

Analyses of four centuries of bounty hunting on seals in Zeeland, SW-Netherlands

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Abstract: For centuries, bounty hunts for seals (*Phoca vitulina*) were conducted in the Province of Zeeland (SW-Netherlands). Records of bounties paid for seals hunted in that area have been archived by the province of Zeeland from the 16th until the 20th century. These hunting records were used to reconstruct the numbers of seals caught each year in order to subsequently investigate the effect of social and historical events on the hunt. Based on the type of records we discerned three periods in the bounty hunts: 16th until 19th century, 19th century, and 20th century. During these periods large fluctuations in numbers of seals killed were observed. In the first period, high yields were achieved when experienced hunters (Frisians) came to the area, whereas the presence of privateers - and to a much lesser extent war activities - lead to significant lower seal catches. The effects of these events on the hunt appear to be so significant that it impairs the reconstruction of the population size in the pre-20th century period. This is different for the 20th century. Besides the periods during the two World Wars, no large scale changes in environmental conditions occurred. Efficacy of hunting methods took effect from 1900 onwards, when firearms became increasingly accurate. When bounty payments stopped in 1934, the seal hunt still continued and catches were registered. When the hunt was finally closed in 1961, the population in the SW-Netherlands had been decreased to approximately five percent of its estimated size around 1900. It has not recovered since then, mainly due to lack of immigration, high mortality, excessive disturbance, and low reproduction.

Keywords: seal hunting, bounty scheme, SW-Netherlands, privateers, hunting methods, Zeeland.

Introduction

For centuries, harbour seals (*Phoca vitulina*) have been considered to impact fisheries. They were therefore hunted throughout their range of distribution, including the Netherlands, where hunting was encouraged by the provincial government by means of imposing bounties. There was a highly developed fishery in

the Province of Zeeland and seals were considered to be a threat, being by competition, gear damage or depredation. The authorities expected to promote seal hunting by providing bounties. The payment of bounties for each seal killed has a long history in the Netherlands. This was especially the case for the hunt in the waters around the Province of Zeeland (figure 1). This bounty system was particularly well documented and was introduced as early as 1591, continuing though with some interruptions, throughout the cen-

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Figure 1. Map of the Netherlands around 1800.

turies until 1934. Most of the information on the magnitude of the seal hunt presented here has been given in earlier publications written in Dutch (de Vooy et al. 1999, de Vooy 2003, de Vooy 2006). In theory, this data could be used to analyse changes in the local seal population, assuming a relation between population size and hunting success (Reijnders 1992). However, next to the population size, the success of these bounty hunts aimed at strongly reducing the seal population might have been affected by social and historical events. This would render it impossible to estimate the population size in historic times, solely based on numbers of seals killed and retrieved. Therefore we study here the possible effects of prevailing social and historical events in Zeeland on the bounty hunt during four centuries. The usage of the word

seal or seals refers to harbour seals, as in the time period covered there were no observations on occurrence of other seal species such as the grey seal (*Halichoerus grypus*).

Material and methods

data sources

The main source of data used to determine the seal hunting activities in Zeeland are the bounty payments recorded in the archives of the Province of Zeeland. The different types of archives are the basis for the separation into three periods.

For the first period of bounties in the 16th, 17th and 18th centuries (1591 until 1810) we

