Habitat quality for Grey Seals in the Dutch Wadden Sea

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Cover photograph by Roger Kirkwood: A grey seal ponders its next move

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Contents

Conte	nts	
Summ	nary	5
List of	Tables	57
List of	figure	s
1	Introd	uction & Methodology9
	1.1	Conservation status of grey seals in the Wadden Sea9
	1.2	Research questions and aims10
	1.3	Methodology10
2	Grey	seals in the Netherlands12
	2.1	Grey seal identity12
	2.2	Grey seal biology
		2.2.1 General
		2.2.3 Moult
	2.3	Grey seal population status
		 2.3.1 Population changes in Europe
		2.3.3 Grey seals in the Delta region
3	Greys	seal habitat requirements and usage19
	3.1	Habitat at sea19
	3.2	Habitats on land: haul-outs and breeding colonies20
	3.3	Processes of colonisation
	3.4	The Dutch Coastal area
		3.4.1Breeding habitat availability in the Netherlands233.4.2Wadden Sea breeding sites25
	3.5	Grey seal breeding site requirements
		3.5.1Physical properties of breeding sites323.5.1.1Frequency of submergence32
		3.5.1.2 Access to shore 32
		3.5.2Other properties of breeding sites
		3.5.2.2 Presence of other grey seals
		3.5.2.3 Predators and Disturbance
	3.6	Conclusions
4	Greys	seal pup survival and mortality
	4.1	Overview
	4.2	Pup survival and mortality in the Netherlands

		4.2.1 Natural pup survival/ mortality in the Wadden Sea4.2.2 Impact of weather events on grey seal pup counts in the Dutch	39
		Wadden Sea	40
		4.2.2.1 Observations in 2013	
		4.2.3 Anthropogenic influences on survival in the Netherlands	
		4.2.3.1 Fisheries impacts	
		4.2.3.2 Collisions	
		4.2.3.3 Disturbance	
		4.2.3.4 Captive-care and release 4.2.3.5 Environmental contamination	
		4.2.3.6 Habitat change	
5	Excha	inge of grey seals with other areas	49
	5.1	Local breeders, annual immigration and seasonal visitors	49
	5.2	Photo-ID of grey seals	50
		5.2.1 Introduction	
		5.2.2 Methods	
		5.2.3 Results	
		5.2.4 Conclusion	55
6	Concl	usions & recommendations	57
	6.1	Summary points	57
	6.2	Adequacy of the habitat for grey seals	59
	6.3	Survival of grey seals in the Netherlands	
	6.4	Exchange of grey seals between Dutch waters and other areas	61
	6.5	Recommendations	61
7	Refere	ences	63
8	Qualit	ty Assurance	71
-			
9	JUSTITI	cation	12
Apper	ndix A.	Baltic grey seals	73
Apper	ndix B.	Grey seals and the Farne Islands, UK	74
Apper	ndix C.	Potential for antagonism between seal species?	76

Summary

Atlantic grey seals (*Halichoerus grypus grypus*) commenced recolonising Dutch coastal waters, following >2000 years of rarity caused primarily by human hunting - the first pup-birth was recorded in 1985. Growth in numbers has seen the Netherlands become a strong-hold for grey seals in continental Europe.

Conservation of grey seals in the Netherlands is managed by the Ministry of Economic Affairs in accordance with the European Commission's Habitats Directive. This directive requests Member States to undertake surveillance of, and seek a 'favourable' status for, habitats and species of Community interest.

In the Dutch Natura 2000 species profile document for the grey seal, the habitat quality for grey seals was assessed to be 'unfavourable' due to disturbance of pupping sites and it was not sufficiently clear how a 'favourable' conservation status could be achieved. There are knowledge gaps concerning the survival of grey seal pups born on potentially sub-optimal breeding sites and the importance of an influx of seals, mainly from the UK.

Accordingly, the Ministry for Economic Affairs commissioned the project presented in this report and posed two central questions:

- 1. "Is the favourable status of the habitat quality of the grey seal in the Netherlands dependent on the presence of undisturbed, permanently dry breeding sites, or do the current sites, which are considered sub optimal, suffice for a long term survival of the species in the Netherlands?"
- 2. "How strongly is the growth in the Netherlands influenced by immigration from other areas?"

In this report, these questions are addressed as three topics:

- a) Adequacy of habitat in the Netherlands, especially pupping/ breeding habitat (Chapter 2)
 b) Survival primarily of pups, which are the most likely age-group to have reduced survival if breeding sites are inadequate (Chapter 3).
- 2. Exchange of seals between the Netherlands and other areas (mainly UK) (Chapter 4).

1a-Adequacy of breeding habitat

- 1. Grey seals require land habitat to rest, moult, have pups and breed. All current pupping sites of grey seals in the Netherlands are flooded by extreme high tides and by high storm surges (i.e. that reach approximately 2-m above NAP Amsterdam Ordnance Datum). Grey seal pups usually do not swim until 3-7 weeks after birth (3-weeks of maternal support and up to 4-week of post-weaning period). If flooding coincides with the pupping period (November to January in the Netherlands), dependant pups can be separated from their mothers and dependant and weaned pups could be drowned or washed away from the site. Because of the vulnerability to inundation, current pupping sites can be considered as sub-optimal for pup survival.
- 2. Within the Netherlands, alternative habitats for the seals to colonise are available, including coastal beaches and adjacent dunes of the mainland and Wadden Sea islands. At such places, the seals may stay dry for as long as needed. They avoid these sites, however, and the most likely reason for this is to avoid human disturbance. Future colonisation of such sites might occur provided disturbance is minimised, particularly during the first years of colonisation.
- Grey seals currently give birth to pups at five key locations in the Netherlands all in the Wadden Sea: Richel (67% of the pups born); Engelschhoek (14%); Griend (2% and increasing); Razende Bol (5%); and Steenplaat (4%). These are critical locations for the sustainability of the current recolonisation of grey seals in the Netherlands. The natural development of the grey seal

population in the Netherlands requires these locations to be adequately protected from human interference, particularly during pupping periods. A few pups are born at other sites, including on inhabited islands. Currently, there is no policy for special protection measures at such sites.

4. There is also a strong selection pressure for the most appropriate moult locations. Currently, the most important grey seal moult location in the Netherlands is Engelschhoek. In the past 5 years, an average of 75% of seals seen in the Dutch Wadden Sea moult there. Other key moult sites include Razende Bol (11%) and Steenplaat (5%).

<u>1b-Survival</u>

- 5. Adult grey seal survival rates in the Netherlands are in line with levels found in other areas (Brasseur et al. 2014). However, there is an indication that the rate of first year survival in the Wadden Sea (~59%) is lower than rates at other sites (Brasseur et al. 2014). There is a high probability that the lower survival is related to the regular flooding of the breeding sites in the Wadden Sea.
- 6. The sustainability of grey seal breeding (and pupping) in the Netherlands will be influenced by survival rates of seals. Possible human-related impacts on survival include altered feeding possibilities due to fisheries takes, entanglement and by-catch in fishing gear, and disturbance (e.g. visual disturbance on land and acoustic disturbance underwater).
- 7. A further potential influence on grey seal survival-rates in the Netherlands is the high level of collection, captive-care and release of first-year seals. It is unknown how this could have impacted on natural mortality, population growth, or distribution of pupping.

2-Exchange

- 8. Modelling of grey seal population data collected in the Netherlands confirms that a proportion of the seals, born in the UK, are incorporated into Dutch colonies (Brasseur et al. 2014). Approximately 35% of the one-year-old grey seals in the Wadden Sea are estimated to come from the UK. Also, a larger numbers of grey seals that breed in the UK occupy Dutch waters and coastlines outside the breeding period. The exchange between the Netherlands and the UK is also registered in telemetry studies collected in the past decade.
- 9. Quantification and a better understanding of the underlying mechanisms for the migrants requires a longer-term study (photo-ID plus genetics). This is of importance to further understand the inter-dependency of the colonies in the North Sea.
- 10. A photo-ID program was commenced in the framework of this project, in cooperation with researchers at the Sea Mammal Research Unit (SMRU, St Andrews, Scotland). SMRU researchers developed the photo-ID method for grey seals and have a data base of over 20 000 seals mostly from UK colonies. Initial processing and pattern matching of a proportion of the images from Dutch waters represented a pilot study and no matches were made of individuals between areas.
- 11. Further gaps still remain in our knowledge of local habitat quality and sustainability, pupping success and population demography, quantification of links to other populations, prey species and foraging behaviours, and impacts of anthropogenic factors that may influence survival including fisheries interactions and disturbance.

List of Tables

Table 1. Pup production at colonies in the Dutch Wadden Sea. 25
Table 2. Summary and description of habitat qualities which are assumed to play a role in the grey seal
females' choice for breeding sites (based on available literature *) and relative effect on usage and pup
survival. Site selection: low = will not prevent selection, moderate = likely to influence selection, high =
will influence selection. Potential to effect pup survival: low = might influence survival rate, moderate =
will influence survival rate, high = likely to prevent survival
Table 3. Grey seal (Halichoerus grypus) pup mortality at colonies in the UK, indicating colony description,
% mortality, main causes of mortality and reference
Table 4. Means of mortality of grey seal (Halichoerus grypus) pups at colonies in the UK (data from
references in Table 3)
Table 5. Previously estimated survival rates for grey seals aged 0-1 year old. 39
Table 6. High water events (>2m) that coincided with grey seal pupping in the Wadden Sea, and likely
caused some flooding. Shading combines data for pupping seasons
Table 7. Locations and dates of grey seal photography for photo-ID pattern matching
Table 8. Processing outcomes of grey seal photo-ID images taken in the Netherlands between March and
May 2013
Table 9. Number of females, males and 'sex unknown' grey seal in photo-ID images taken in the
Netherlands between March and May 2013 55

List of figures

Figure 1. Grey seal pup production at eastern UK breeding colonies (southern Scotland and England). An exponential curve is fitted to the totals for the period 1980 to 2008 and indicates a growth rate of 5.7%
(Thompson & Duck 2010)
Figure 2. Numbers of grey seals counted in the Wadden Sea (by IMARES) and in the Dutch delta region
(counted by RWS/Province of Zeeland) between 1960 and 2012
Figure 3. Trend in numbers of grey seal pups recorded during surveys in the Wadden Sea between
1985/86 and 2012/13 (Brasseur et al. 2013)
Figure 4. Examples of movements by grey seals from the Wadden Sea, data from 10 seals tracked in the
years between 2004 and 2008 (Brasseur et al. 2010)
Figure 5. Examples of grey seal pupping habitats (photos accessed from the web)
Figure 6. Expansion of the distribution of grey seals in the Dutch Wadden Sea from 1985-2010 (Brasseur
et al. 2013). Engelschhoek (also known as Engelsehoek) was the first pupping site; Richel is now the
most important pupping site
Figure 7. Water depth and modelled water velocity (Brinkman & Bult 2002) in the Wadden Sea, indicating
drainage patterns as well as relative channel depths and flow rates between the islands24
Figure 8. Recorded locations of grey seal pup births in the Dutch Wadden Sea since 1985 25
Figure 9. Annual maximum of grey seals (bars) and pups (dots; right axis) counted during different
seasons on the Engelschhoek
Figure 10. Aerial photos (from bing maps and google earth) of important grey seal pupping sites in the
Wadden Sea, indicating changes in shape over time
Figure 11. Grey seal pupping habitat on Richel, Vlieland in the background (photo RK)
Figure 12. Locations of grey seal pups recorded during surveys in the Dutch Wadden Sea between
1999/2000 and 2012/13
Figure 13. Grey seal pupping habitat on Griend (Group 13 in Figure 14; photo RK)
Figure 14. Distribution of grey seals on Griend, 15 December 2013
Figure 15. Modelled (lines) and observed (markers) pup production distinguishing between counts that
were not influenced by prior storms (solid triangles) and those that were (open circles) (Brasseur et al.
2014)
Figure 16. Water levels (cm) at Vlieland harbour (near Richel and Engelschhoek) indicating the rise over
predicted levels caused by storm conditions on the 5-6 December 2013
Figure 17. Movement from Richel to Griend of an adult female grey seal with a tracker, following the high
tide that flooded Richel on 5-6 December 2013 (see Figure 16; google map, inset photo RK)
Figure 18. Grey seals with fishing net around their necks (photo RK)
Figure 19. Estimated pup production compared to counts and number of grey seals brought in to captive-
care for years 2000 to 2013 (Ecomare pers. com. and diverse public media). Captive-care cases were
only included if dates for capture were in the period 1 Dec. to 15 May. Only six of 271 grey seals brought
in to captive-care were older than a few months (Brasseur et al. 2014)
Figure 20. Steps in the technique used by pattern recognition software to convert the 3-dimensional
shape of a seal into a 2-dimensional image of pelage pattern (photos SMRU)
Figure 21. Pattern recognition techniques used for individual pelage recognition of lateral head shots
(Hiby et al. 2007), plus example photographs from 2013 (photos RK and Oscar Bos)
Figure 22. Example photographs of grey seals at Wadden Sea haul-outs that enable individual recognition
by photo-ID (photos by RK and GA)
Figure 23. Pup production and number of adult females and pups killed during the population control
program at the Farne Islands. Fitted lines are exponential curves – 7.4% per year between 1956 and
1971, -6.2% between 1972 and 1984 and 1.8% after 1984 (Thompson & Duck 2010)74

1 Introduction & Methodology

1.1 Conservation status of grey seals in the Wadden Sea

The grey seal *Halichoerus grypus* is one of two species of pinniped seals that lives and breeds in the Netherlands; the other is the harbour (or common) seal *Phoca vitulina vitulina*. The greatest numbers of both species in the Netherlands are observed at haul-outs in the Wadden Sea region; the other area for hauling-out is the Delta region (i.e. Zeeland and part of South Holland). During recent decades, the numbers of both species have increased in both regions.

The primary level of governance for management of grey seals in the Netherlands is the Ministry of Economic Affairs (*Economische Zaken*). This ministry defines the conservation status of habitats (HD Annex I) and species (HD Annex II) protected under the Habitats Directive (HD) and sets conservation objectives (both at a national level and at a Natura 2000 site level). The objectives strive to achieve an at national level 'favourable' conservation status for each of these habitats and species.

The conservation status for a species is defined in Article I of the Habitats Directive as the sum of influences acting on the species, which may affect the long-term distribution and abundance of its' populations. Status is taken as 'favourable' when:

- 1. population dynamics data on the species concerned indicate that it is maintaining itself on a long term basis as a viable component of its natural habitat;
- 2. the natural range of the species is neither being reduced nor is likely to be reduced for the foreseeable future; and
- 3. there is, and probably will continue to be, a sufficiently large habitat to maintain populations on a long-term basis.

The national conservation status of the grey seal in the Netherlands is described in the Natura 2000 species profile

document: <u>http://www.synbiosys.alterra.nl/natura2000/documenten/profielen/soorten/Profiel_soort_H13</u> 64_2014.pdf

The status was assessed on the basis of the population distribution, population size, habitat quality and future perspectives, following the Natura 2000 systematics. While the other components were assessed 'favourable', the habitat quality was assessed 'unfavourable/ inadequate' (due to disturbance at pupping sites), and hence the overall assessment was 'unfavourable'. However, since the population of grey seals was growing in the Netherlands, the Ministry did not opt for an 'improvement target' ('*verbeteropgave*'), but for a target to conserve the situation as it was when the Natura 2000 site 'North Sea Coastal Zone' ('*Noordzeekustzone'*) was placed on the list of sites of Community Importance (SCI, '*behoudsopgave'*). The same conservation target was set for the Natura 2000 area 'Wadden Sea' (also '*behoudsopgave'*).

In 2011, the Dutch high court (*Raad van State*) (case 200902398/1/R2) argued that the minister had not made sufficiently clear how a 'favourable' conservation status for the grey seal could be achieved, given that the habitat quality for the grey seal in the profile document was assessed to be 'unfavourable' due to disturbance of pupping sites. Given the overall unfavourable conservation status, it was not clear to the high court for which reasons the target for the grey seal in the Wadden Sea, as described in the site designation decree, was not an improvement target, but a conservation target. The ministry and appellants did not dispute the fact that there was a knowledge gap with respect to both the survival of grey seal pups born on potentially sub-optimal breeding sites in the Netherlands and the importance of an influx of seals, mainly from the UK, that had to be closed. This report addresses these knowledge gaps.

It is noted that in 2013, during the course of this study, the Dutch high court declared that grounds for appeal against the conservation objective for the grey seal failed (case

201104368/1/A4, <u>http://www.raadvanstate.nl/uitspraken/zoeken-in-uitspraken/tekst-</u> <u>uitspraak.html?id=74490</u>). The knowledge gaps remain and the Ministry considered that further research was required on grey seal habitat quality and status.

1.2 Research questions and aims

Two central questions were posed by the Ministry:

- "Is a favourable status of the habitat quality of the grey seal in the Netherlands dependant on the presence of undisturbed, permanently dry breeding sites, or do the current sites, which are considered sub optimal, suffice for a long term survival of the species in the Netherlands?". Sub questions were:
 - a. How many pups are born at sub-optimal locations and how many at optimal locations?
 - b. What are the risks (frequency of inundation, effects on survival, etc)?
 - c. Which permanently dry locations in the Wadden Area (North Sea Coastal Zone, islands, Wadden Sea) are disturbed now, but could serve as pupping locations when not disturbed?
 - d. Which part of the population growth can be explained by immigration?
- 2. How is the growth influenced by immigration from other areas (i.e. the UK)?"

