponds to that source.

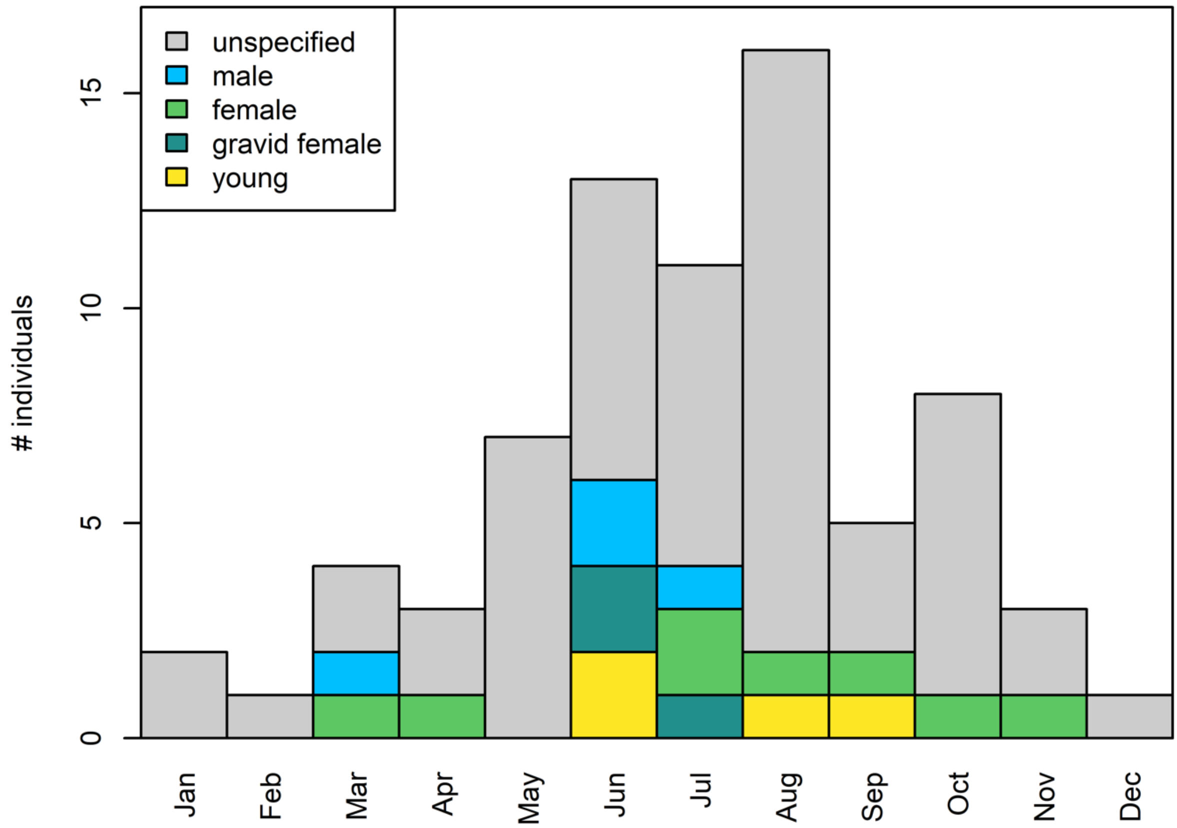

Figure 3. Distribution of catch month for Angelsharks in the Dutch coastal waters (1840-1973). Sex and life-stage, including pregnancy status, are indicated separately.