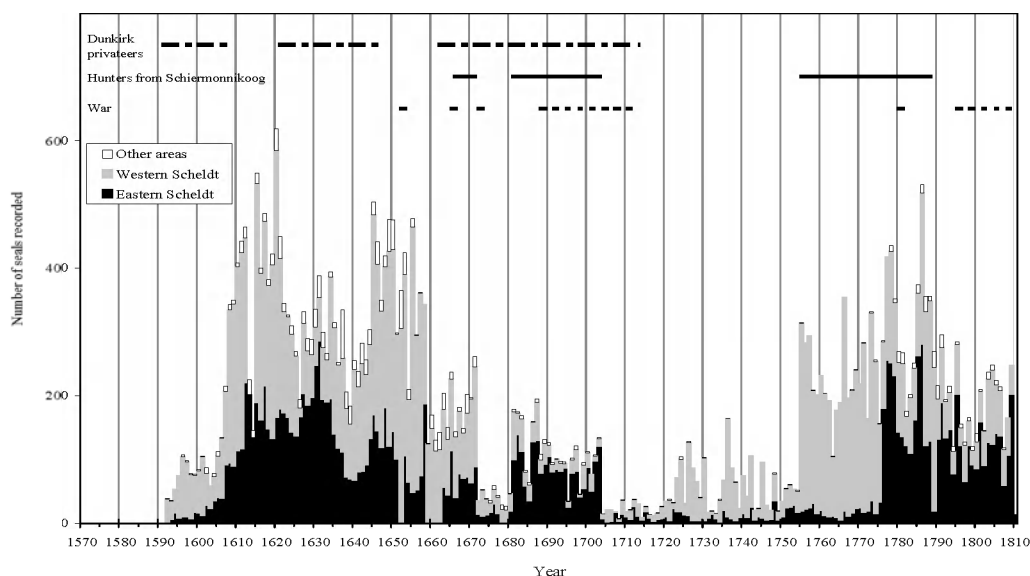


Figure 2. Number of harbour seals killed for bounties in the 17th and 18th centuries in Zeeland. Factors influencing numbers caught are indicated.

used the general archive of Zeeland (Zeeuws Archief, Middelburg). For the 17th and 18th centuries they can be found under the numbers: Rekenkamer (Audit-office) van Zeeland 1319-1805, Rekenkamer B (ZA No. 505), Rekenkamer II (ZA No. 512), Rekenkamer varia (ZA No. 513). These archives contain the receipts of the bounties paid to the hunters. In the 19th century (1825) the Fishery Board of Zeeland (*Bestuur der visscherijen op de Schelde en de Zeeuwse Stroomten*) was founded. From then on (second period, 1826-1856), bounties were paid for each seal or harbour porpoise (*Phocoena phocoena*) killed. This was considered the second period. Until 1840 seals were recorded separately. However after that, only the total amount of animals killed (seals and porpoises together) was registered. Bounties were paid for each seal or porpoise caught. Registrations of payment of these bounties were preserved in the Zeeuws Archief (17.1): No. 838 (1825-1844) and No. 839: (1845-1867). For these years the number of seals killed could be estimated based on the reported total seal catch in the period 1840-1849 and for the

period 1850 -1856 we assumed that the ratio seals-to-porpoises was similar to the period before (de Vooy 2003).

For the third period of bounties, from 1900-1934, payments for captured seals were recorded, now for the whole of the Netherlands. The numbers for the Wadden Sea in the north, and Zeeland, were given separately in the yearly reports on Dutch fisheries. Registration of bounties paid in the 20th century can be found in: Verslag van den Staat der Nederlandse Zeevisscherijen (1900-1910); Jaarverslagen der Visscherijinspectie (1911-1920) and from 1920 onwards: Verslagen en Mededelingen van de afdeling visserijen, Departement van Landbouw, Nijverheid en Handel.

Historical Background

Presumably, seal hunting was never the only source of income of a person involved, even when bounty systems were operative. However, it could have been a lucrative supplementary income. Discussions were held repeatedly