These questions were addressed as three topics:

- a) The adequacy of the habitat for grey seals, especially the breeding areas (Chapter 3)
 b) The survival of the seals in the Netherlands, primarily the pups as these are the most likely to suffer if the breeding sites would be inadequate (Chapter 4).
- 2. The exchange of seals between the different areas (mainly UK) and the Netherlands (Chapter 5).

The answers to these questions will help the Ministry of EZ to determine whether a change in the current grey seal policy is needed. The answers should help the ministry to:

- 1. Adapt the Natura 2000 grey seal species profile document and make a clear choice for the description of the quality of the species' habitat (extra space needed or not).
- 2. Provide a thorough underpinning for decision making, in case extra space for seals is needed, including possible protection measures.

1.3 Methodology

To address the topics of habitat quality and survival rates (topic 1a and 1b see previous paragraph), a combination of literature study, field studies and population modelling was undertaken. It was realised there were many misconceptions amongst the public and policy makers concerning the population status, biology and ecology of grey seals. This report represents a suitable means for compiling and making available such data in a single and current report. Accordingly, the literature review (provided in Chapter 2) is broader than would be required for the topics of habitat quality and survival, alone.

The population modelling was an in-depth statistical analysis of data available counts of grey seals in Dutch waters since the 1980s. The detail of this modelling is beyond the scope of this report but has been incorporated into a peer-reviewed publication for the journal Marine Mammal Science (Brasseur et al. 2014).

Information on the exchange of seals between the Netherlands and UK was reviewed. The data were found to be largely anecdotal with minimal quantifiable records. Hence, a designated project was commenced to facilitate quantification of the exchange. This involved development of a collaboration with researchers from the Sea Mammal Research Unit (SMRU, St Andrews, Scotland) who had an established photo-ID program with grey seals at UK colonies. A pilot study to obtain suitable photographs of grey seals in the Netherlands was commenced. Methods and results from that pilot study are described in this report.

2 Grey seals in the Netherlands

2.1 Grey seal identity

There are two sub-species of grey seals: the Baltic grey seal *H. g. macrorhynchus* and the Atlantic grey seal *H. g. grypus*. These sub-species differ in their degree of sexual dimorphism (relative size of males and females), behaviour and range. Baltic grey seals are less sexually dimorphic, they give birth on seaice and are restricted in range to the Baltic Sea.

Atlantic grey seals have two distinct stocks: the north-west Atlantic stock and the north-east Atlantic stock. These function as distinct populations with minimal genetic exchange. Grey seals in the Netherlands belong to the north-east Atlantic stock, which occupies the coastlines of Europe from France to the Kola Peninsula in Russia. At present, approximately 90% of north-east Atlantic grey seal pups are born in the United Kingdom (UK). Outside of the UK, the area with the next largest pup production is the Dutch Wadden Sea.

Grey seals overlap in range with and are similar in appearance to harbour seals. Individuals can be difficult to identify to species. Pelage (or fur) pattern assists species recognition, with harbour seals having a more speckled appearance while grey seals exhibiting larger patches, although some individuals (particularly adult males) have a uniform pelage. There is some overlap in patterning though so pelage pattern does not ensure species recognition. Size also helps: grey seals attain larger sizes. A seal appearing larger than 200 cm in length or greater than 150 kg in mass is likely to be a grey seal. Adult grey seals also have a relatively long and robust muzzle, compared to the shorter muzzle of harbour seals. From close up, the nostrils of the grey seal appear to run parallel i.e. 'I I', whilst the harbour seals' nostrils come together forming a 'V' shape. The teeth of the seals also differ: grey seal molars lack the distinctive 'three point' structure of harbour seal molars.

Grey and harbour seals exhibit different breeding strategies. For example, grey seals breed in late summer, autumn, or in winter – the latter being when they breed in the Netherlands. Harbour seals breed in summer. Grey seals have their pups in (often large) colonies on land where 'alpha-males' defend a harem from other males. Harbour seals have their pups in more diffuse colony areas with males patrolling adjacent water-ways. Grey seals generally mate on land, whereas harbour seals mate in the water. Also, grey seal pups (born with a white lanugo)cannot swim properly until they reach several weeks of age, whereas harbour seal pups (born with adult-like fur) can swim independently within hours of birth.

2.2 Grey seal biology

2.2.1 General

In common with many large mammals, grey seals have a long lifespan, delayed maturity, and relatively low rates of adult mortality (Promislow & Harvey 1990). Compared to other phocids, grey seals exhibit a high level of sexual dimorphism; males attain considerably larger sizes than females. Adult males can be up to 300 kg, adult females up to 200 kg. A function of the larger size attained by males is thought to be to dominate reproductive opportunities within densely packed colonies (Anderson & Fedak 1985, Cassini 1999). The greater size comes at the likely expense of longevity, though, with males having shorter life spans. Longevity is up to 26 years for males and 46 years for females, although individuals seldom achieve more than 20 years of age.

2.2.2 Pupping

Like all pinnipeds, grey seals typically give birth to a single pup and may have a pup once a year. Their pupping is highly synchronised. They mate when the pup is weaned, so pupping and breeding periods overlap. Following mating, they have a delayed implantation followed by an 8-9 month pregnancy, so the next pup is born one year after its sibling.

Grey seals have a short suckling period (16-21 days) during which the mother and pup stay close by each other, the mother–pup bond is broken on weaning. Grey seal pups weigh approximately 15 kg at birth and 40 kg at weaning. There is considerable individual variability in weights, however, and weaning weights can range between 20 and 60 kg (Hall et al. 2008). Males are on average slightly heavier than females.

Weaned grey seal pups may stay on land for up to another month after the mother has departed. Over this month, the pups undergo several changes - such as completing their moult and converting fat into muscle (Boyd & Campbell 1971). Some pups will depart within a week of weaning, however, to complete the moult into juvenile pelage away from the colony-site. Between weaning and colony departure, the pups lose weight - they average 30 kg when they depart the colony (Kovacs & Lavigne 1986).

Survival through the first few months away from the colony can be dependent on the amount of stored energy with which they go to sea (McMahon et al. 2000, Hall et al. 2008). Generally, the heavier the pup is on departure, the better its chances of survival. This is because the pups must learn to find and hunt prey, and may expend considerable body reserves in the process.

Sexual maturity in grey seal females is at 3-6 years of age (Hammill & Gosselin 1995). Pregnancy rates are 83 to 94% (Boyd 1985), meaning each year 83-94% of adult females will give birth to a pup.

The mean age of sexual maturity in males is 5.6 years (Hammill & Gosselin 1995), although they do not achieve social maturity (and can hold a territory) until aged 8. To defend a territory, grey seal males may remain on land for up to 2-months without feeding, and thus need to store considerable fat reserves prior to this time of year. Grey seal females arrive at the colony after the males and enter a male's territory. A male may have several females in his territory, termed his harem.

The time of year when grey seals give birth varies between regions, and can be in late-summer to autumn (in western and northern colonies of the UK) or winter (in southern UK colonies, the Netherlands and Germany). Interestingly, a shift in the peak of the pupping time is observed in the Dutch colonies; in 1985 the peak occurred in early January, by 2010 this had shifted to early December (Brasseur et al. 2014). On average, the shift was at a rate of approximately 1.3 days per year.

2.2.3 Moult

Grey seal pups are born with a long-haired, white coat (lanugo). The animals usually complete the moult into a grey spotted pelage during the post-weaning fast (Boyd & Campbell 1971). If pups go to sea too early, their long-haired natal coat reduces their swimming capability and their chance of survival. As the pups remain on land unattended for such a period of time, grey seals probably are more vulnerable to disturbance and hunting than harbour seals, which can swim virtually at birth (Härkönen et al. 2007).

Moult in grey seals involves shedding of the entire coat over a period of several weeks (Ling 1970). Not all seals moult at the same time and the moulting period may therefore last for several months, February to April and even into May for some late moulters. There is a gradual turnover of moulting seals at the

haul-outs. Moulting seals can appear shabby due to the browner colour of their fur, loss of fur, accumulation of dirt and a drop in body condition.

Disturbances during the moult period can scare seals into the water, which greatly increases energetic costs, and can influence the seal's survival and future breeding success (Boily 1996, Worthy et al. 2009).

Aerial surveys demonstrate that during moult the highest number of seals seen on land can be attained. Therefore, counts taken during the moult period are used to index annual changes in numbers of seals in the Wadden Sea (see http://www.waddensea-secretariat.org/monitoring-tmap/topics/marine-mammals).

2.3 Grey seal population status

2.3.1 Population changes in Europe

North-east Atlantic grey seals have occupied the Wadden Sea, which fringes the North Sea coastlines of the Netherlands, Germany and Denmark, since the sea's formation through sea level rise 10,000 BP (Clark 1946, Joensen et al. 1976, Reijnders et al. 1995). Historically, grey seals may have been more abundant in the Wadden Sea than harbour seals. Excavations dated to between 6000 and 1000 BC from more than 50 settlements in the Danish Wadden Sea reveal the remains of exclusively grey seals (Joensen et al. 1976), and grey seals have been the most commonly encountered seal in excavations of prehistoric sites in both the German and the Dutch Wadden Sea (van Bree et al. 1992, Clason & Zeiler 1993, Reijnders et al. 1995). The greater prevalence of grey seal remains over harbour seals reflects both a high proportion in the Wadden Sea area, and that grey seals, especially the pups, were easier for prehistoric hunters to catch.

Through the Middle Ages (500 – 1500 AD) grey seal numbers in the Netherlands area decreased. Potentially, the low grey seal numbers was caused by increasing hunting pressure, biased for grey seals, and human disturbance (Reijnders et al. 1995, Prummel & Heinrich 2005). Major dyke systems protecting human inhabitants from floods were constructed and more humans colonised the area. By 1000 AD, numbers of the grey and harbour seals were approximately equal (Reijnders et al. 1995). Thereafter in continental Europe, grey seals became scarce, and after 1500 AD, grey seals were rare visitors to continental European waters south of Denmark (Joensen et al. 1976, Reijnders et al. 1995). Those that arrived would have been readily harvested.

During the middle ages on islands around the north of the United Kingdom, hunting also was undertaken, but isolated breeding groups of grey seals persisted. Hunting on those islands reduced during the 1800s, as human settlements there were abandoned. Consequently, seal numbers increased (Boyd 1963, Summers 1978). As they increased on the distant islands, seals stated to appear at and colonise sites closer to the mainland of the UK.

In 1914, an assumed low number of grey seals in the UK triggered the introduction of the <u>Grey Seals</u> (<u>Protection</u>) <u>Act</u> which prohibited seal hunting during the local pupping period. An amended <u>Grey Seals</u> (<u>Protection</u>) <u>Act of 1932</u> increased the duration of the closed season. These Acts enabled grey seal numbers to grow further across northern UK (Figure 1).

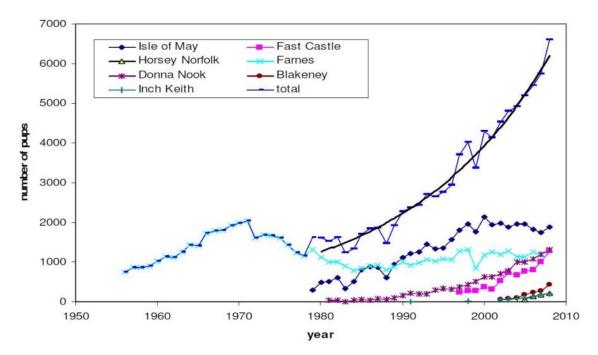


Figure 1. Grey seal pup production at eastern UK breeding colonies (southern Scotland and England). An exponential curve is fitted to the totals for the period 1980 to 2008 and indicates a growth rate of 5.7% (Thompson & Duck 2010).

Along with the increases in the UK, after centuries of rarity in continental Europe, grey seals became more frequently sighted. During the 1960s, they regularly utilised sandbars near the island of Amrum in the German Wadden Sea (Drescher 1979). By 1967, a small colony had developed near Amrum (Drescher 1979, Vogel & Koch 1992, Abt et al. 2002).

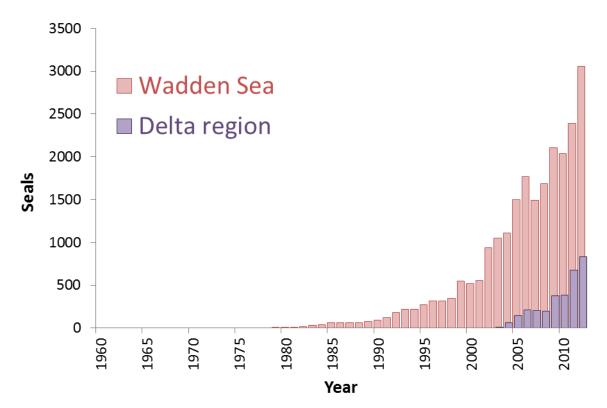
By 2005, the number of grey seals in continental Europe had grown to over 2500, with 2000 counted in the Dutch Wadden Sea (Härkönen et al. 2007). In addition to seals that pup at sites in continental Europe (residents), each year potentially thousands of grey seals from the UK travel eastwards to forage over the North Sea and many choose to haul-out at sites in continental Europe .

To summarise, north-east Atlantic grey seals undoubtedly declined in number between 2000 and 1000 years ago, and were suppressed to low level until the 1900s. Compared to the extended period of suppression, dramatic increases have occurred in the last 100 years. At present, the Dutch colonies form the most important strong-hold for these grey seals outside of the UK.

2.3.2 Recolonisation of the Dutch Wadden Sea

After centuries of virtual absence in the Dutch Wadden Sea, grey seals were recorded more often during the 1950s (van Haaften 1975, Reijnders et al. 1995). During the 1970s, seals were observed hauling-out at sandbars between the islands of Vlieland and Terschelling, particularly at Engelschhoek (Reijnders et al. 1995). Between 1980 and 1983, annual maxima at these sandbars grew from 10 to 40. In 1985, at Engelschhoek, there were approximately 40 seals present and the first pup-birth in the Netherlands was recorded (Reijnders et al. 1995). Prior to 1985, grey seal pups occasionally had been brought to Dutch rehabilitation centres, but these likely had been weaned at UK sites and had crossed the North Sea.

Surveys of grey seals in the Netherlands commenced in 1985 and have recorded exponential increases in numbers (Figure 2). Prior to 2001, the seals were monitored from vessels. As they spread to different sites, aerial surveys were needed. The surveys are timed to coincide with annual events: the pupping period (November-February) and the moulting period (March-April). Harbour seal surveys allow for numbers in summer (June-September) to be recorded as well, which is the grey seals' most intensive foraging period (Beck et al. 2003). Haul-outs in the Dutch Delta region were established in 2003. Numbers at these are counted monthly during local bird surveys (Strucker et al. 2006).



Data from <u>http://www.compendiumvoordeleefomgeving.nl/indicatoren/nl1231-Gewone-en-grijze-zeehond-in-Waddenzee-en-Deltagebied.html?i=19-135</u> last accessed 8 July 2014.

Figure 2. Numbers of grey seals counted in the Wadden Sea (by IMARES) and in the Dutch delta region (counted by RWS/Province of Zeeland) between 1960 and 2012.

The Wadden Sea pup surveys in midwinter can be underestimates in some years because extreme weather conditions can inundate the low sandbars on which the pups are born. Still, the long-term data set provides a good monitor of population changes. (Figure 3). During the 1980s, fewer than five grey seal pups were born annually in the Dutch Wadden Sea (Reijnders et al. 1995). By 2000, this had increased to 50 and, in 2009-2010, a maximum of 380 pups was counted .

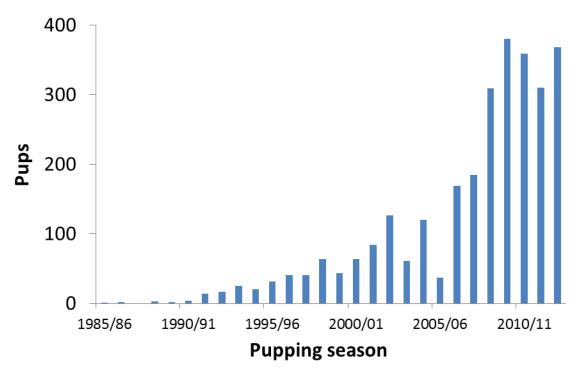


Figure 3. Trend in numbers of grey seal pups recorded during surveys in the Wadden Sea between 1985/86 and 2012/13 (Brasseur et al. 2013).

Overall, the increase in pup numbers between 1985 and 2013 followed an exponential pattern at a rate of 19% per year (Brasseur et al. 2014). This rate is higher than the 11% maximum rate of annual increase for a closed population of grey seals, which is reported in other demographic analyses (Harwood 1978, Harding & Harkonen 1999). Initially, when the colonies were founding in the Dutch Wadden Sea, the unstable population structure could have explained a higher growth rate. However, the high growth rates persisted over more than 30 years, and were evident in counts during breeding, moulting and in summer. This persistent high growth cannot be explained by a founding effect. The rate greatly exceeds growth rates within the same period for grey seal pup production at other locations: averaging 5-7% at colonies on the North Sea coast of the United Kingdom (Thompson & Duck 2010).