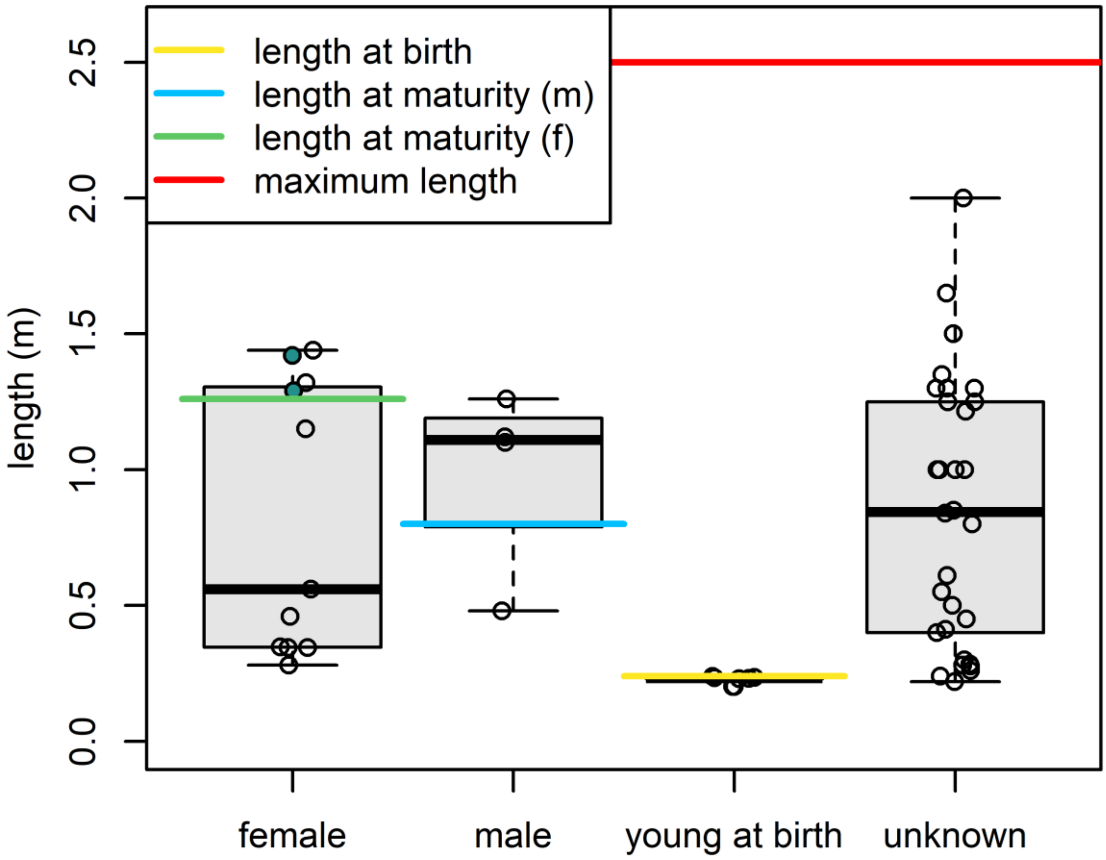

Figure 4. Size distribution of individual Angelsharks caught in the Dutch coastal waters (1840-1973). The jittered points are the raw data. Filled points refer to females that gave birth on deck. Lines refer to length at birth (Miller, 2016), length at maturity for males and females, and maximum length (see legend; Roux et al. cited in Heessen et al 2015).

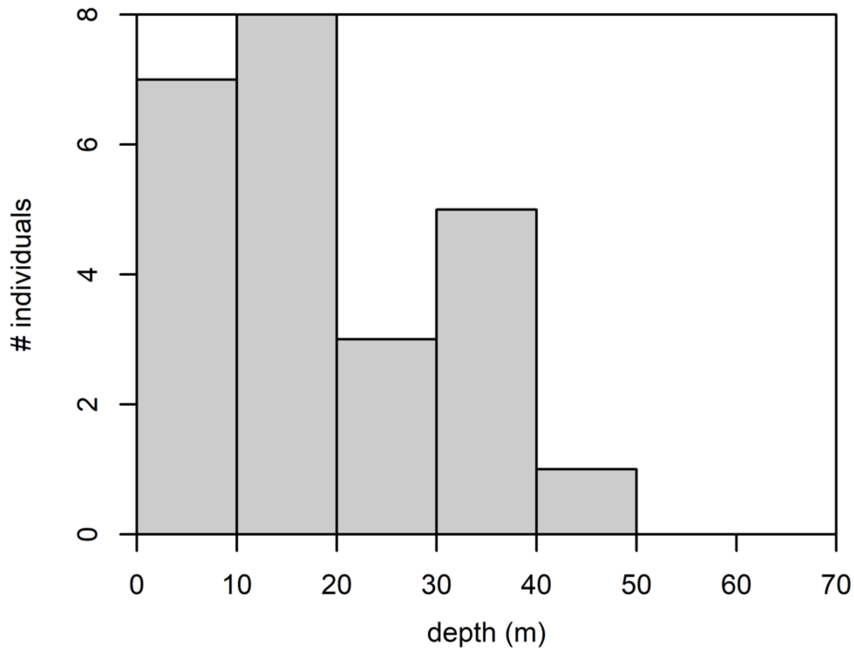

Figure 5. Catches of Angelsharks in relation to water depth in the Dutch coastal waters (1840-1973). The maximum depth of the Dutch part of the North Sea is 70 m.

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