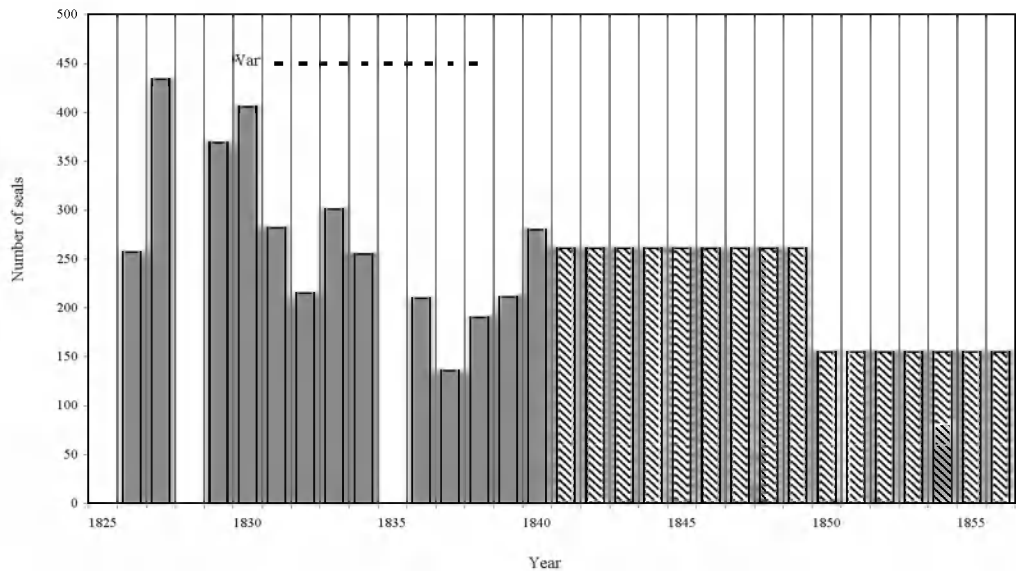


Figure 3. Number of harbour seals killed for bounties in the 19th century in Zeeland. Filled bars are registered numbers of harbour seals killed and hatched bars are estimated numbers of harbour seals killed. --- Period of Belgian Independence War.

Table 1. Privateers and Naval wars which restricted and were destructive for Dutch fishery and merchant fleet (Boxer 1977).

	Period	Under protection of / against	Duration (years)
Dunkirk Privateers	1583-1609	Spain	26
	1621-1646	Spain	25
	1662-1713	France	51
Naval wars	1652-1654	England	2
	1665-1667	England	2
	1672-1674	England & France	2
	1701-1713	France	12
	1780-1784	England	4
	1795-1813	England	18
	1830-1839	Belgium	9

in the parliament on the efficacy of the bounty system (de Vooys 2006). It was questioned whether the bounty system would contribute significantly to seal hunting to generate a sound source of income. As an example, reference was made to a small business in West-ernieland (Province of Groningen, the Netherlands) which existed from 1860-1905 and caught about 200 seals per year without bounties. However, this company did not depend

solely on seal hunting. The people involved were primarily fishermen and salvage workers (de Vooys et al. 1999).

Seal hunting in Zeeland is assumed to have been influenced by the varying social and historical events occurring in the area during the study period. In 1581 the Seven United Provinces proclaimed independence from the government of the Habsburg King Philips II, King of Spain. The war ended in 1648, when

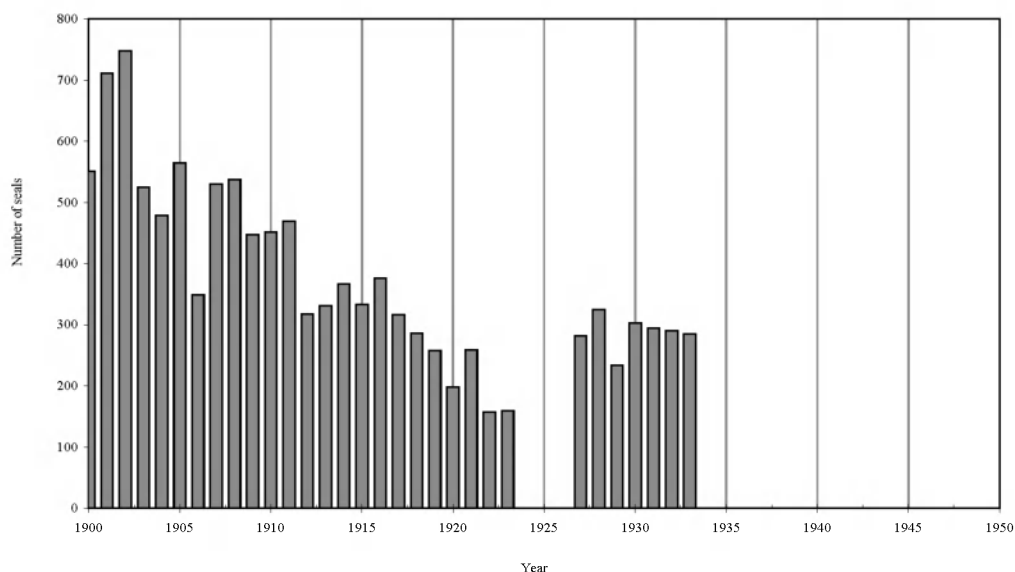


Figure 4. Number of harbour seals killed for bounties in the 20th century in Zeeland.

Dutch independence was recognised by the Spanish government. During this period, the Spanish commander-in-chief Parma founded an Admiralty in Dunkirk aimed at causing maximal damage to the Dutch merchant fleet and fishery (Boxer 1977). An overview of the historical events is presented in table 1.