Reasons for the high growth rate in the Wadden Sea could partially be a result of high intrinsic growth supported by enhanced juvenile survival, but are most likely caused by high immigration rates. Brasseur et al. (2014) show in a population model that on average 1.3% of the pups born on the east coast of the UK immigrate into the Dutch breeding population each year. This amounts to slightly less than 35% of the annual growth of the breeding population in most recent years.

2.3.3 Grey seals in the Delta region

Both species of seals, harbour and grey seals, were absent from the Delta region until the 1980s. Harbour seals started to return in the late 1980s, but no grey seals were reported until 2001. Thereafter, despite the lack of births in the area, the growth rate in grey seal numbers has been approximately 42% per year (Aarts et al. 2013).

Up to 2013, there were no definitive records of grey seal pups being born in the Delta region. Several sightings that have been investigated were paint-marked weanlings that had travelled from the Farne

Islands (UK) or harbour seals lying adjacent to grey seals. Therefore, absolute growth in the numbers in the Delta has been entirely the result of immigration (Aarts et al. 2013).

Grey seals moving into and through the Delta region could come from the UK, the Wadden Sea or the smaller colonies in France. The largest source is likely to be the UK, where in 2009 an estimated 7637 pups were born (Duck 2010), compared with about 440 in the Dutch Wadden Sea in 2012 (Brasseur et al. 2014) while no births are recorded in Northern France. Recent tracking data show that a proportion of grey seals tracked in spring from the Baie de Somme (Northern France) transit to Dutch waters and back (unpublished data, Université de La Rochelle / CNRS, Parc naturel marin d'Iroise, Océanopolis, Picardie Nature, Région Bretagne, Région Poitou-Charentes). In 2013, grey seals were tracked from both the Delta region and the Wadden Sea to record movement along the intervening coast (Kirkwood et al. 2014). Five of 15 grey seals tracked traversed the Dutch coast between the two regions, demonstrating a strong connection.

Despite the relatively low numbers of grey seals in the Delta region compared with in the Wadden Sea region, there is a high occurrence of dead grey seals encountered on Delta region beaches. For example, in 2011 there were ~10 dead grey seals (and ~30 dead harbour seals) on shorelines (S. Brasseur unpublished data). One theory is that a proportion of the mortalities could be related to by-catch in trap fisheries in the Delta region.

3 Grey seal habitat requirements and usage

Pinniped seals forage at sea and return to land or sea-ice to rest, moult, breed and avoid predation. Their energy demands for thermoregulation, prey capture and assimilation, growth and reproduction are constrained by both aquatic and terrestrial conditions (Whittow 1987, Costa & Williams 1999). Typically, grey seals spend approximately 10-30% of their time on land, and 70-90% of their time at sea. Descriptions here of aquatic habitat and land habitat use outside the breeding periods are brief as the report focusses on breeding (and moulting) habitat.

3.1 Habitat at sea

Grey seals go to sea primarily to feed, but also utilise the sea to transit from one area to another. Radio and satellite tracking of seals has demonstrated that outside the breeding and moulting periods, grey seals can travel great distances in short periods (McConnell et al. 1992, Brasseur et al. 2010). For example, a male grey seal tagged at Donna Nook (N. Humberside, UK) travelled to the Farne Islands, 265 km away, in 4-days (McConnell et al. 1992). Seals tagged in 2005 in the Netherlands travelled to the Farne Islands and to northern Scotland, almost 1000 km distance (Figure 4) (Brasseur et al. 2010). Recent tracking studies give similar results, even showing that animals tagged in the Netherlands leave to breed in the UK (e.g. Kirkwood et al. 2014). Between feeding trips, grey seals appear to use several haul-outs throughout their range, probably chosing a haul-out based on its proximity to the area where they are feeding, and prior knowledge.

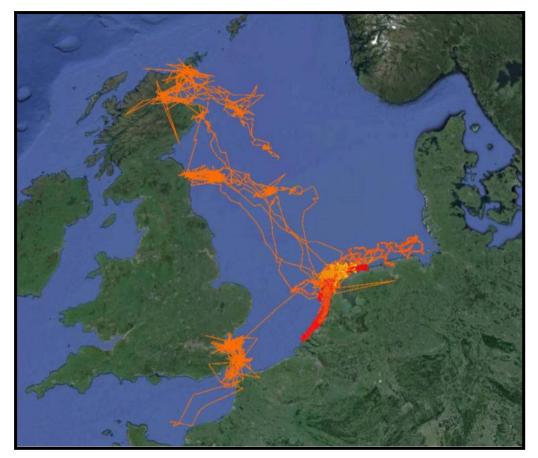


Figure 4. Examples of movements by grey seals from the Wadden Sea, data from 10 seals tracked in the years between 2004 and 2008 (Brasseur et al. 2010).

Atlantic grey seals forage in a range of habitats, including inshore, offshore, shoals, shelf breaks and slope waters, and over both soft or hard substrates (McConnell et al. 1992, Hammond et al. 1994). They appear to target prey in and around the sea floor rather than in the water column (Thompson et al. 1991). In the Dutch North Sea, depth seldom is greater than 50 m which is not limiting as grey seals can dive to depths of several hundred metres. Diet of grey seals can vary seasonally, spatially and individually (Prime & Hammond 1990, Beck et al. 2007). Important prey in the east Atlantic and UK North Sea include sand eels (family Ammodytidae), cod *Gadus morhua*, saithe *Pollachius virens*, haddock *Melonagrammus aeglefinus*, whiting *Merlangius merlangus* and flounder *Platichthys flesus* (Harwood & Croxall 1988, Prime & Hammond 1990, Hammond et al. 1994).

3.2 Habitats on land: haul-outs and breeding colonies

Although seals can sleep underwater, they regularly haul out on land to rest. Hauling out allows them to conserve energy, enhance blood flow in their skin and, in some areas, avoid predation. Grey seals tolerate a broad range of land habitats, including hard and soft substrates, and vegetation. Different qualities are required from a site depending on whether the seal is hauling out to rest, to moult or to breed. If resting between feeding trips, the seals require an area that remains dry for several hours, so are likely to select sites that are adjacent to where they are feeding. Grey seals tend to aggregate on haul-outs, which is a common pinniped trait. For moulting and pupping, grey seals tend to haul-out at sites that remain dry for weeks or more, such as on permanently exposed islands and coastlines (see Figure 5). This site-selection is reflected in the seasonal distribution of the seals, such that breeding and moulting activities may occur on sites that are almost seal-free in other periods.

Throughout their distribution, grey seals occupy a large variety of substrate types. The largest colony in the world (of north-west Atlantic grey seals) is on the long, sandy beaches of Sable Island, Canada (Bowen et al. 2003b) (Figure 5, a-b). The habitat available at Sable Island is similar to the beaches of the islands in the Wadden Sea. In the United Kingdom, grey seal colonies are on a range of substrates from sand to grass (Figure 5, c-i). Even on the same island, seals may have pups on rock and sand beaches, or on inland grass and mud surfaces (e.g. Isle of May, Scotland; Figure 5, e-h). At Donna Nook, on the English, North Sea coast, approximately 1000-2000 pups are born each year on a flat, sand beach, similar to that available on island coastlines of the Wadden Sea (Figure 5, i). In the Baltic Sea, Baltic grey seals pup on sea-ice (Figure 5, j).



Figure 5. Examples of grey seal pupping habitats (photos accessed from the web).

3.3 Processes of colonisation

In recent decades, the recolonistion of many formerly overharvested pinniped populations has been documented (Payne 1977, Bester 1982, Roux 1987, Bradshaw et al. 2000). The process typically exhibits four phases: discovery, establishment, development and maturity (Roux 1987). The 'discovery' phase extends from the cessation of depletive human exploitation to the initiation of breeding. The 'establishment' phase is the period when breeding commences at a few founding colonies. In the 'development' phase, numbers increase and new colonies arise rapidly, often in response to a shortage of space at the founding colonies. Finally, the 'maturity' phase is identified by a decline in the rate of growth, caused by density-dependent factors such as an absolute shortage of either space ashore or food at sea. The phases overlap and their durations vary depending on location-specific circumstances. In the Wadden Sea, grey seals appear to have re-established breeding and are in stage 3, the 'development' phase. The maturity phase is difficult to recognise due to inter-annual variability, and is most evident in hind-sight.

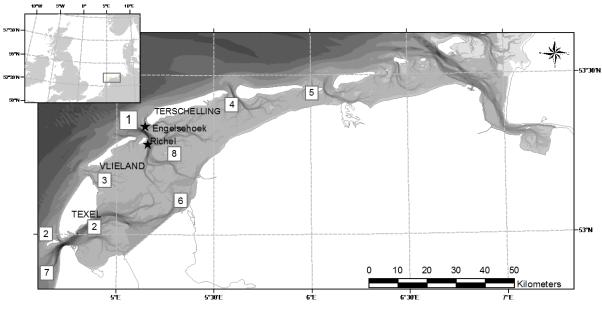
During the establishment phase, breeding sites can develop from haul-out sites. Pupping would initially be by first-time breeders, who had yet to secure a fidelity to a site (Gentry 1998). Pups born to an unexperienced female at an establishing site would have a low chance of survival. However, if the site has sufficient qualities for a pup to survive, and the female continues to pup at the site and her ability to rear a pup improves, other females will be attracted. Eventually pups will be successfully reared to weaning age (Baker 1978). Gradually, the haul-out will establish as a breeding site. This process of colonisation through occupation of a haul-out can result in establishment of a colony at great distances from other colonies.

The process of progression from a haul-out to breeding site in a new area is likely to have occurred in the Wadden Sea, at the island of Amrum and the sandbar of Engelschhoek (Figure 6). Both these sites were haul-outs for grey seals prior to the commencement of pupping. They were not necessarily the best habitats in the region for pups to survive.

Both the breeding sites of Amrum and Engelschhoek suffered degradation after their establishment. This was mostly a natural process of sandbar movements within the Wadden Sea. At Engelschhoek, the degradation included complete submergence of the sandbank for two years in the early 2000s. Due to the submergence, the seals that had established a breeding fidelity to the site had to pup elsewhere. Potentially, the site most females shifted to was the sandbar Richel, several kilometres south-east of Engelschhoek. At Amrum, the degradation included disturbance due to high levels of uncontrolled human visitation (Abt et al. 2002). On re-emergence of Engelschhoek, grey seals re-commenced pupping there (see further discussion on Engelschhoek in section 3.4.2).

A second and distinctive process by which colonisation can occur is through the 'spill-over' effect (Bonner 1968, Bradshaw et al. 2000). This happens when there is insufficient space to breed. Presumably, first-time females that are not established at the colony are more likely to colonise nearby sites. The 'spill-over' effect results in the clustering of breeding colonies within a region (Bradshaw et al. 2000). The observed development of new breeding sites within the Wadden Sea may be a consequence of a 'spill-over' effect from the initial sites. Growth in numbers at the new sites may exceed that at the initial site, if the habitat proves better for pup rearing.

During colonisation, immigration and intrinsic growth combine to give total growth. As of 2013, ~35% of growth in grey seal numbers in the Dutch Wadden Sea was a result of immigration from elsewhere (Brasseur et al. 2014). There was no indication that the colonies had approached a maturity phase.



1. first area colonized by grey seals in 1980; pupping started in 1985;

2. first grey seal observed in 1988; first group >5 in 1997 (2 areas);

3. first grey seal observed in 1988; first group >5 in 2000;

4. first grey seal observed in 1989; first group >5 in 1998;

5. first grey seal observed in 1998; first group >5 in 2001;

6. first grey seal observed in 1997; first group >5 in 1998;

7. first grey seal group >5 in the Dutch delta area 2003 (Strucker et al. 2006);

8. first grey seal observed in 2009

Figure 6. Expansion of the distribution of grey seals in the Dutch Wadden Sea from 1985-2010 (Brasseur et al. 2013). Engelschhoek (also known as Engelsehoek) was the first pupping site; Richel is now the most important pupping site.

3.4 The Dutch Coastal area

The Netherlands evolved into its current geographic form as a result of sea level rise about 7,500 years ago (Flemming 2002). In the Wadden Sea area, there was an outer barrier of sand-dunes fronting low-lying land. As sea level rose, the low-lying land behind the dunes was flooded. The sand-dunes remained as an island chain and on-going siltation of the hinterland kept pace with sea level rise, maintaining a shallow water system. The result is one of the largest intertidal systems in the world (Wolff 1983). Over the past 2000 years, humans have been drivers of change in the Wadden Sea. Activities causing change include building of dykes for land reclamation, dredging, fishing, hunting and harvesting, pollution, and extraction of peat and subterranean petroleum products (Lotze 2005, Lotze et al. 2005). In recent decades, rates of human-induced change to the landscape have slowed due to conservation measures that aim to protect and enhance ecosystems as they currently stand (CWSS 2008). Examples of conservation measures include the inclusion of the Wadden Sea as a Natura 2000 Site and the 2009 designation of the Wadden Sea as a World Heritage Area.

3.4.1 Breeding habitat availability in the Netherlands

Grey seals are capable of pupping along most coastlines in the Netherlands. All the larger islands and much of the coast bordering the western part of the country contain sand beaches that are comparable to sites currently occupied by grey seals in Canada and the UK, including the largest grey seal colonies in existence. Potentially, the only areas within the Wadden Sea where there are physical barriers to

occupation are those that would require extensive travel across mud, such as sections of the mainland coast and those with man-made barriers.

Currently, locations where breeding colonies have established within the Wadden Sea are in association with the channel systems between the major islands. These afford fast-moving, deep water access to relatively calm beaches, and lay slightly higher than the other tidal flats (Figure 7). Breeding colonies have not yet established in the Delta area, although suitable pupping habitat is available.

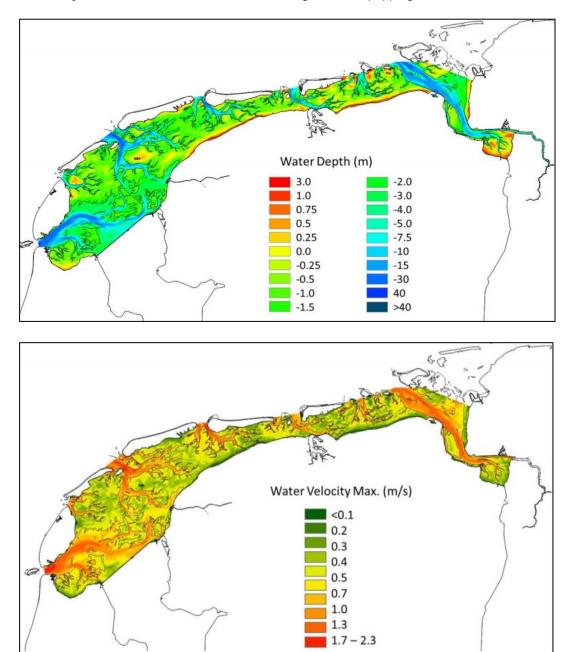


Figure 7. Water depth and modelled water velocity (Brinkman & Bult 2002) in the Wadden Sea, indicating drainage patterns as well as relative channel depths and flow rates between the islands.

3.4.2 Wadden Sea breeding sites

A grey seal requires different qualities from a haul-out site than a pupping (or colony) site. In general, haul-outs require a degree of proximity to feeding areas, need to remain dry for the duration of their rest (at least a few hours, up to several days) and should provide protection from disturbance. Because grey seal feed minimally during the pup support and territory tenure, pupping sites do not need to be close to deeper waters. They do need to have a greater temporal stability, including remaining dry for weeks.

Although there are several reports of grey seals giving birth on the main Islands, for example Texel, Vlieland and Terschelling, colonies have not developed. Locations in the Wadden Sea where grey seals have had pups are predominantly sandbars (Figure 8). Coastal sand substrates are normal pupping sites for grey seals. Elsewhere in there range, grey seals occupy similar sandy beach habitats. Grey seal pup births in the Wadden Sea have predominantly taken place in the western side, with a focus around the drainage channels between the large islands of Vlieland and Terschelling. These include the sandbars of Engelschhoek, Richel, Razende Bol and Steenplaat, and the small island of Griend (Table 1). Pups were also see on the Blauwe balg (maximum 3 in 2009 and 2011; none after this) and on the Rif (one in 2011).



Figure 8. Recorded locations of grey seal pup births in the Dutch Wadden Sea since 1985.

Colony	Average percent of births per year 2008 to 2012	Comment
Richel	67%	
Engelschhoek	14%	Maximum in 2010/11
Griend	2%	Growing since 2007
Razende Bol	5%	No pups in 2012/13*
Steenplaat	4%	Less in 2011
Blauwe Balg	>1%	Regularly after 2008, but
		none after 2011

Table 1. Pup	production	at colonies	in the	Dutch	Wadden	Sea.
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*Pupping probably was deterred at Razende Bol in 2012-13 by a high disturbance level with visitation to a stranded whale. The first recorded births of grey seal pups in the Dutch Wadden Sea were at the Engelschhoek sandbar, which is exposed to the North Sea off the western tip of the island of Terschelling. Although an ideal site to establish a haul-out, due to its proximity to North Sea feeding grounds, Engelschhoek. In the 1990's, currents and storms caused major changes to the area (which are yet to be documented well) and the sandbar became subject to frequent inundation. Between 2004 and 2006, most of the Engelschhoek remained submerged continuously. It re-emerged in 2006 and by 2012 had re-established as the largest grey seal haul-out in continental Europe (more than 2500 seals April 2012, 63% of all grey seals counted in the Wadden Sea. A maximum of 73 pups have been recorded there in a single breeding season (2010/11). The importance to grey seals of Engelschhoek may relate to the fact that, compared with other Wadden Sea sandbanks, it is relatively high, gives good access to the North Sea, and was rarely visited by humans (although visitation may be increasing).

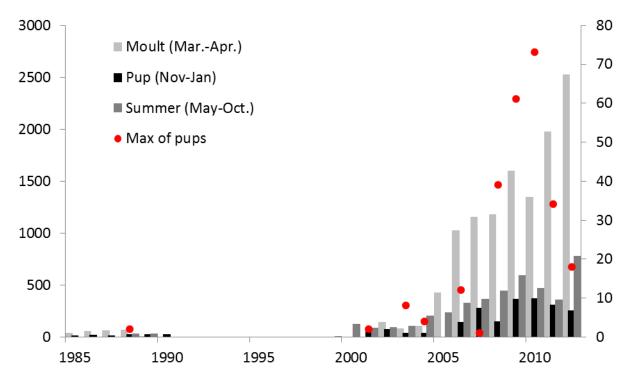


Figure 9. Annual maximum of grey seals (bars) and pups (dots; right axis) counted during different seasons on the Engelschhoek.

All islands and sandbars of the Wadden Sea are subject to on-going processes of erosion and deposition, and due to the absence of hard substrates, changes can be rapid. The four most important pupping sites, Engelschhoek, Richel, Razende Bol and Griend, have altered shape noticeably within the past 10 years (Figure 10). As they change shape, the availability of pupping habitat within them also changes. Grey seals may adapt to such changes by tolerating changes in density or by shifting to another site. The degree of change each year is influenced by habitat availability, habitat quality, habitat site fidelity of the individual and density-dependent factors - such as tolerance to nearest neighbours. Consequently, the relative importance of individual sites within the Wadden Sea for grey seal pupping fluctuates over time.



Figure 10. Aerial photos (from bing maps and google earth) of important grey seal pupping sites in the Wadden Sea, indicating changes in shape over time.

The most important pupping site for grey seals in the Netherlands is currently Richel (Figure 11). Richel is situated five kilometres south west of Engelschhoek; it is less exposed to the North Sea than Engelschhoek. Every year for the past 15 years, the majority of grey seal pups born in the Netherlands have been on Richel (Figure 12). In the past five seasons, recorded numbers of pups for Richel have been fluctuating. This could be an artefact of the survey method, which is dependent on tides, that are not always in sync with the pupping peak, or the winter storms affecting the number of pups. Currently, Richel is not utilised by grey seals as an important haul-out site outside the pupping period, with the nearby site of Engelschhoek preferred.



Figure 11. Grey seal pupping habitat on Richel, Vlieland in the background (photo RK).

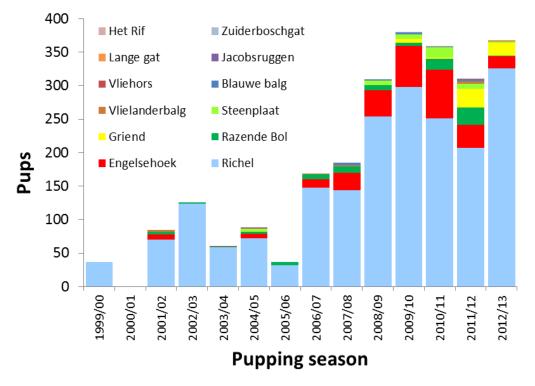


Figure 12. Locations of grey seal pups recorded during surveys in the Dutch Wadden Sea between 1999/2000 and 2012/13.

Despite its importance, Richel is also flooded when high-tides, often storm-enhanced, achieve levels greater than 2 m above NAP (Dutch Ordnance Datum). Such high water-levels may happen several times within a pupping period. Between 1987 and 2007, three inundations occurred in November, nine in December and six in January; there were only six pupping seasons (November to January) when the Richel was not flooded (see Table 6 in section 3.2.2). December and January storms are of more consequence for pup survival because, in those months, many un-weaned and post-weaned pups are present (also in the 1980s and 1990s, the peak in pupping was in January – the peak has shifted from early January in 1985 to early December in 2012). It is difficult to determine the exact loss of pups as a result of inundations. Aerial surveys monitor pup numbers three times per pupping season, so (for example) pups may be born and removed by floods between surveys.

Interestingly, the on-going inundations of Richel during have not stimulated the seals to abandon this site. Either alternative sites are not apparent to them or the flooding is not a strong mechanism to trigger a change in pupping site for the female grey seals, which display high site fidelity.

After Richel and Engelschhoek, the sites of next greatest pup production in the Netherlands have been Razende Bol and recently, Griend (Figure 13). Razende Bol, between Texel and the mainland, is exposed to the North Sea and thus may be considered a better haul-out site than a pupping site. It also receives, though mostly in summer, disturbances by human visitation, including use as a military shooting zone. The northern part of the Razende Bol is closed for public for a large part of the year (1 May to 1 November). However, being relatively easy to access and enforcement being limited, disturbances do occur, such as by tourists walking over the sandbar and kite- surfers landing in the closed area. As a further example of disturbance there, in December 2012 during the grey seals' breeding season two whales were beached on the northern part of the sandbank. Rescue efforts and publicity trips would have disturbed the seals and was likely the main reasons for an absence of pup-births there that year.

Griend is a small island within the Wadden Sea. It receives strict legislative protection largely due to its importance as a summer breeding location for seabirds. The first grey seal pup births recorded on Griend were in six pups present on 14 December 2007 (in hut log-book). This pre-dated the first winter aerial surveys of Griend in 2009/10. Due to the relative stability of this island and its level of protection, there is great potential for pup production at Griend (Figure 14).

Other sites within the Wadden Sea where grey seal pups have been recorded represent incidental or occasional pupping locations. They may not have had sufficient time to establish as permanent pupping locations or may not have established due to either frequent inundation or human disturbance. Grey seals have now had pups at more than 10 locations in Dutch waters. Occasionally pups are born on the main islands (such as Texel, Vlieland and Terschelling). However, these are typically single births. Efforts to prevent disturbance of these animals by members of the public have increased in recent years. However, given the levels of human disturbance that could occur on the main islands, occasional birth-sites, at present, are unlikely to develop into colonies.

Continued growth and distribution of grey seal pupping in the Netherlands is dependent on geomorphological developments at the current breeding sites. For example, the current growth of pioneer vegetation on Richel suggests that the sandbar is getting higher and potentially more stable. This development suggests the site could continue to grow in importance for the seals through coming decades. On the other hand, erosion is currently reducing the size of Griend and thereby reducing the pupping capacity that could be achieved there. The geomorphology of current breeding habitats in the Wadden Sea is an important factor influencing the long-term sustainability of a viable breeding population. More detailed measurements, for example of the height and stability of the sites, including prediction on possible changes and storm probability, are necessary.



Figure 13. Grey seal pupping habitat on Griend (Group 13 in Figure 14; photo RK).

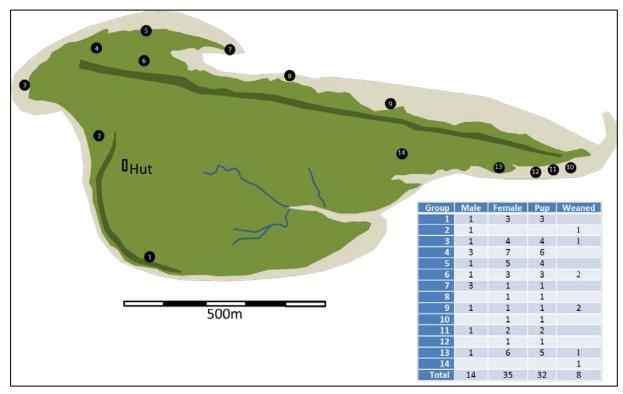


Figure 14. Distribution of grey seals on Griend, 15 December 2013.

3.5 Grey seal breeding site requirements

The initial factors which determine where breeding colonies of grey seals are located are unclear, but there are key habitat qualities that can induce or deter colonisation of a location (Table 2).

Table 2. Summary and description of habitat qualities which are assumed to play a role in the grey seal females' choice for breeding sites (based on available literature *) and relative effect on usage and pup survival. Site selection: low = will not prevent selection, moderate = likely to influence selection, high = will influence selection. Potential to effect pup survival: low = might influence survival rate, moderate = will influence survival rate, high = likely to prevent survival.

Habitat quality	Description	Importance to site selection	Potential to effect pup survival
Physical properties			
Frequency of submerging	Pups should be able to stay on land for the duration of the suckling period and the post weaning fast, in total up to 60 days	Mod	High
Substrate type	Grey seals can give birth on a range of substrate types. Sand, cobble, rock, snow and ice, and vegetation are all suitable. Unsuitable substrates include sharp and angular rock, and thick mud.	Mod/Low	Mod/low
Access to shore from the water and access to open water from land	Require relatively easy access/ secure passage to open water.	Mod/Low	Mod/low
Proximity to feeding area	Seals may pup great distances from feeding areas, however, a pupping site near to a feeding area affords advantages – seals may feed up to the time they come ashore to pup and may feed shortly after returning to the water post-weaning.	Low	Low
Slope	If terrain is too steep it is not a suitable pupping site and may cause mortality	Mod	Mod
Other properties			
Previous knowledge of site	Having attended a site either to haul-out or to pup in previous years provides a strong attraction.	High	High
Presence of other grey seals	Having other seals present indicates a degree of quality to the site – provides an attraction. High densities of seals (densities above a site specific level) may lead to aggression, and diseases	High/Mod	High/Mod
Predators	Land predators are likely to deter females from pupping at a site	High	Low in NL
Disturbance	Disturbance that is perceived to be a threat could deter females from pupping at a site.	High	High

* (Davies 1949, McLaren 1967, Bartholomew 1970, Kenyon 1972, Anderson et al. 1975, Cox & Le Boeuf 1977, Anderson 1978, Anderson et al. 1979, Boness & James 1979, Renouf et al. 1981, Boness et al. 1982, Trillmich & Trillmich 1984, Gerrodette & Gilmartin 1990, Kovacs & Innes 1990, Riedman 1990, Boness et al. 1992, Campagna et al. 1992, McConnell et al. 1992, Amos et al. 1993, Kamil et al. 1993, Brasseur & Reijnders 1994, Pomeroy et al. 1994, Twiss et al. 1994, Allen et al. 1995, Boness et al. 1995, Hersteinsson & Macdonald 1996, Twiss et al. 1998, Wartzok & Ketten 1999, Pomeroy et al. 2000a, Pomeroy et al. 2000b, Cassini 2001, Henry & Hammill 2001, Twiss et al. 2001, Boren et al. 2002, Blumstein et al. 2003, Matthiopoulos 2003, Twiss et al. 2003, Matthiopoulos et al. 2005, Pomeroy et al. 2005, Boness et al. 2006, Härkönen et al. 2006, Härkönen et al. 2007, Curtin et al. 2008, Shaughnessy et al. 2008, Beijder et al. 2009, Jansen et al. 2010a, Lancaster et al. 2010, Higham & Shelton 2011, Andersen et al. 2012, Culloch et al. 2012, Stafford-Bell et al. 2012)

3.5.1 *Physical properties of breeding sites*

3.5.1.1 Frequency of submergence

Grey seal pups must stay on land while being suckled (about 3-weeks). They are also likely to remain out of the water during much of their post-weaning fast (up to 1-month), although some pups can depart the colony immediately after weaning and complete part of their post-weaning past away from the colony. Grey seal mother-pup pairs do not swim together (although swimming together is a behaviour of harbour seal mother-pup pairs). Grey seal pups have a coat of long, white hair, that protects them on land but absorbs water readily, which retards floatation and enhances hypothermia. This coat is replaced during the post-weaning fast.

In the Netherlands, most grey seals breed on sandbars that can be flooded by extreme high tides or storm surges. As mentioned in the previous section, flooding events during the pupping period can move pups away from colony sites, causing some to drown.

3.5.1.2 Access to shore

It is logical that a female grey seal cannot pup at a shore-line that it cannot access. Even so, grey seals can give birth to pups in marginal places, including adjacent to, intertidal zones that receive high waveaction, such as in Pembrokeshire, England (Davies 1949). Such sites are unlikely to develop into large colonies but are likely to remain as ephemeral breeding sites with high inter-annual variability in pup survival. Grey seal females may also climb relatively steep slopes and move hundreds of metres inland to breed.

In the Wadden Sea, access to the shore is unlikely to be limiting where grey seals will come ashore to have pups. The entire coastlines of all Wadden Sea islands and sandbars are accessible to grey seals. However, inaccessible areas could include much of the mainland coast of the Wadden Sea, where access is restricted by extensive mudflats bordered by shallow waters, and human modified coastlines. Steep dykes, water barriers and wharf areas are less accessible to grey seals.

3.5.2 Other properties of breeding sites

3.5.2.1 Previous knowledge and site fidelity

Grey seals have a strong connection to traditional breeding sites and have a high level of fidelity to their site of first breeding (Boness & James 1979, Twiss et al. 1994). They also have a tendency to return to their birth site – a behaviour which is termed philopatry – although this is not as strong as the fidelity to the first breeding site (Allen et al. 1995, Pomeroy et al. 2000b).

Behavioural studies of marked individuals at North Rona, Scotland, over many breeding seasons have shown that the median distance between the positions of adult males in successive seasons was 53 m (Twiss et al. 1994), for adult females it was 55 m (Pomeroy et al. 1994). The fidelity of females to specific pupping sites was maintained even when a female had pupped unsuccessfully in the preceding year, or had not pupped at all. A similar degree of pupping site fidelity has been recorded for female grey seals on Sable Island, off the coast of Nova Scotia (Boness & James 1979). However, not all animals remain faithful to a site. Some return to the site sporadically, others may depart permanently even following several years of successful pup-rearing at a site (Amos et al. 1993, Pomeroy et al. 1994, Twiss

et al. 1994). Male grey seals tend to exhibit less fidelity to natal sites than do females (Pomeroy et al. 2000b).

Strong site fidelity relates to site familiarity and a habituation to local conditions. It is also linked to a resistance to go elsewhere due to an uncertainty about the ability to breed effectively in novel areas. This motivation is comparable to having a foraging site fidelity; individuals resist switching foraging sites even if prey catch rates decline because the availability of prey elsewhere is uncertain (Kamil et al. 1993). At times, individuals could be forced to shift pupping sites, for example due to density pressure, habitat reduction (such as the flooding of Engelschhoek in 2004-06) or due to disturbance at the familiar site (Pomeroy et al. 1994).

In the Wadden Sea, grey seals are establishing a familiarity with many sites and breeding has taken place for over 25 years. Individual seals undoubtedly have developed strong links with particular locations. The majority of pups have been born at Richel, so it is expected this sandbar will continue to support substantial numbers of breeding grey seals into the future, provided the habitat remains available.

Grey seal philopatry and strong breeding site fidelity has many advantages, but it also retards colonisation of new sites and enhances vulnerability because individuals are less prepared for catastrophic change (Matthiopoulos et al. 2005). Also, strong philopatry and site fidelity retards genetic mixing, leading to strong population structure and the potential for more rapid speciation, although the high levels of individual variability in pinniped populations can negate this effect (Lancaster et al. 2010).

3.5.2.2 Presence of other grey seals

One outcome of having strong site fidelity is that kin associations could develop. Individuals could recognise and become familiar with the behaviour of neighbours, and may even be genetically related to them (Pomeroy et al. 2000b). This may reduce the need for vigilance, allowing females to expend more resources on improving the fitness of their pup (Pomeroy et al. 2005).

Grey seals are more likely to come ashore and bear their pup at a place where other grey seals are present. Colonial breeding in social pinnipeds is a dramatic example of gregariousness in mammals (Boness 1990, Riedman 1990). Breeding in colonies does have several disadvantages, such as pup mortality due to crowding, aggression and enhanced disease transfer (Boness et al. 1982, Härkönen et al. 2006). However, the advantages must outweigh these for colonial breeding to have been retained. Colonial breeding enables these top marine predators that disperse widely to finding a mate at a predictable time and place (Bartholomew 1970). At most times of the year, grey seals gather beside oneanother when they are ashore. Once their pup is born, however, females become intolerant of other seals near to them (Anderson et al. 1975). Intruders within a certain range are threatened or attacked. This aggression during pupping establishes a maximum density within a colony, and possibly limits the size to which a colony can grow (Boness et al. 1982). The features and quality of individual pupping sites influences the proximity of conspecifics that will be tolerated by post-partum females (Boness et al. 1982). A closer proximity may be tolerated where conspecifics may be hidden by undulating ground, than in flat and open terrain. As numbers within a colony approach a maximum density, there is pressure on the females to relocate to an alternative site in which to pup (the 'spill-over effect, see section 2.3). Established breeders are most likely to remain at the established site forcing younger females to new sites.

Females breeding in colonies derive genetic benefits from mating with the fittest, most dominant adult males, which hold territories at the colonies, while avoiding subordinate individuals (McLaren 1967, Cox & Le Boeuf 1977). Females that pup individually or in small groups are vulnerable to harassment of

themselves and their pups by subordinate males, and as a consequence, elevated levels of pup mortality (Trillmich & Trillmich 1984, Campagna et al. 1992).