The Admiralty succeeded to damage the Dutch fleet considerably and this continued until 1646, when the French occupied Dunkirk. Before that, this practice had only been interrupted during the “twelve year truce” lasting from 1609–1621 (van Vliet 2004). In 1662 however, the privateers started again, now under French protection and this lasted until 1713.

On top of these privateer activities, the seal hunt could also have been affected by the four naval battles the Netherlands fought with England, and the two battles against France during the 17th and 18th centuries (table 1). During these wars Dutch fishery and coastal activities were practically impossible, as for example curfews were in effect.

The Congress of Vienna in 1815 united the Netherlands and present-day Belgium into one country under King William I of Orange. However, the Belgians revolted against the

Dutch government in 1830. After nine years, a peace treaty was concluded on 19 April 1839. During the war the Western Scheldt was closed by English and French warships, and shipping at night on the Western Scheldt was forbidden (van den Broeke & Paul 2004). As seal hunting was often carried out with nets, and often practiced at night, hunting in the Western Scheldt must have been severely hampered. On the other hand, seal hunting in the Eastern Scheldt could have continued unhindered in that period.

Interestingly, from the mid-17th century to the second half of the 18th century the majority of seals were caught by Frisians coming from the island of Schiermonnikoog in the North of the Netherlands, and not by local people. This could be deduced from the receipts in the archives in Zeeland as well as the archives of Schiermonnikoog. The naval wars and especially privateer activity, must have also affected the traveling of the Frisian fishermen to Zeeland. The presence of Frisian hunters was only recorded reliably for the period after 1666.

The number of hunters and the amount of bounties paid out to each of them is known

Table 2. Analysis of Deviance. Terms added sequentially (first to last); Df = degrees of freedom, Resid. Df. = residual degrees of freedom, Resid. Dev. = residual deviance.

	Df	Deviance	Resid. Df	Resid. Dev
NULL		287.0		19134.0
Area	1	268.9	286	18865.1
Frisians	1	8109.0	285	10756.1
Privateers	1	1466.2	284	9290.0
War	1	120.8	283	9169.2
Area : War	1	229.0	282	8940.2
Area : Privateers	1	178.0	281	8762.1
Area : Frisians	1	5.6	280	8756.5

in the 19th and 20th centuries (de Vooy 2006), but not in the 17th and 18th centuries.

centuries considered, large variations in yearly yields occur, from a maximum of about 700 per year to almost none in some years.

Statistical Treatment

In order to determine how historical events affected the number of harbour seals harvested in Zeeland, data for the first period up to 1810 was analysed. The number of seals caught was related to the binary factors Area (East or West, representing respectively the districts Eastern Scheldt and Western Scheldt, as defined in 't Hart 2007), War (Yes or No), Privateers (Yes or No) and presence of Frisian hunters (Yes or No).

A log-linear model was fitted using main effects and first-order interactions with the factor Area. These interactions were included in order to examine whether the factors War, Privateers and Frisian hunters differed between Areas. A Poisson-like error was assumed and a correction for overdispersion was made (Crawley 2005, R Development Core Team 2009).

Reliable information on the presence of Frisian hunters was only available for the period after 1666. Data before 1666 was therefore excluded from the statistical analysis.

Results

Annual yields for the period 1590-1934 are given in figures 2-4. Data show that for all

Effects of historical events

For the first period of bounties, the analysis of deviance showed that all main effects and the interactions Area : War and Area : Privateers were significant ($\alpha=0.01$, $\chi^2=6.64$, and table 2). The contributions of the main effect War and of all its interaction effects Area : War and Area : Privateers were, however, small and difficult to interpret. For example, the number of seals caught increased slightly during a war period in the West but decreased slightly in the East (figure 5). As we are dealing with time series where the data are probably auto-correlated, the risk of over-fitting is large and we have therefore chosen to leave the main effect War and all interaction effects out of the final model. For the entire period, the coefficients of the final model point to an average number of 50 seals caught per year in the Western Scheldt district (West) and 41 in the Eastern Scheldt district (East), bringing the total to over 90 seals. But this holds only for those periods when neither privateers nor Frisians were around. When privateers were active the total number caught decreases to an average of 47 seals compared to the situation when privateers were absent. When Frisians were around many more seals, 354, were caught (almost 4 times as much)