3.5.2.3 Predators and Disturbance

Bartholomew (1970) stated that an absence of land predators is an important factor determining whether grey seals will pup at a site. Historically, the most avid land predator of grey seals has been man. Polar bears could be land predators in the Arctic, and both Arctic (in Iceland) and red foxes (England) predate weak pups at some sites, although they mostly scavenge (Hersteinsson & Macdonald 1996, Culloch et al. 2012). In the Netherlands land predators are not a threat to the seals.

Seals are predominantly aquatic animals and despite having aquatic predators in some areas they generally return to water when threatened, indicating that is where they sense the greatest safety (Riedman 1990). When ashore and disturbed, individuals weigh-up the potential consequences of remaining ashore and defending themselves (and their pups), or fleeing into the water (Kenyon 1972). Such decision making and responses cause stress and can reduce fitness.

Disturbance may play a central role when the grey seals are seeking a breeding site. Examples of natural disturbances include unexpected atmospheric (storm, hail, strong wind) and oceanographic (large waves, peak high tide) events, or incidental events, such as a flock of birds lifting up and the arrival of a potential predator. By far, most disturbances that have been monitored previously have been anthropogenic. On land seals have acute hearing and a refined sense of smell, but blurred vision (Wartzok & Ketten 1999). Unfamiliar or strong, sounds or odours can greatly disturb seals (Shaughnessy et al. 2008). Objects that break the horizon or appear taller than themselves, are unfamiliar, or are familiar and previously have been associated with a threat, can also disturb seals (Kenyon 1972, Cassini 2001, Stafford-Bell et al. 2012).

Within the Netherlands, a primary source for disturbance is approaches by humans either over water (any boat, vessel, kayak, wave-board, jet-ski etc.) and land (pedestrian, vehicle), or by air. The majority of beaches in the Netherlands are exposed to frequent human visitation and are accordingly not used by seals.

The responses by seals to a disturbance depend on a range of factors, including individual disposition, distance from the water's edge, behaviour of other seals around them, previous experience and time of year. For instance, when strongly bonded to land during breeding and moult, seals exhibit a reluctance to flee approaching disturbers (Renouf et al. 1981, Kovacs & Innes 1990, Henry & Hammill 2001). Seals may habituate to a benign stimulus that occurs frequently and/or regularly and consequently have a minimal response (Higham & Shelton 2011). Alternatively, they may become highly sensitised to a disturbance and flee on suspicion that it might recur (Bejder et al. 2009). Ultimately, repeated disturbances can cause a gradual abandonment of established sites (Bejder et al. 2009)

Long-term consequences of human disturbance are complicated to assess. One example of an impact has been for endangered Hawaiian monk seals, *Monachus schauinsland*, on the main Hawaiian Islands. The monk seals were displaced by humans from more suitable breeding beaches to less suitable sites, and a consequence was that pup mortality rates increased (Kenyon 1972, Gerrodette & Gilmartin 1990). To quantify an instantaneous effect of human disturbance, studies often measure the distance at which the animals flee from an approaching person or vessel (Brasseur & Reijnders 1994, Blumstein et al. 2003, Shaughnessy et al. 2008, Jansen et al. 2010b). In such studies, fleeing to the water is considered to be an ultimate response, which comes with metabolic consequences and potential injury. Other studies have monitored pre-flight responses such as modified behaviour (van Polanen Petel et al. 2008) and elevated levels of stress, detected through increased heart-rate (Giese 1996, Marechal et al. 2011). These represent a cost to the seal and are precursors to fleeing.

There is limited quantified data on responses of grey seals to human approaches. At Ramsey Island, Pembrokeshire (UK), grey seals at a haul-out were aware when tourist vessel approached within 150 m and became visibly disturbed if the vessel came closer (Strong & Morris 2010). In the Mew Stone, Devon (UK), tourist vessels adopted voluntary precautionary procedures at a grey seal haul-out, including a 25 m exclusion zone and reduced approach speeds (Curtin et al. 2008). However, a study at the site found that vessels approaching to 50-100 m elicited a response on 60% of approaches and stampedes into the sea on 11% (Curtin et al. 2008). Data on long-term effects of disturbance on grey seals are lacking. However, there is some indication that a high level of disturbance at the Farne Islands in the UK has stemmed growth at that colony.

Seals may appear to become accustomed to particular human approaches and site-specific tolerances may develop over time. This could be an habituation by the seals present or a steady exclusion of less tolerant individuals. One site of note for this is Donna Nook, in Lincolnshire (UK). One section of the colony is exposed to thousands of tourists each year, another section is owned by the air force and is closed to the public. In a study of maternal behaviour at Donna Nook (James 2013), it was observed that females in the less exposed section seemed less tolerant of regular disturbances (such as a vehicle driving past) whereas those in the public section could be more tolerant to regular disturbances.

3.6 Conclusions

Following the recommencement of pup-births in the Netherlands in 1985, after centuries of absence, grey seals now have pupped at at-least 10 locations in the Wadden Sea, breeding colonies have developed at five of these, the sandbars of Engelschhoek, Richel, Razende Bol and Steenplaat, and the island of Griend.

Grey seals are capable of pupping at most coastal sites in the Netherlands, provided the coast is accessible from the sea, not occupied by humans, and not covered by sharp stones or separated from water by a great expanse of mud. The absence of grey seals on the beaches of the mainland and inhabited islands of the Wadden Sea, indicates that the greatest factor likely to regulate the distribution of grey seal pupping sites within the Netherlands is human disturbance. The concentration of grey seals on the Richel, suggests the seals are also driven by intrinsic factors, such as prior experience and site fidelity, as has been observed in other areas. Throughout the almost 30 years that grey seals have been pupping in the Netherlands, pups have been born at novel sites, but few have developed into colonies.

All current grey seal colony sites in the Netherlands are prone to flooding at extreme high-tides, particularly if enhanced by storms. The threat of inundation differs between sites. At the largest colony on Richel, in two out of three years since 1985, storms have caused the inundations during the pupping period. The impact the inundation would have varied depending on its timing in relation to the ages of the pups present.

Excessive flooding and eventual submergence at the Engelschhoek in the late 1990s and early 2000s, probably stimulated the colonisation of other sites, notably the Richel. It may be that such a dramatic disturbance as submergence, or long-term gradual-change, is required to cause seals to abandon an established colony.

Inundation at pupping sites in the Wadden Sea undoubtedly influences the breeding success of grey seals in the Netherlands. If colonies had established on beaches that were not inundated frequently, pup

survival and population growth are likely to have been higher. It is difficult to conclude if current breeding sites are sufficient for the needs of grey seals breeding in the Netherlands. The occupied colonies are also subject to on-going change and new sites are likely to be colonised if the numbers continue to grow. Further data on the height and stability of current colony sites, including predictions of possible changes and storm probabilities, are necessary to better discuss habitat quality.

4 Grey seal pup survival and mortality

The terms survival and mortality represent different ways of expressing the same process: Survival rate + Mortality rate = 1

In research of wild populations, the term survival is used more often than mortality, however, mortality is applied when describing the mechanisms for death. For clarity in this report, we apply both terms.

4.1 Overview

Rates of mortality of grey seals vary with age. Generally, mortality is highest in the first-year of life then declines exponentially through to maturity. Compared with the juvenile years, mortality rates for adults tend to remain constant, irrespective of age. Within the first year, there are two periods of mortality. The first coincides with birth and the first weeks of life and the second coincides with the post-weaning period.

During the pupping period, grey seal females come ashore, give birth, suckle the pup for approximately 3-weeks, mate, and then return to the sea. Upon weaning, the young seals can remain at the colony for 1-4 weeks as they convert fat into muscle and undertake their moult into a juvenile pelage (Nordoy & Blix 1985b, a, Noren et al. 2008, Bennett et al. 2010). Individuals may depart the colony prior to completing their moult, and as such healthy weaned juveniles can be confused with unhealthy 'starving' juveniles or even pups. On their first trips at sea, weaned pups may travel hundreds of kilometres (Thompson & Duck 2010).

High rates of mortality occur during birth and the 3-week period of maternal support. Over this period, mortality rates average 15% but may range up to 60%. Causes and rates of grey seal pup mortality during the pupping period appear to be site-specific (Table 3). Rates can be highest at crowded sites, where there is limited access to water and on storm-washed beaches (Summers et al. 1975).

Numerous factors have been proposed as primary causes of natural mortality of grey seal pups during the maternal support and post-weaning period (Table 4). Pups fail in their first week either by being stillborn or suffocating during birth (Davies 1949, Coulson & Hickling 1964). In this period, the role of the mother seems eminent; her inexperience could for example lead to starvation or misadventure, disease, trauma or drowning. Other drivers of pup mortality include poor quality of the habitat (e.g. near cliff, intertidal, disturbance) and climatic events, storms and high wave action (Coulson & Hickling 1964, Twiss et al. 2003). Necropsies in the UK showed a prominent cause for young-pup mortality was peritonitis, due to infection of the navel (Baker 1980, Baker et al. 1980, Baker 1983, 1984, 1988, Baker & Baker 1988). Infection rates were highest in poorly-drained, muddy and densely occupied habitats and lowest in open, relatively clean, grasslands or sand beaches.

Island	Year	Trend	Habitat	Pups	%	1° cause	2° cause	3° cause	Reference	
				born	mortality					
Ramsey	1947		Rock beach		15.0				Davies 1949	
Ramsey	1976	stable	Rock beach cliff back	300	35.0	drown	disease	trauma	Anderson et al 1979	
Auskerry	1977	growing	Shingle beach	555	14.1	disease	starve	drown	Anderson et al 1979	
Farnes	1956-62	growing	Various	~1000	2.5 - 21.1	starve	stillborn	injury	Coulson & Hickling 1964	
North Rona	1959	stable	Low grass	2300	15.0				Boyd & Laws 1962	
North Rona	1960	stable	Low grass	2200	13.0				Boyd & Laws 1962	
North Rona	1962-68	stable	Low grass	~2200	14 - 25				Boyd & Campbell 1971	
North Rona	1972		Low grass	~2200	30.0				Summers et al. 1975	
North Rona	1980	stable	Low grass	~2200	15.1	starve	peritonitis*	liver issue	Baker 1984, 1988	
North Rona	1985	stable	Low grass	~2200	7.5	starve	peritonitis*	stillborn	Baker 1988	
North Rona	1986	stable	Low grass	~2200	12.0	starve	peritonitis*	trauma	Baker 1988	
North Rona	1997		Low grass	~2200	14.6				Twiss et al. 2003	
North Rona	1998		Low grass	~2200	14.4				Twiss et al. 2003	
Ceann Ear	1981		Sand beach	645	14.3	drown	starve	peritonitis*	Baker 1984	
Ceann Ear	1981		Sand dune	49	18.4				Baker 1984	
Shillay	1982		Mud, stream	130	14.6	peritonitis*	starve	trauma	Baker 1984	
Shillay	1982		Sand beach	82	23.2	starve	peritonitis*	trauma	Baker 1984	
Isle of May	1986		Sand beach	166	15.7	peritonitis*	starve		Baker & Baker 1988	
Isle of May	1986		Rock	399	13.0	starve	bites	peritonitis*	Baker & Baker 1989	
sle of May	1986	1	Gullywallow	275	14.2	starve	peritonitis*	asphyxia	Baker & Baker 1990	

Table 3. Grey seal (Halichoerus grypus) *pup mortality at colonies in the UK, indicating colony description,* % *mortality, main causes of mortality and reference.*

* peritonitis is inflammation of the membrane that lines the abdominal cavity

Table 4. Means of mortality of grey seal (Halichoerus grypus) pups at colonies in the UK (data from references in Table 3).

Condition	Ramsey Island	Auskerry Island	Ceann Ear - beaches	Shillay - wallow	Shillay - beach	North Rona	North Rona	North Rona	Isle of May- beach	Isle of May - rock	Isle of May - wallow	Total
	1976	1977	1981	1982	1982	1980	1985	1986	1986	1986	1986	
Autopsied n =	24	32	49	16	18	78	78	62	20	29	19	425
Starvation	2	9	23	3	6	20	20	15	8	16	11	133
Peritonitis/ navel ill	1	6	6	4	2	18	29	15	10	4	5	100
Stillborn	2	1	2	3	2	1	7	4		1		23
Drowned	4	3	3			1	4	3		1		19
Disease	7	6	11	3	4	15	14	13	1	4	3	81
Birth defects	3	3	0	1	0	4	5	5	2	1	0	24
Trauma/ fall	3	1	4	3	4	2	3	9	1	2	3	35
Other	3	3	3	1	1	13	10	4	1	0	0	39

A second peek in mortality occurs post-weaning, when the seals that have not succeeded in finding and capturing prey, succumb – usually due to starvation. Pups that are larger at weaning are more likely to survive the first months than smaller ones, because they carry more body reserves (Hall et al. 2002, 2008).

Survival estimate of grey seals in their first year range between 20 to 90% (Baker & Baker 1988, Mohn & Bowen 1996, Pomeroy et al. 1999, Hall et al. 2002, Trzcinski et al. 2006, Hall et al. 2009, SCOS 2011) (Table 5). Adult grey seal survival rates each year range between 85 to 97% (Mansfield & Beck 1977, Harwood & Prime 1978, Wiig 1991, Mohn & Bowen 1996, Schwarz & Stobo 2000, Manske et al. 2002, Trzcinski et al. 2006, SCOS 2011).

Survival rate (age 0-1)	Year published	Source
90.2	1988	Baker and Baker
70.6	1996	Mohn and Bowen
83.2	1999	Pomeroy et al.
19.3 (♂); 61.7 (♀)	2002	Hall et al.
90.0	2006	Trzcinski et al.
47.5 (♂); 63.9 (♀)	2009	Hall et al.
70.0	2011	SCOS

Table 5. Previously estimated survival rates for grey seals aged 0-1 year old.

In summary, during the 3-week period of maternal support, grey seal pups at colony sites suffer a natural mortality of approximately 15%, but this can range up to 60%. Mortalities are caused by intrinsic factors, such as mother quality, and extrinsic factors, such as disturbance, disease and seasonal storms. Pups that are removed (e.g. by storm surge) from a colony while they are still dependant on their mothers will most likely die from drowning or starvation. After weaning (at 3-weeks of age) and in their first months of self-support, mortality rates remain high but diminish over time. In the first year, the mortality rate ranges between 10 and 80% of pups born (thus survival is between 90 and 20%). Because factors that affect mortality vary from year to year and between locations, there is considerable variation in this mortality-rate.

Box : Stranded seals?

Seals deliberately come ashore to rest, socialise, pup, breed and moult. Coming ashore also enables them to reduce the metabolic costs of swimming and, especially during moult, to keep warm, and could assist in maintaining pelage and skin condition. When out of the water, seals can enhance blood flow in their skin without losing excessive amounts of heat. In some areas (although not the Netherlands), seals also avoid marine predators (large sharks and killer whales) by coming on to land. The term 'stranding' is not appropriate for an animal that choses to come ashore and often must come ashore to survive. Stranding is more appropriately applied to marine animals that are incapable of free movement on land, such as whales, fishes and zooplankton.

4.2 Pup survival and mortality in the Netherlands

4.2.1 Natural pup survival/ mortality in the Wadden Sea

As monitoring in the Netherlands currently is limited to aerial surveys, it is difficult to estimate pup survival directly. Recently, a Bayesian demographic model was developed based on data from the aerial surveys (Brasseur et al. 2014). Preliminary results estimate that pup survival in the first year of life in

the Wadden Sea area is approximately 59% (SD 18%), while for animals older than one year, annual survival is estimated at about 95%. Compared with elsewhere, the survival rates of first-year seals is low while that of older seals is high.

Specific features of sites in the Wadden Sea that may alter natural mortality rates from those experienced elsewhere include that many pupping habitats are open sandbars and that seals have recently colonised (or recolonised) the sites (Reijnders et al. 1995). Natural mortality on sand where most grey seals are born in the Netherlands differs to natural mortality on a rocky or muddy habitat. As stated above crowded, muddy, habitat is found to be more conducive to the spread of disease than open sand bars (Baker & Baker 1988). Thus, mortality due to the spreading of disease between individuals might be less at Wadden Sea sites.

Sandbars and low sand beaches are also exposed to inundation by storm events. At the Donna Nook (UK) grey seal colony, which is comparable in structure to sites in the Wadden Sea, a high storm surge on 28 November 2011 separated many mothers and pups, causing the death of many pups (James 2013). Storms could also increase pup mortality at sites in the Netherlands (see also section 4.2.2). They may wash not only live but also dead and moribund pups off sandbars. In the Netherlands between 1990 and 2008, starvation was the main cause of death for grey seal pups found dead on beaches (Osinga et al. 2012). The dead pups may have starved after weaning, some could have weaned prematurely (for example, through storm-induced separation from mothers), and others could have been carcases or starving seals that were washed away from birth sites. The data do not indicate relative causes of mortality at the colonies.

There are several other reasons why pup mortality at places that are in a colonisation phase could differ to that at more established breeding locations. During the colonisation phase, the age structure of seals is likely to be biased toward younger seals, and younger (as well as senescing) females tend to be less capable than middle-aged females of rearing healthy pups to weaning (Bowen et al. 2006). Also, during establishment there is likely to be a greater proportion of adult males to pregnant females. Thus, each female is likely to be harassed by males at a greater frequency than they would at an established colony. Higher levels of male harassment have been correlated with lower pupping success, as the female has less time to suckle her pup (Boness et al. 1995). Additionally, few seals are involved during colony establishment so there is a greater chance for individuals to mate with near relatives than there is at larger, established colony. Mating events between related individuals can affect offspring survival and susceptibility to disease, known as inbreeding depression (Crnokrak & Roff 1999). Bean et al. (2004) found that grey seal pups with higher than average levels of parental relatedness had significantly lower survival rates. Finally, during the colonisation phase, seals are attracted to places where other seals reside, which may not be the optimal available habitat for pups to survive. Upon attraction, seals exhibit a strong fidelity to sites where they have previously pupped, so shifts to more optimal pupping habitat may take a strong environmental perturbation or generations of gradual shift.

4.2.2 Impact of weather events on grey seal pup counts in the Dutch Wadden Sea

To assess the effect of a storm event on the removal or mortality of pups, it is first necessary to know how many pups would be present if no storm took place. To do this, an age-specific population model was developed based on the pup counts in the Dutch Wadden Sea (Brasseur et al. 2014). The model describes the changes in pup numbers as a function of annual mortality, reproduction, immigration and birth, and departure rates during the pupping season. This model was fitted to all pup count data. The greatest impact on grey seal pupping would be weather conditions that result in unusually high tides. Therefore, all pup counts after a storm when water levels at Vlieland harbour exceeding 2m NAP, which is known to result in complete flooding of the Richel, were excluded (Table 6).

Pupping season	Date_time	Height (m)		
85/86	6-11-1985 11:00	2.15		
85/86	14-01-1986 22:00	2.34		
87/88	20-11-1987 19:00	2.07		
88/89	5-12-1988 04:00	2.34		
88/89	24-12-1988 20:00	2.13		
89/90	17-01-1990 23:10	2.22		
89/90	25-01-1990 20:40	2.07		
89/90	26-01-1990 07:20	2.16		
90/91	12-12-1990 16:40	2.51		
90/91	2-01-1991 21:20	2.04		
91/92	20-12-1991 06:20	2.61		
91/92	20-12-1991 18:00	2.29		
91/92	26-12-1991 23:30	2.10		
92/93	20-11-1992 03:10	2.02		
92/93	11-01-1993 21:50	2.08		
92/93	12-01-1993 22:40	2.17		
92/93	22-01-1993 20:10	2.35		
92/93	24-01-1993 21:20	2.20		
92/93	25-01-1993 09:30	2.26		
92/93	25-01-1993 21:10	2.11		
93/94	14-11-1993 20:00	2.01		
93/94	9-12-1993 15:00	2.10		
93/94	19-12-1993 23:40	2.43		
93/94	28-01-1994 08:30	2.73		
93/94	28-01-1994 19:40	2.55		
93/94	30-01-1994 21:40	2.31		
R	-	•		

Pupping season	Date_time	Height (m)
94/95	1-01-1995 07:00	2.04
94/95	1-01-1995 19:40	2.72
94/95	2-01-1995 08:00	2.14
94/95	10-01-1995 12:50	2.08
97/98	5-01-1998 00:50	2.04
99/00	6-11-1999 18:20	2.05
99/00	4-12-1999 03:40	2.22
99/00	30-01-2000 02:00	2.57
01/02	28-12-2001 18:20	2.17
03/04	21-12-2003 17:10	2.38
04/05	18-12-2004 00:10	2.06
05/06	16-12-2005 20:00	2.10
06/07	1-11-2006 03:10	2.65
06/07	1-01-2007 17:20	2.02
06/07	4-01-2007 20:20	2.04
06/07	12-0-2007 00:40	2.62
06/07	18-1-2007 19:50	2.47
07/08	9-11-2007 06:30	3.02
07/08	25-11-2007 07:50	2.05
07/08	25-11-2007 19:50	2.05
10/11	12-11-2010 11:20	2.10
11/12	25-11-2011 20:00	2.02
11/12	27-11-2011 21:00	2.47
11/12	4-12-2011 01:20	2.07
11/12	9-12-2011 18:00	2.33
11/12	29-12-2011 10:40	2.05
11/12	5-01-2012 15:50	2.17
12/13	30-01-2013 22:10	2.04
13/14	6-12-2013 00:00	2.75

Table 6. High water events (>2m) that coincided with grey seal pupping in the Wadden Sea, and likely caused some flooding. Shading combines data for pupping seasons.

Data are presented as a series of annual graphs that model data on pup presence through to 2010, and then predict the curves of pup presence in 2011 and 2012 (Figure 15). The comparison between the observed pup counts after storm events and the model estimates indeed shows that lower numbers of pups were observed than expected when storms preceded the count dates. This is apparent in the figure by open circles appearing below the trend line. For example, in 2005 there was a storm on 16 December that probably removed a proportion of pups present. The aerial survey (open circle) was conducted after the storm and fewer pups were recorded then than were expected by the model – with the difference between the observed and expected numbers potentially attributable to storm losses.

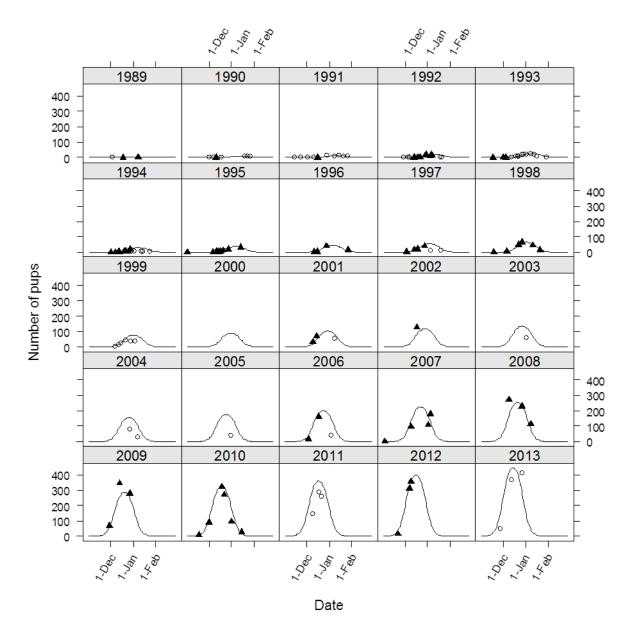


Figure 15. Modelled (lines) and observed (markers) pup production distinguishing between counts that were not influenced by prior storms (solid triangles) and those that were (open circles) (Brasseur et al. 2014).

Further interpretations can be made from the modelled data. For example, in 2011, many storms took place during the pupping season (Figure 15), but these did not cause large discrepancies between the number of pups estimated and the model estimates. One possible explanation could be that storm swells in that year were not sufficiently high to flood the main pupping sites or came from a direction that did not impact as strongly as in other years. Provided un-weaned pups are sufficiently old, they are capable of swimming and remaining beside the cow during brief inundations, particularly if these do not involve a strong surge. Although not always completely moulted, some weaned pups could survive by swimming to safety. Another possibility is the changing height of the sand bank from year to year.

Initially, the raw count data for 2011 and 2012 may suggested that pup growth was levelling off. The model shows however that in 2011, the apparent decrease in growth could be explained by several storm events preceding the counts. Then in 2012, lower pup counts could be explained by the fact that they were conducted before the actual peak in pup numbers was reached. In 2012, 340 pups were counted. The model predicts that, in fact, approximately 440 pups were born.

Also evident in the modelled data is the exponential increase in pup numbers and gradual progression to earlier pupping dates (see also section 2.3.3 of this report).

4.2.2.1 Observations in 2013

In 2013, a significant north-westerly storm occurred on the night of 5 December resulting in a 2.75m high tide at midnight at Vlieland harbour (Figure 16), which is beside the colony sites of Richel and Engelschhoek. The 5 December storm coincided with the expected period of maximum pup production. Effects of that storm on pup production will become apparent at a later time when aerial count data are tallied.

One outcome from the storm, however, was that it provided an example of storm-induced relocation by a grey seal. A female grey seal that had been fitted with a GPS tracker earlier in the year was present at the Richel for several days prior to the storm and likely had a pup there. During the night of 5 December, the female departed Richel at 10 pm, spent 7-hours in the water then haul-out at Griend (Figure 17). It is unknown if she had a pup, nor if the pup travelled with her. She was sighted on Griend on 14 December without a pup directly at her side but in the vicinity of a pup that had just weaned and might have been her pup.

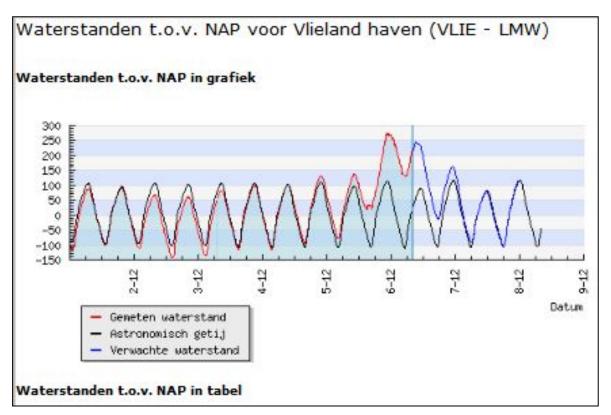


Figure 16. Water levels (cm) at Vlieland harbour (near Richel and Engelschhoek) indicating the rise over predicted levels caused by storm conditions on the 5-6 December 2013.

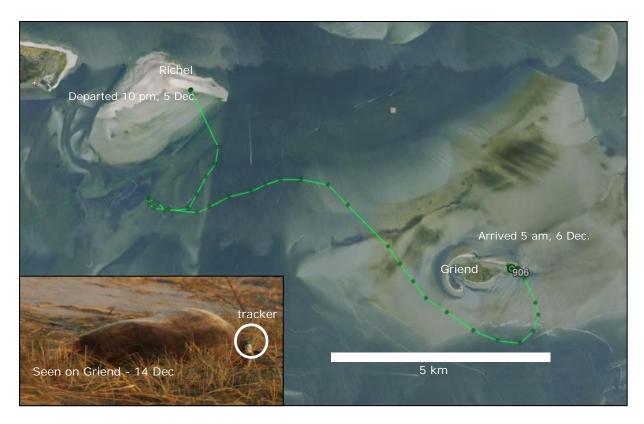


Figure 17. Movement from Richel to Griend of an adult female grey seal with a tracker, following the high tide that flooded Richel on 5-6 December 2013 (see Figure 16; google map, inset photo RK).

4.2.3 Anthropogenic influences on survival in the Netherlands

Grey seals are vulnerable to a range of human activities, these include:

- 1. <u>fisheries impacts</u> through by-catch, and entanglements or alter prey availability (e.g. influences parental condition, and post weaning survival)
- 2. collisions at sea
- 3. disturbance on land and at sea(e.g. stress, particularly to mother-pup bond)
- 4. <u>captive-care/ release</u> could this alter natural survival rates and distribution?
- 5. <u>environmental contamination</u> enhances disease susceptibility/ propagation
- 6. <u>habitat change</u> such as land reclamation or climate change.

4.2.3.1 Fisheries impacts

As fisheries intensity in the Wadden and southern North Seas is high (Jennings et al. 1999, OSPAR 2010), interactions with the seal population is to be expected. Seal interactions with fisheries can be direct (operational) or indirect (ecosystem). Fisheries may directly impact on grey seal survival through drowning in fishing gear or entanglement in fishing debris (Morizura et al. 1999), and see Figure 18. In Norway, a study on post weaning seal mortality revealed that out of 259 grey seals found dead, 169 (65%) had died in bottom set nets, and another 35 (14%) in other fishing gear (Bjørge et al. 2002). In the Netherlands, many set nets are used but as systematic monitoring of by catch lacks, there is thus very little information on by-catch. A recent study of stranded animals (Osinga et al. 2012) suggests by-catch could result in a high level of mortality.

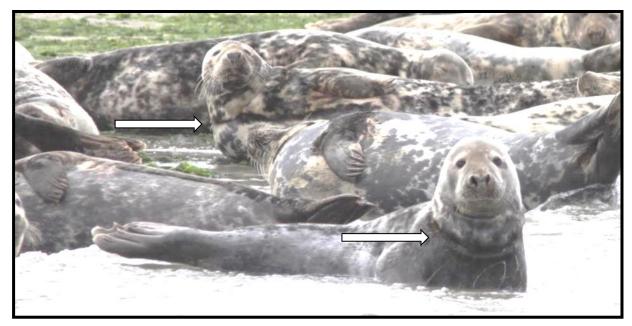


Figure 18. Grey seals with fishing net around their necks (photo RK).

In contrast to direct interactions, indirect interactions are difficult to quantify and relate to fisheries and seals being high level predators within the same ecosystem (Goldsworthy et al. 2003). Fisheries may regulate population sizes and ranges of seals by removal or enhancement of prey resources.

In the most obvious example of an indirect interaction, the same species and age classes of a prey are targeted by both consumers in the same area. This becomes more complicated when the same ageclasses of the same prey are targeted in different areas, or different age classes of the same species are targeted, or one consumer targets a species that is a predator or prey of the species targeted by the other consumer (Butterworth et al. 1995). Such interactions between fisheries and seals are likely to be more substantial than direct interactions. Marine food-webs are complex. Moreover, fisheries and seals target a range of species. Thus the impacts of one on the other can be exceedingly convoluted and difficult to estimate(Lavigne 2003).

Regulating population and range change is a gradual and long-term impact. In the shorter term, fisheries may also influence the body condition or seals, altering their reproductive capacity in a given year. For example, it is important for pup survival that investment by the cow is maximised. Cows that attain insufficient body reserves to rear a pup will abort, produce undernourished pups or prematurely abandon their pups. Thus, a fishing venture that temporarily lowers prey stocks in a region that is important to the seals during the lead up to pupping, could reduce pup survival in that year.

4.2.3.2 <u>Collisions</u>

Recently, a relatively large number of seals were found dead in the UK with what was described as extensive lacerations (i.e. deep cuts or tears of the flesh) (Bexton et al. 2012). These seem to have been caused by collisions with propellers, and are thought to be decimating seals in some areas. Although in the Netherlands this has not been examined, it is possible that collisions with vessel propellers cause a some mortality, especially given the large number of vessels traversing Dutch waters.

4.2.3.3 Disturbance

Disturbance may affect the seals in many ways, above the choice of (breeding) haul outs in relation to disturbance is discussed, here we elaborate more on the direct effect on survival. This could differ depending on the age and situation of the animal.

A comparative study of grey seal mother-young relations found that at a minimally disturbed beach, cows consistently and exclusively suckled their own pups (Fogden 1971). At a frequently disturbed beach, there was frequent break-down of the mother-pup bond resulting in poor recognition of pups, abandonment and higher pup mortality rates (Fogden 1971). Suckling female grey seals would be reluctant to flee from a disturbance, and therefore be perceived as more tolerant. Multiple disturbances during this period could however lead to higher stress levels and ultimately lower survival.

In Devon, UK, voluntary codes reduced disturbance from tour operators on grey seals at a haul-out, however, there were still disturbances mainly from private vessels (Curtin et al. 2008). A survey indicated tourists were aware of their potential impacts upon the wildlife and were generally supportive of the voluntary codes (Curtin et al. 2008).

After the pups are weaned, disturbance on land may startle the seals, causing them to flee toward the water, and thus consume valuable energy reserves. Effects of disturbance underwater (often by underwater noise) are still poorly understood. This would lead to displacement of animals, limiting their distribution and feeding possibilities, ultimately affecting survival. This could especially be a problem for young animals discovering their environment.

4.2.3.4 Captive-care and release

Most grey seal pups and juveniles go unnoticed by humans. However, each year a proportion of the pups comes onto shore-lines near inhabited areas where they may receive public scrutiny. The proportion varies between years, largely dependent on the timing and severity of storms during the breeding season. Specially in the Netherlands, great efforts have been made to take these animals into captivity, interpreted as a rescue. Motivation for taking a seal into captivity normally is to improve its chance of survival, although in some situations it may be to remove a seal from a place where it may upset, or be harassed by, people. Seals that are taken into captivity have several possible outcomes. They might be retained and released back into the wild at a later time, they might die soon after coming in, including by euthanasia, or they could be retained for the rest of their lives in captivity. The outcome that has the greatest potential to influence wild populations is captive-care and release. For instance, one consequence of captive-care and release is that individuals that might otherwise die of natural causes, survive and could contribute to total numbers and genetic composition of future generations. Also, diseases could be redistributed from the facilities to the wild population. In both examples, issues are more likely to occur if the proportion of animals taken into captivity is high relative to the population size.

Exact data on all rescue efforts in the Netherlands are not available. For some years, however, approximate effort for young grey seals has been reconstructed by Brasseur et al. (2014) based on records available from one captive care centre (Ecomare) and various public media (see Figure 19). It was clear that in some years rescue effort was extremely high. For example in 2004, the number of rescued pups was approximately the same as the estimated pup production in that year.

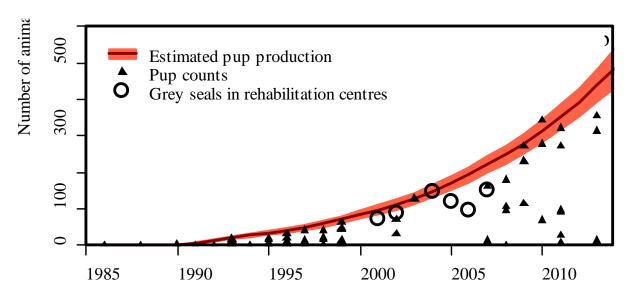


Figure 19. Estimated pup production compared to counts and number of grey seals brought in to captivecare for years 2000 to 2013 (Ecomare pers. com. and diverse public media). Captive-care cases were only included if dates for capture were in the period 1 Dec. to 15 May. Only six of 271 grey seals brought in to captive-care were older than a few months (Brasseur et al. 2014).