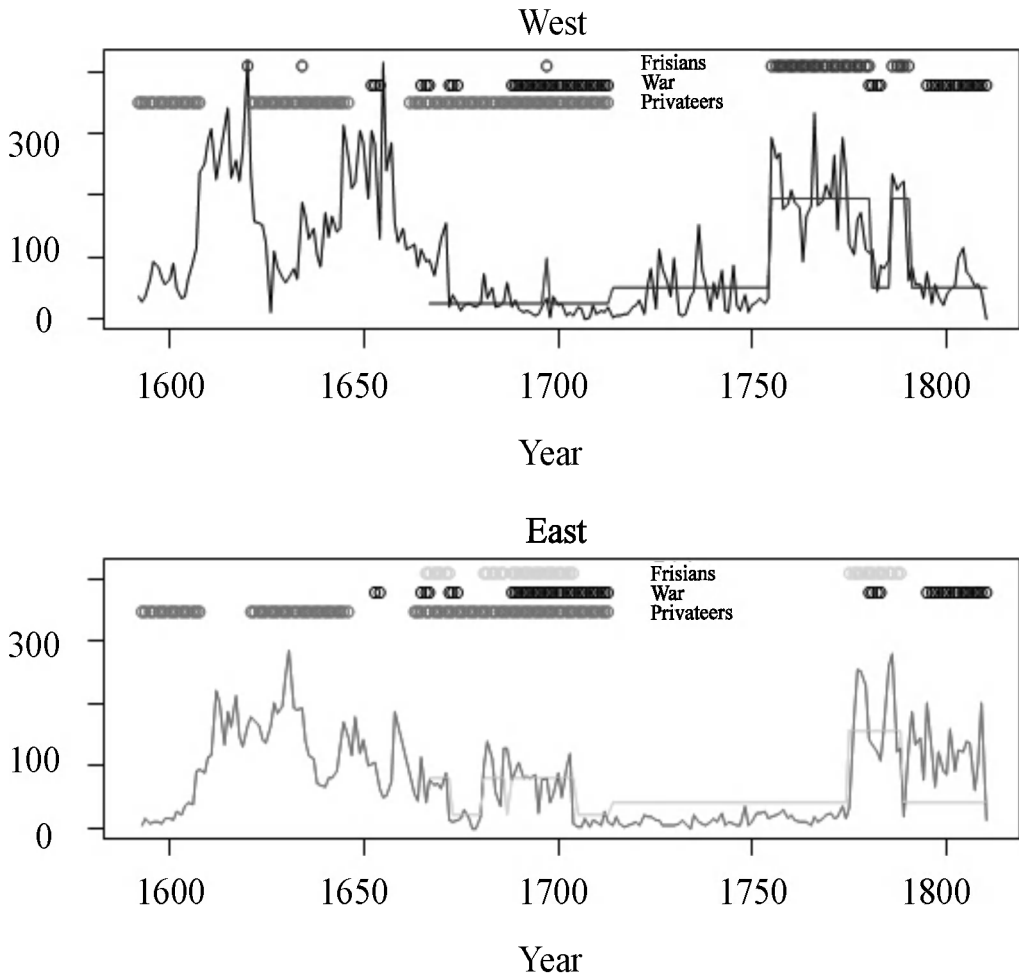


Figure 5. The number of harbour seals caught versus time in the West and the East, with data and model predictions. Straight lines represent model outcome.

compared to the situation when these hunters were absent. Figure 5 shows the data and the model fit for both areas separately.

For the second period of bounties, which was not subject to the statistical analysis, the influence of the Belgian Independence War and subsequent tumult (1830-1839) seem to have suppressed the yield (figure 3).

In the third period of bounties, the reported numbers caught strongly decreased over time (figure 4).

Records for the 19th and 20th centuries were given in more detail. They show that seal hunt-

ing effort was concentrated around the third quarter of the year (figure 5). This coincides with the pupping and moulting period of the harbour seals. During the late summer, the animals spend relatively more time on the sandbanks as they attend to their young and subsequently moult. Seal hunting was therefore a seasonal activity.

Discussion

The analyses of bounty payments in rela-

tion to circumstances during the first period of bounties show that a dominant influence was exerted by both Frisians coming to the southern Delta area to hunt and privateers who posed a threat to vessels sailing in the area. The influence of the naval wars on the seal hunt was less, as can be deduced from the deviances in table 2. This is also the case for differences between areas. The model does not fit well in all periods. Apparently, other factors must have played a role here. Shifts of interest could explain the relative low yields of seals in the Netherlands in part of the 18th century. Next to seals, bounties were paid for several other species of mammals and birds in Zeeland from 1712 onwards. This also applies to the Province of Friesland from 1720 onwards, and in the Province of Groningen from 1703 onwards ('t Hart 2007).

In the second period of seal bounties a decrease in the yield can be observed from 1831 to 1838. This could have been influenced by war. During the revolt of the Belgians (1830-1839), fishing in the Western Scheldt was prohibited during the night. This might have hindered seal hunting as well (Broeke & Paul 2004).

The large variations in hunting yield seen in the Netherlands are not unique. Similar large fluctuations are known for the long-term harvest of Cape fur seals (*Arctocephalus pusillus*) in South Africa. Reconstruction of that harvest operating from 1653-1899 revealed that hunting effort was the dominant factor influencing the yield (David & van Sittert 2008). The low fur seal yields in the period 1840-1860 could be explained by high prices of guano occurring in the same region, and local people shifted to guano collection instead of seal hunting.

Changes in hunting methods – from clubbing and netting to firearms – might have played a role in the hunting efficacy, and hence yield during the centuries studied. Clubbing can be effective when seals can be taken by surprise or when they are less mobile, for instance when mothers are accompanied by

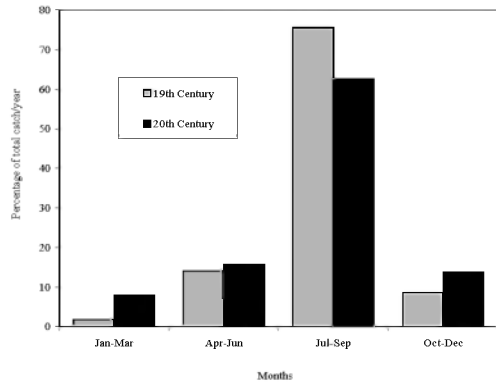


Figure 6. Percentages of total catch of harbour seals in different seasons in the 19th and 20th centuries.

a young pup. Until the beginning of the 20th century in the Netherlands hunting with nets was often practiced (Anonymus 1852, Kuelper 1912). In the 19th and the beginning of the 20th century seals were sometimes caught alive, and could be sold to zoological gardens and circuses (Anonymus 1852). In Germany seals were hunted in the Elbe estuary and the coast of Schleswig-Holstein. Here old sturgeon-nets were used. Different hunting techniques were used, depending on the width and depth of the gully and the strength of the current. If the gully could be closed off at low tide, seals would be caught in the net. In wider gullies, nets were used to contour the seals on the bank, and when the seals flush into the water, the net would be tightened. When the depth of the gully extended beyond the depth of the net, the current was used to float the net along the seal bank. When the net reached the bottom, the seals are hunted into the water and the net was contracted.

Hunting of seals by means of firearms was hardly practiced before the end of the 19th century, and only seals on sandbanks were shot. Both the precision of the firearms (often muskets) and the quality of the ammunition was rather inferior. Only after 1900 rifles became increasingly effective. With the improved firearms seals could be killed when swimming in the water, and this could increase the catch. The efficiency of the new

firearms could account for the relative high number of seals killed in the beginning of the 20th century onwards, when bounties were re-introduced (third period of seal bounties 1900-1923). Firearms gradually superseded older hunting methods. The hunt was so efficient that it affected the population size. This could explain the decrease in catch from 1920 onwards (figure 4).

After termination of bounties in 1934, hunting on seals was continued, licensed under the Dutch Hunting Law of 1954. But the character of hunting changed. After the Second World War many seals, especially young ones, were killed for the fabrication of fur coats. Finally, the seal hunt was banned in the SW-Netherlands in 1961 and in the Dutch Wadden Sea in 1962. The extent of this hunt had a devastating influence on the seal population (Reijnders 1976).

Currently, the estimation of the size of seal populations is carried out based on aerial or boat surveys. In the Netherlands, seal counts have been conducted from the late 1950s onwards. In addition, back calculations using hunting statistics to estimate more historical population sizes have been carried out for the Dutch Wadden Sea (Reijnders 1992) and Zeeland (Reijnders 1994). These techniques have enabled back calculations to 1900. The size of the harbour seal population in the SW-Netherlands in 1900 will have been close to 11,500 animals.