An important consideration for captive-care and release of grey seals in the Netherlands is 'could it affect the status of the wild seals?' There are several scenarios where this may be the case. Given the low levels of pup production between 1980 and 2000, and the high proportion of pups that received captivecare, captive-care could have contributed to the survival of the pups and, therefore, in addition to the annual immigration, to growth of the breeding population. However, it is not possible to define the extent of this (Brasseur et al. 2014).

Another potential impact of captive-care on wild seals is the interference with the development of the pup after weaning. In a normal setting pups are left after weaning to discover their environment during the first months and develop strategies to optimally feed and haul out. It is unknown how the seals are affected when they are deprived of their environment in these first months. Also medicine administered during the captive care, and infections potentially caught in the facility could influence the immune development of the young animals or even unnaturally spread new diseases in the wild populations (for example the herpes virus). This has been the strongest argument against rescue and rehabilitation in Denmark, for example. Finally, removal of pups could influence the breeding or haul-out range of the grey seals. For example, it is normal behaviour for grey seal pups to be left ashore by their mothers who may depart on brief trips into the water e.g. to feed or avoid a disturbance. If such pups are removed, the females may be less likely to return to pup at the site, and the site would be unlikely to develop into a colony.

4.2.3.5 Environmental contamination

Anthropogenic environmental contaminants include heavy metals, PCBs, DDTs and petroleum products. These can have impacts on individual seals and populations. Contaminants are not discussed in depth. Briefly, however, high levels of environmental contaminants during the 1900s were implicated in substantial population declines of Baltic grey seals (Sormo et al. 2003) and of harbour seals in the Dutch Wadden Sea (Reijnders 1986). Chronic exposure to high levels of oil and exposure to fresh oil spills can alter behaviour and cause mortalities of grey seals (Jenssen 1996). Environmental contaminants are also deleterious to fishes, reducing prey availability for seals, or can accumulate in fish resulting in and are then passed on to seals through consumption (Jenssen et al. 1995, Jenssen 1996, Jenssen & Skaare 1996). In the Netherlands pollution is currently not considered an immediate threat to the seal populations, although locally it may affect individual animals.

4.2.3.6 Habitat change

Grey seals are reliant on certain habitats and change at those habitats can influence pup production and pup survival. Potential processes for human habitat change include infrastructure development, dredging, land reclamation, dams and human-induced climate-change. There are few data sources for impacts on grey seals of anthropogenic habitat change, however, so connections are largely speculative.

One land reclamation activity that might be of benefit to grey seals could be the replenishment procedures at the island of Griend during the 1970s, undertaken to sustain the habitat for breeding birds. Over centuries, the island had steadily reduced in size and probably would not exist if the replenishment had not taken place. Griend is now an important grey seal pupping site.

5 Exchange of grey seals with other areas

Grey seals in the Netherlands belong to a north-east Atlantic stock, whose range extends from France to the Kola Peninsula in Russia. Approximately 90% of north-east Atlantic grey seal pups are born in the UK, with the next largest pup production being in the Dutch Wadden Sea. Grey seals on the east coast of Britain are treated as a single ecological unit, within which discrete breeding populations exist (Hammond et al. 1993, Thompson et al. 1996). The group of grey seals that produces pups in the Netherlands, likewise might be considered as a 'population'. However, it is distinctly not a discrete population. Grey seals in Dutch waters comprise two components, those associated with local pup production if the breeding population' and visitors that are not associated with local pup production. Levels of isolation and overlap between these components are difficult to assess, but are important factors for understanding the identity and sustainability of grey seals in the Netherlands.

5.1 Local breeders, annual immigration and seasonal visitors

Based on the estimate of 440 pups in 2012, the group of grey seals associated with pup production in Dutch waters (defined as the local breeding group) was estimated at slightly over 3000 animals in 2013 (Brasseur et al. 2014). This included pups of the year, juveniles and breeding age animals. The observed growth of 19% per year since the first breeding in 1985 can only be explained if, in addition to the pups born in the Wadden Sea, new animals immigrate into the population annually. Given the fact that breeding animals are very site faithful this influx can only be achieved by young animals moving into the area. To achieve the observed growth, an estimate of 1.3% of the grey seal pups born on the UK- North Sea colonies immigrate annually into the Dutch waters (Brasseur et al. 2014). So the local breeding group comprises those involved in local pup production and growth, plus young immigrants that decide to breed in the Wadden Sea.

In addition to the local breeding group, there are indications for seasonal visitors. Surveys carried out during the moult and in summer have recorded more grey seals than can be accounted for by the local breeding group. For example, in 2012, there was a maximum count of 3081 grey seals ashore at sites in the Netherlands, while the population estimate based on the pup counts was about 2770 (Brasseur et al. 2014). Not all seals are haul-out at one time and so the counts underestimate the total number of grey seals in the Netherlands. It seems evident that the local breeding group is augmented by seasonal, visitors from other regions, and these seals apparently return to those other areas to breed. It was calculated that in recent years a minimum of 200-250 animals come to the Netherlands outside the breeding season (Brasseur et al. 2014). One factor preventing the estimation of the actual number is that during the moult not all seals haul out at the same time.

Data obtained from tracking of individual seals provide some indication of the levels of local and regional movement (see paragraph 2.1). However, the numbers of animals tracked are low compared to the population size and they do not provide longer-term data on migration behaviours, nor allow for quantification of the proportions of seals present that are local breeders or seasonal visitors. More data are needed on movements of individual seals. One means of obtaining such data is through broad-scale mark-resight programs. Traditional methods involve physical capture of large numbers of seals and individual marking with either flipper tags, for which there are high rates of tag loss and loss of readability, and branding, which is very time consuming and is an invasive procedure. An alternative means of identifying and following life-time movements of individuals is through photo-identification.

In 2013, a grey seal photo-identification (photo-ID) program was established in the Netherlands. This included a collaboration with the Sea Mammal Research Unit (SMRU), in Scotland, which developed a photo-ID technique for grey seals (Hiby & Lovell 1990, Vincent et al. 2001, Hiby et al. 2007, Hiby et al.

2012, Paterson et al. 2013). Since the 1990s, SMRU have collated images of grey seals from across the United Kingdom and France.

5.2 Photo-ID of grey seals

5.2.1 Introduction

Recognising an individual over time allows interpretations of life-history traits and behaviour. For example, information can be gathered on where the individual travels and how frequently or for how long it rests at one place. It also has applications for estimations of population size by applying a mark-recapture (recognise-resight) technique. Standard techniques for enabling identification of individuals include tagging and branding. Such techniques require the animal to be captured, however, which can be difficult and invasive and give rise to ethical discussions.

The photo-ID technique of individual recognition takes advantage of the fact that individual animals can have unique markings on their fur. Several software programs are designed to assist computer-based pattern matching. The technique has been applied successfully to a wide range of animals, including tigers, zebras and grey seals (Hiby et al. 2007, Hiby et al. 2009). In grey seals, pattern-matching of individuals can result from photographs taken on land: head, neck and flank profiles, and at sea: head and neck profiles (Hiby et al. 2012, Paterson et al. 2013).

Not all grey seal individuals are useful candidates for photo-ID. For example, recognising individual adult males is more difficult than recognising individual females. This is partly because the pelage of males darkens considerably with aging. Adult males can also have extensive scarring around the neck, caused by fighting, which makes pattern matching even more difficult. In adult females, individual patterns can last for their whole life (Paterson et al. 2013). Some darkening of female pelage with age serves to strengthen the contrast between dark and light areas, making identification by pelage recognition easier as animals get older (Vincent et al. 2001).

In order to be able to monitor movements of individual grey seals over several years across the extent of their possible range, this project has the objective of establishing a North Sea wide program of photo recording and pattern matching. In this framework, photographs from Denmark were added to the database and procedures are underway to incorporate seals from German haul-out sites. The project has stimulated greater efforts to undertake photo-ID at sites in the UK, particularly those from which grey seals might undertake movement to the Netherlands. One site of particular interest is the Farne Islands, which has a strong link with grey seals in the Netherlands.

In the UK during the 1950s, routine tagging of grey seal pups commenced with the aim of monitoring their dispersal (Bonner 1972, Harwood 1978). During the 1960s and 1970s, all resights of UK tagged seals in the Wadden Sea had come from the Farne Islands (Hewer 1974). Potentially, not all grey seals entering the Wadden Sea at that time came from the Farnes, but undoubtedly many did, and that link could still be strong. Due to the link between the Farne Islands and the recolonisation of the Netherlands by grey seals, a review of research and activities at the Farnes is presented in Appendix B.

The ultimate aims of the photo-ID project in the Netherlands is to establish what proportions of seals that are resident or seasonal visitors, to gain information on immigration rates, and record movements of females that are pupping in the Netherlands, which are the critical component of the current breeding group. These results will facilitate identification of grey seals in Dutch waters and provide data for their conservation.

5.2.2 Methods

Photographs of grey seals were taken during research visits to haul-out and breeding sites of grey seals in the Netherlands and during opportunistic visits via tourist vessels to haul-outs (Table 7). Visits were also made to two important breeding sites in the UK, the Farne Islands and Fast Castle, where photo-ID data were not being collected, to stimulate collaborative data collections. Potentially a more regular exchange of information with the personnel active on the Farne Islands in the future will yield more photographs of animals breeding locally. This was particularly important for the Farne Islands due to its link with the recolonisation of the Netherlands, and because a research team remain on the island throughout the grey seal pupping period. Considerable effort also went into obtaining photographs of breeding females at the important Wadden Sea pupping sites of Griend and Richel.

Area	Location	Date	Photographs	Processed by July 2014
Wadden Sea	Steenplaat	2013-03-12	339	yes
Wadden Sea	Steenplaat	2013-03-13	502	yes
Delta region	Renesse	2013-03-19	74	yes
Delta region	Aardappelbult	2013-03-21	593	yes
Wadden Sea	Steenplaat	2013-04-29	230	yes
Zeeland	Aardappelbult	2013-05-15	289	yes
Wadden Sea	Steenplaat	2013-05-23	422	yes
Wadden Sea	Steenplaat	2013-08-17	1267	no
Wadden Sea	Steenplaat	2013-08-27	139	no
Wadden Sea	Steenplaat	2013-09-25	302	no
UK North Sea coast	Farne Islands	2013-11-05	227	no
UK North Sea coast	Fastcastle	2013-11-08	406	no
Wadden Sea	Griend	2013-12-14 to 17	1224	no
Wadden Sea	Richel	2013-12-17	975	no
			6989	

Table 7. Locations and dates of grey seal photography for photo-ID pattern matching.

The photographs were collated and supplied to SMRU for further processing. At SMRU, an overview of seals present was obtained by stitching together a selection of images. Then images were graded as suitable or unsuitable for extracting patterns in the pelage of individual seals. Unsuitable images comprised blurry photographs (poor focus or excessive movement), repeat photographs, photographs of only harbour seals, or photographs in which the pelage of grey seals present was not clear (poor lighting, poor angle of view, only males with unclear patterns etc). Not all pictures were analysed prior to submission of this report.

In suitable images, patterns from the head, neck and flank of each seal (mostly female) were extracted where possible. Extraction involved processing the 3-dimensional shape of the seals' body into a 2-dimensional map of the patterns of light and dark patches, which are unique to each seal (Figure 20, Figure 21). This provided up to six extracts per seal if both sides were photographed successfully and linked in records. These extracts were added to the photo-ID database using the computer-aided matching software '*ExtractCompare*', and compared with all the patterns in the data base. The data base produced the most likely matches, if any existed, which could then checked by eye.

The photographs were scanned to look for 'recaptures' within the Dutch sampling dates – internal matches, and to look for 'recaptures' of animals seen in UK waters (photographs in the SMRU data base – SMRUPOT) in the Dutch sampling.

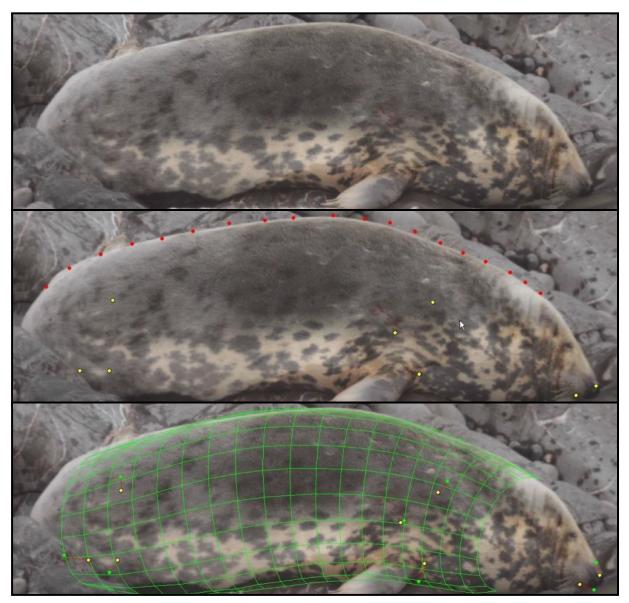


Figure 20. Steps in the technique used by pattern recognition software to convert the 3-dimensional shape of a seal into a 2-dimensional image of pelage pattern (photos SMRU).

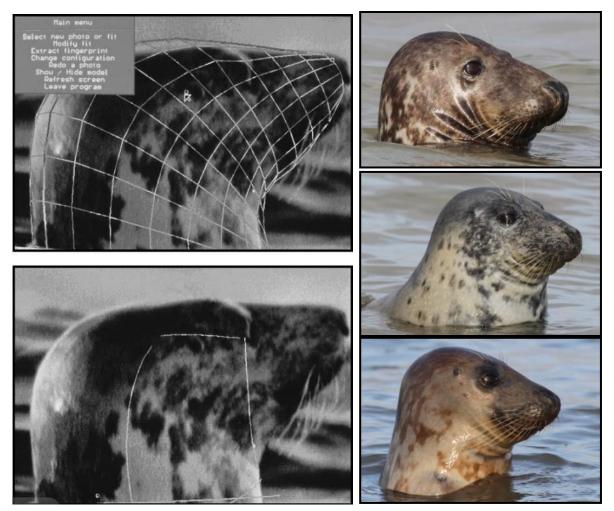


Figure 21. Pattern recognition techniques used for individual pelage recognition of lateral head shots (Hiby et al. 2007), plus example photographs from 2013 (photos RK and Oscar Bos).

5.2.3 Results

At the time of report preparation, images from seven sampling trips only had been processed (total of 2449 images). These were collected between March and May 2013. Further sample dates, including photographs of females from UK and Wadden Sea pupping sites, are yet to be processed. Numerous individual patterns in the pelage were recognised (Figure 22).

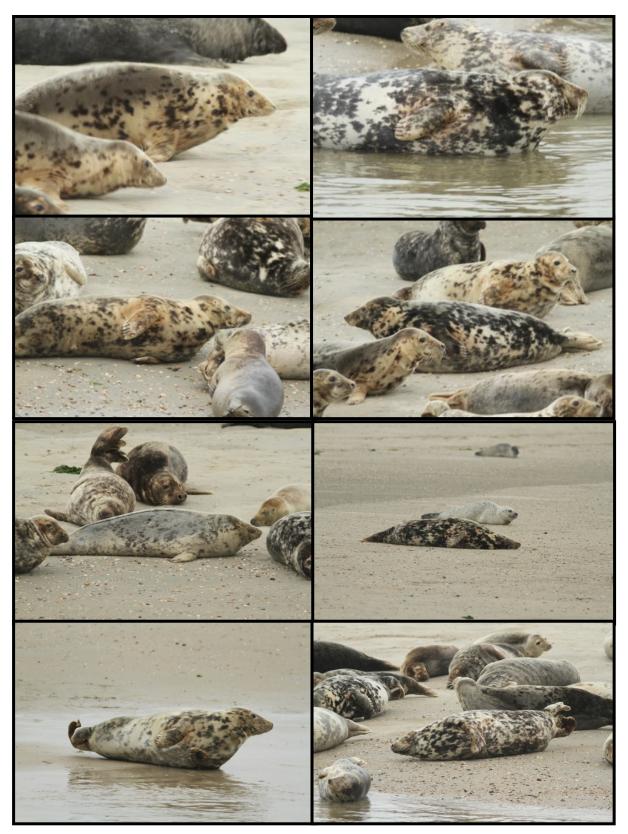


Figure 22. Example photographs of grey seals at Wadden Sea haul-outs that enable individual recognition by photo-ID (photos by RK and GA).

The photographs from March to May 2013 were taken on research trips that involved going ashore at haul-out sites. In the process, all seals entered the water and thus few were available for close-up photographs of pelage patterns. A total of 108 females were identified as suitable for pattern extraction [55 head (30 left, 25 right), 19 neck (13 left, 6 right) and 11 flank (10 left, 1 right)] (Table 8, Table 9). A further 76 images of males also were recorded (technically suitable for pattern extraction if they were suitably patterned). These equated to 53 female individuals and 92 males (more than one male was present in some images).