Similar studies were carried out in the Skagerrak-Kattegat (Heide-Jørgensen & Härkönen 1988, Marboe 2004) and show a negative influence of hunting on population size.

To go further back to estimate the seal population in Zeeland, a definite link had to be made between the yield of the hunt and the seal population size. In this study we show that human societal factors were in times determinant for the number of seals taken. Therefore we deem it not possible to estimate the size of the population for the 17th, 18th or 19th century in Zeeland.

Calculations estimating population size

in retrospect, using hunting statistics have been carried out for the 20th century. These showed clearly that hunting as carried out in the mid-20th century was not sustainable for the seal population. When the hunt stopped in the SW-Netherlands in 1961, the size of the population was then less than 5 percent of its estimated size around 1900, and only 350 harbour seals were counted (Reijnders 1994). Given the centuries long period of bounty hunt with strongly fluctuating but generally relatively low number caught, it is unlikely that the hunt in the preceding centuries would have had a similar impact. Probably the inefficacy of hunting techniques, and the further complications rendering the hunt sometimes impossible, prevented a significant decimation of the seal population throughout the centuries.

Contrary to the Wadden Sea harbour seal population, which recovered during the 20th century after the complete ban of hunting including Denmark and Germany in the mid-1970s, the seal population in the SW-Netherlands did not recover (Reijnders 1994). Particularly disturbance and lack of immigration are considered initial causes hampering recovery from overhunting. In addition a general lack of reproduction and extremely high mortality in the area prevents recovery.

Conclusion

Here we show that social and historical events such as long periods of war, privateers and visiting hunters have had a strong influence on the success of hunting harbour seals in the Province of Zeeland. Despite the excellent records of the seal bounty hunt in that area, spanning more than three centuries, it appears that the bounty records cannot be linked to population size in these periods. For seal populations in the Netherlands in the 20th century, and in other areas, it was possible to use bounty records to back-calculate the original population size. This was possible, as



Frans Snyders. Flemish Fish market, depicting a.o. two harbour seals and a harbour porpoise. Painted 1618-1621. Royal Museum of Fine Arts, Antwerp, Belgium © Lukas - Art in Flanders vzw. Photograph: Hugo Maertens.

a few independent population estimates enabled checking of the calculated population trajectories. One can however conclude tentatively that in these earlier days the population must have been extremely large, to sustain, sometimes years on end, the loss of hundreds of animals per year. However, the intensified and efficient hunt in the first half of 20th century was apparently unsustainable, from which the population could not recover until now.

References

- Anonymus 1852. De robbenvangst. Sloet's Tijdschrift voor Staathuishoudkunde en Statistiek 7: 195-208.
- Boxer, C.R. 1977. The Dutch seaborne empire 1600-1800. Hutchinson & Co, London, UK.
- Crawley, M.J. 2005. Statistics: An introduction using R. John Wiley, Chichester, UK.
- David, J. & L. van Sittert 2008. A reconstruction of the Cape (South African) fur seal harvest 1653-1899 and a comparison with the 20th century harvest. South African Journal of Science 104: 107-110.
- de Vooy, C.G.N. 2003. Premies voor de jacht op zeehonden in Zeeland, 1826-1856. Nehalennia 142: 34-39.
- de Vooy, C.G.N. 2006. Zeehondjacht in Zeeland: het effect van premies. Zoogdier 17 (3): 9-12.
- de Vooy, C.G.N., S.M.J.M. Brasseur & P.J.H. Reijnders 1999. Visserij en zeehonden in de vorige eeuw. Waddenbulletin 34 (3): 40-41.
- Hart, P. 't 2007. Zeehondjacht in Nederland 1591-1962. PhD Thesis. Vrije Universiteit, Amsterdam, the Netherlands.
- Heide-Jørgensen, M.P. & T. Härkönen 1988. Rebuilding seal stocks in the Kattegat-Skagerrak. Marine Mammal Science 4: 231-246.
- Kuelper, W. 1912. Der Seehundsfang an der deutschen Nordseeküste. Mitteilungen Deutschen Seefischerei-Vereins 28: 245-258.
- Marboe, A.H. 2004. Seals, Seal Hunting and Fishermen - The seal population in Denmark's Coastal Waters, c. 1750-1889. In: P.J. Moree, A. Poldervaart, A.P. van Vliet & J.P. Voort (eds.). Fish, War and Politics, 1300-2003, International Conference Amsterdam/Middelburg. Netwerk, Jaarboek Visserijmuseum 15: 120-126. Visserijmuseum, Vlaardingen, the Netherlands.
- R Development Core Team 2009. R: A language and

- environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reijnders, P.J.H. 1976. The harbour seal (*Phoca vitulina*) population in the Dutch Wadden Sea: size and composition. *Netherlands Journal of Sea Research* 10: 164-179.
- Reijnders, P.J.H. 1985. On the extinction of the Southern Dutch harbour seal population. *Biological Conservation* 31 (1): 75-84.
- Reijnders, P.J.H. 1992. Retrospective Population Analysis and Related Future Management Perspectives for the Harbour Seal *Phoca vitulina* in the Wadden Sea. *Netherlands Institute for Sea Research Publication Series* 20: 193-197.
- Reijnders, P.J.H. 1994. Historical population size of the harbour seal, *Phoca vitulina*, in the Delta area, SW Netherlands. *Hydrobiologia* 283: 557-560.
- van den Broeke, W. & P. Busse 2004. De betekenis van de visserij voor de Zeeuwse economie in de periode 1795-1849: niets dan vel en graat? In: P.J. Moree, A. Poldervaart, A.P. van Vliet & J.P. Voort (eds.). *Fish, War and Politics, 1300-2003*. International Conference Amsterdam / Middelburg. Netwerk, Jaarboek Visserijmuseum 15: 59-69. Visserijmuseum, Vlaardingen, the Netherlands.
- van Vliet, A.P. 2004. Vissen in oorlogstijd. De Zeeuwse zeevisserij in de zestiende en zeventiende eeuw. In: P.J. Moree, A. Poldervaart, A.P. van Vliet & J.P. Voort (eds.), *Fish, War and Politics, 1300-2003*. International Conference Amsterdam / Middelburg. Netwerk, Jaarboek Visserijmuseum 15: 50-58. Visserijmuseum, Vlaardingen, the Netherlands.

Samenvatting

Het verloop van vier eeuwen premiejacht op zeehonden in Zeeuwse wateren

Eeuwenlang vond in de Zeeuwse wateren premiejacht op zeehonden plaats. De uitbe-

taalde premies van de in de 16^e tot in de 20^e eeuw buitgemaakte dieren werden geregistreerd in Zeeuwse archieven. In deze studie worden die jachtstatistieken gebruikt om het aantal jaarlijks geschoten dieren te reconstrueren. Vervolgens wordt het effect van sociale en historische gebeurtenissen op het jacht succes onderzocht. Er worden drie perioden van premiejacht onderscheiden op basis van het systeem van registratie: 16^e tot begin 19^e eeuw, de 19^e en de 20^e eeuw. Gedurende deze perioden treden grote fluctuaties op in het geregistreerde aantal gedode zeehonden. In de eerste periode waren er hoge opbrengsten wanneer ervaren jagers (Friezen) in het gebied kwamen, terwijl de aanwezigheid van kapers en in veel mindere mate oorlogsactiviteiten, leidden tot significant lagere vangsten. De invloed van die gebeurtenissen op de vangstopbrengst was in de periode 16^e tot 20^e eeuw dermate groot, dat het niet mogelijk is op basis van de jachtgegevens een reconstructie van de populatiegrootte voor die tijd uit te voeren. Dat is anders voor de 20^e eeuw. Afgezien van de duur van de twee wereldoorlogen waren er geen grootschalige veranderingen in omgevingsomstandigheden. Wel nam de doelmatigheid van de jachtmethoden toe vanaf circa 1900, toen vuurwapens steeds nauwkeuriger werden. Ondanks het stoppen van de premiebetalingen in 1934, werd de zeehondenjacht toch voortgezet en werden de aantallen gedode zeehonden geregistreerd. Toen de jacht in 1961 tenslotte werd gesloten, was de populatie in ZW-Nederland gedaald tot ongeveer 5% van de geschatte omvang omstreeks 1900. Die heeft zich sindsdien amper hersteld, hoofdzakelijk door het ontbreken van immigratie, verstoring, hoge mortaliteit en lage reproductie.

Received: 20 April 2012

Accepted: 4 June 2012