Out of the female individuals, none matched with any individual from the existing UK database. There were four matches within sampling dates but no matches between sampling dates within the Dutch samples. Due to the small number of images and different individuals processed to date, this is expected. The value of the data base comes with repeated and multi-year sampling, particularly at the pupping sites. The lack of matches detected between the Netherlands and UK is undoubtedly a sample size issue.

Table 8. Processing outcomes of grey seal photo-ID images taken in the Netherlands between March and May 2013.

	Female	Male	Total
Number of suitable images	108	76	184
Number of suitable individual seals	53	92	145
Number of matches with SMRU data base	0	NA	0
Dutch photo matches within sampling dates	4	NA	4
Dutch photo matches between sampling dates	0	NA	0

Table 9. Number of females, males and 'sex unknown' grey seal in photo-ID images taken in the Netherlands between March and May 2013.

Sample date	No. of females	No. of males	Sex unknown	Total
2013-03-12	74	13	0	87
2013-03-13	33	6	0	39
2013-03-19	8	0	0	8
2013-03-21	50	23	0	73
2013-04-29	4	33	0	37
2013-05-15	40	173	34	247
2013-05-23	38	20	18	76
Total	247	268	52	567

5.2.4 Conclusion

It is clear that photo-ID of individuals provides a valuable technique for the long-term marking and recognition of individual seals, and for understanding how the populations of grey seals in the southern North Sea are structured. Further data collection and analysis will clarify how dependent the Dutch animals are on the exchange of individuals between areas.

In addition to the recording of seals at different haul-outs and between different countries, the photo-ID data base provides opportunities for studying individual behaviours over the long-term within the Netherlands. There is the potential, for example, to record time-spent at haul-outs and movement between haul-outs, which will greatly augment data being collected by tracking of individual seals.

Of particular interest is the ability to monitor breeding females at the colony of Griend. Photo-ID of these individuals provides the possibility to monitor fidelity of individuals to this site and to individual breeding areas within this site. It also enables recordings of immigrations to this site from UK populations, and relocations from other sites within the Wadden Sea (such as from Richel) as well as recruitment of locally born individuals. Long-term data sets of individuals will furthermore allow the recording of important demographic parameters, such as fecundity rates, providing valuable data on the breeding group of grey seals within the Wadden Sea.

It will be necessary to increase sample sizes from both sides of the North Sea to make a statistically reliable estimate of recapture likelihood. To this end, photo-ID programs are being encouraged across the North Sea, particularly at UK sites from where movements between UK and the Netherlands are most likely to occur e.g. east and south-east England (Fast Castle, Farne Islands, Donna Nook, Blakeney Point and Horsey). Substantial efforts to acquire such images are in progress and additional breeding season surveys will take place in 2013 in the UK. Greater efforts will also be made within the Netherlands to obtain regular data from some haul-outs and a greater spread of sampling. Particular attention will be paid to obtaining photographs of females at pupping sites.

6 Conclusions & recommendations

6.1 Summary points

1a-Adequacy of breeding habitat

- Grey seals require land habitat to rest, moult, have pups and breed. They utilise different locations for different purposes. Location selection is a balance between proximity to feeding sites, and likelihood of remaining dry and undisturbed for the shore period (hours to rest or weeks to rear a pup). In Dutch waters, the land habitats most utilised by grey seals are sandbanks that could be flooded at high tide.
- 2. Grey seal pups usually do not swim until 3-7 weeks after birth (3-weeks of maternal support and up to 4-week post-weaning). Therefore, elevation above water level is important to maximise the chance of pup survival.
- 3. All current pupping sites of grey seals in the Netherlands are flooded by extreme high tides and by high storm surges (i.e. that reach approximately 2-m above NAP). If flooding coincides with the pupping period (November to January in the Netherlands), dependant pups can be separated from their mothers and/or drowned. Storms may also drown or disperse weaned pups to other beaches. Because of their vulnerability to inundation of current pupping sites, they can be considered sub-optimal for pup survival.
- 4. Breeding sites that are sub-optimal for pup survival are utilised by grey seals, though. This is because the sites serve other purposes than just optimising survival of the young. For example, important considerations include site fidelity, previous experience with the site, chance of encountering a suitable breeding partner, levels of disturbance and ease of access. These are all relevant to how optimal breeding adult seals might consider a site to be.
- 5. Within the Netherlands, alternative habitats are available for grey seals to colonise, including on coastal beaches and adjacent dunes of the mainland and larger Wadden Sea islands. At such places, the seals may avoid the chance of inundation. They have not colonised these sites yet, however, and the most likely reason for this is to avoid human disturbance. Future colonisation of such sites might occur provided disturbance, particularly during the first years of colonisation, is minimised.
- 6. Although single births have been recorded elsewhere, grey seals currently give birth to pups at five key locations in the Netherlands all in the Wadden Sea: Richel (67% of the pups born); Engelschhoek (14%); Griend (2% and increasing in importance); Razende Bol (5%); and Steenplaat (4%). These are critical locations for the sustainability of the current recolonisation of grey seals in the Netherlands. The natural development of the grey seal population in the Netherlands requires these locations to be adequately protected from human interference, particularly during pupping periods.
- 7. There are indications that there also is strong selection pressure for the most appropriate moult locations. Currently, the most important grey seal moult location in the Netherlands is Engelschhoek. In the past 5 years, an average of 75% of seals seen in the Dutch Wadden Sea moult there. Other important moult sites include Razende Bol (11%) and Steenplaat (5%).

<u>1b-Survival</u>

- 8. Adult grey seal survival rates in the Netherlands are in line with levels found in other areas (Brasseur et al. 2014). However, there is an indication that the rate of first year survival in the Wadden Sea (~59%) is lower than rates at other sites (Brasseur et al. 2014). There is a high probability that the lower survival is related to the regular flooding of the breeding sites in the Wadden Sea.
- 9. The sustainability of grey seal breeding (and pupping) in the Netherlands will be influenced by survival rates of seals. Possible human-related impacts on survival include entanglement in fishing gear, altered feeding possibilities due to fisheries takes, and energetic challenges due to disturbance. The degree of variation in these impacts across the seal's range is unknown.
- 10. A further influence on grey seal survival in the Netherlands is the high degree of effort put into capture, captive-care and release of seals (especially of young dependant and independent individuals). These efforts might affect the wild population. Next to altering the development of young animals by extracting them from their natural habitat, the holding in captivity and administration of drugs could influence the seals' immune system and unintentionally infect the animals that are then released. The relatively high rescue efforts in the recent past may have influenced the survival rates of first-year seals. For example, they could have enhanced survival rates such that without such efforts, the low level of first year survival might have been lower. To better understand the relationship between captive-care and demographics of the local breeding group, more detailed studies are required, e.g. following individual pup survival and movement over time. A further potential impact of the high level of capture of first-year seals is that it may be a disturbance mechanism that influences colony site selection and distribution.

2-Exchange

- 11. Modelling of grey seal population data collected in the Netherlands confirms that a proportion (~1.3%) of the seals born in the UK immigrate into the Dutch colony (Brasseur et al. 2014). Moreover, a numbers of grey seals that breed in the UK use the Dutch waters outside the breeding period. The exchange between the Netherlands and the UK is also registered in telemetry studies collected in the past decade.
- 12. To obtain information on the magnitude of the exchanges and better understand the underlying mechanisms and interdependence of the different colonies, a photo-ID program was commenced in the Netherlands in the framework of this project. This was achieved in cooperation with researchers at the Sea Mammal Research Unit (St Andrews, Scotland), who developed the methods and have a data base of over 20 000 seals photographed at breeding sites in the UK and elsewhere. Initial processing and pattern matching of images represented a pilot study with a small sample size and no matches were made of seals between areas.

6.2 Adequacy of the habitat for grey seals

The first habitat to consider is the marine habitat, where grey seals feed. There is no indication that, at present, feeding habitat for grey seals in the Netherlands is limited. On the contrary, the growth in grey seal numbers (and also in the number of harbour seals, porpoises and other (avian) top predators) suggest there is ample prey available.

Prey quality might have improved in recent years. Brasseur et al. (2014) suggest a forward shift from the mean pupping date from early January in 1985 to early December in 2013 might have been induced by improved prey availability. Reijnders et al. (2010) suggested similarly that altered prey abundance might have caused a forward shift in pupping of harbour seals in the Netherlands.

Grey seals also require land habitat. Primary uses of land are as sites to rest, places to moult, and places to have pups and breed: they utilise different land habitats for different purposes. For all uses, though, sites selection is a balance between likelihood of remaining dry for the required period (hours or days), likelihood of minimal or no disturbance, and proximity to feeding sites. In Dutch waters, grey seals often utilise sandbanks in the Wadden Sea that could be flooded at high tide. Although some grey seals are seen on lower sandbanks that are submerged for most of high tides, contrary to harbour seals, they seem to prefer higher than average sandbanks, which permit them to haul out for longer periods.

The Engelschhoek currently appears to be the most attractive haul-out for grey seals in the Netherlands during the spring moult period (March and April) and summer (May to October). During the spring moult, more than 2000 animals are recorded on Engelschhoek (see Figure 9). Important qualities for a haul-out are that it enables rest and is near to feeding sites and, less explicitly, that it affords the ability to socialise with other seals. Engelschhoek is more exposed to the North Sea than other sandbanks of the Wadden Sea and, thus, provides slightly better access than most other sandbanks to where the seals feed, out in the North Sea.

During the peak of moult, individual seals remain out of the water for days at a time. Entry into the water while moulting results in great energetic costs for the seals, because they have a high blood flow to their skin during the peak of moult. Moulting sites require greater selection than routine rest sites, to further minimise the chance of having to enter the water. Thus, the primary requirement of a site is that it provides the seal with the ability to rest and remain dry without disturbance.

During pupping and breeding periods, elevation above the high tide level is a necessity for the survival of young pups and for breeding success (allowing colony structure and mating opportunities). Selecting sites close to feeding opportunities is not a concern and the seals might even tolerate some level of disturbance, which they would not at a rest or moult site, provided it had less chance of inundation. Grey seals now breed in at least 10 locations, most of them in the western part of the Wadden Sea. Only five have developed into breeding colonies: Richel (67% of the pups born); Engelschhoek (14%); Griend (2%); Razende Bol (5%); and Steenplaat (4%).

Despite being the highest sandbanks in the region, all current breeding sites are still flooded in extreme tides and high storm surges (currently approximately 2 m above NAP). Depending on the timing of the flooding, young pups can be separated from their mothers, and/or drown. Later in the season, mostly weaned pups are attained that are already (partially) moulted. Although some may still die as a result, the storm also disperses the seals on other beaches. Thus, the seals are breeding and moulting at sub-optimal sites.

The concentration of grey seal pupping on the Richel could be because this is the best of the 'suboptimal' sites available to them. The high density of pupping there also demonstrates that the seals are also driven by intrinsic factors, such gregarious behaviour, prior experience and site fidelity, as has been observed in other areas.

Within the Netherlands, alternative habitats for the seals are available, including coastal and island beaches and adjacent dunes. At such places, the seals may stay dry for as long as needed. They avoid these sites, however, and the most likely reason for this is to avoid human disturbance. This might work in two ways: first, the seals are known to avoid the beaches when they detect human activity in general. Second, as breeding occurs in winter, when human activity on the beaches is relatively low, some seals occasionally wander on to the beaches, however the public perceives this as a sign of disease and rescue efforts follow, dissuading the seals to come back to the site. There is a growing effort to discourage approaches of seals; even on the mainland beaches, this however has not led to seals using the beaches on a regular basis. There are indications, however, that breeding sites may tolerate some disturbance. A good example of this is the seals at Donna Nook in the UK. There thousands of tourists come to see the breeding site every year. A fence does prevent the public to wander in between the animals. It is not clear whether the tolerance for the public is general or poses a certain selection, sensitive seals might have relocated to other sites. This also holds for non-human disturbance: for example, seals continue to return to the established pupping sites in the Wadden Sea, even though heavy storms have caused flooding of these in almost two out of every three years.

During the almost 30 years that grey seals have been breeding in the Netherlands, they have been 'testing' new sites. At times seals have attempted to rest ashore, pups are even born on some of the larger islands. But it is likely to require years of nil disturbance for such events to result in the establishment of a colony.

This report focusses on grey seals in the Wadden Sea. Grey seal numbers are likely to also increase in the Delta region and, if so, and providing a lack of disturbance, pupping is likely to commence there in coming years. Currently, the most important moult and haul-out site is the Aardappelenbult sandbank adjacent to Brouwersdam (51.79°N, 3.78°E). However, this site is very exposed to westerly winds and, consequently, winter storms. Hence, pupping is unlikely to develop at this sandbank on a large scale.

6.3 Survival of grey seals in the Netherlands

Adult grey seal survival rates in the Netherlands are in line with levels found in other areas of the seal's range (Brasseur et al. 2014). However, there is an indication that the rate of first year survival in the Wadden Sea (~59%, Brasseur et al. 2014) is somewhat lower than rates at other sites. As the population has been reproducing in the Netherlands for 30 years it is unlikely that inexperience of young females would play an important role in the low survival rates. Furthermore, density dependant factors are unlikely to be influencing the low survival rates of first-years, because the density of seals in Dutch waters is still low relative to other areas and the pups are born on flat and sandy beaches thus are less prone to disease spread which occurs at other colonies. There is a high probability that the lower survival is related to the regular flooding of the breeding sites in the Wadden Sea.

Possible human-related impacts on post weaning survival include entanglement in fishing gear, altered feeding possibilities due to fisheries takes, and energetic challenges due to disturbance. The degree of variation in these impacts across the seal's range is unknown. For example, few studies document grey seal mortality due to entrapment in fishing gear and entanglement in marine debris, but these are known occur across the seal's range (Barnett & Westcott 2001, Bjørge et al. 2002, Kauppinen et al. 2005, Suuronen et al. 2006, Westerberg et al. 2008). Fishing gear identified to cause grey seal mortality in Scandinavia and the UK are used in the Netherlands. In the Netherlands, data on seal mortality related to fisheries are not collected or registered in a structured way.

A further influence on grey seal survival in the Netherlands is the extreme rescue and rehabilitation efforts of recent decades (Figure 19). No studies have examined the results of these efforts at a population level. More detailed studies, following individual pups could help in defining survival rates and defining causes of mortality.

6.4 Exchange of grey seals between Dutch waters and other areas

Tracking data of grey seals have long demonstrated the great movements of individuals, and the strong links between grey seals on the east coast of the UK and those in the Wadden Sea Recent modelling of grey seal count data collected in the Netherlands since the 1980s provides insight into the exchange of grey seals between Dutch waters and other areas (Brasseur et al. 2014). Grey seal numbers in in the Wadden Sea have increased at an exponential growth rate of 19%. Because maximum intrinsic growth rates for pinniped populations are approximately 6%, immigration must be contributing substantially to the growth in seal numbers. Through modelling of grey seal, it was estimated that first-year survival of seals born in the Wadden Sea was likely to be low (~59%) and that at least 35% of the 1-year old animals in the Wadden Sea were immigrants, most likely from the UK east coast (Brasseur et al. 2014). Additionally unexpected high survey results during the moult and in the summer leads to the hypothesis that there are considerable numbers of grey seals that breed in the UK but use the Dutch waters outside this period. A very conservative estimate is that at least 200-250 animals do this. The exchange between the Netherlands and the UK is also registered in telemetry studies.

To obtain information on the magnitude of these exchanges and better understand the underlying mechanisms, a photo-ID program was started in the Netherlands in the framework of this project. This was done in cooperation with the Sea Mammal Research Unit that had developed the methods and already has a data base of over 20,000 animals from different breeding sites in the UK. The project included: Setting up an operational Dutch part to the existing database, learning the methods, testing the photos obtained so far and setting up an appropriate monitoring scheme for the following years.

Initial processing and pattern matching of images represented a pilot study for the photo-ID technique. The lack of matches detected within samples collected between March and May in the Netherlands with seals in the UK was undoubtedly influenced by the small sample size. It will be necessary to increase sample sizes from both sides of the North Sea to make a statistically reliable estimate of recapture likelihood. Particular attention will be made to obtaining reliable photographs from breeding females at Netherlands colonies, to enable movement and life-time data collection from these, and to aid interpretations of immigration and relocation rates. Co-ordinated efforts to acquire quality images from North Sea countries are in progress and additional breeding season surveys will take place in 2014.

6.5 Recommendations

- Maintain monitoring of grey seal numbers during their pupping and moult periods including numbers in the Delta region.
- Ensure adequate protection from disturbance by unregulated human visitation to currently important sites in the Wadden Sea: particularly those for pupping (Richel, Griend, Engelschhoek, Razende Bol), and moult (Engelschhoek, Razende Bol, Steenplaats). In the Delta region, the sandbank adjacent to Brouwersdam is also an important moult site.
- Perform detailed geomorphological measurements (e.g. height and stability) of sites critical to grey seals (Richel, Griend, Engelschhoek, Razende Bol), to predict possible changes and storm impacts.

- Maintain photo-ID program to provide more data on immigration rates and exchange of 'Dutch' grey seals with the UK population. Augment this with a genetics study.
- Data are required on the demographics, breeding success, survival rates and site fidelity of seals at the Dutch pupping sites.
- Further understanding is needed of the consequences of captive-care for grey seal status and distribution in the Netherlands.
- Data are needed on fisheries impacts, including ecosystem overlap (e.g. diet and foraging area) and operational overlap (e.g. by-catch and entanglement).

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8 Quality Assurance

IMARES utilises an ISO 9001:2008 certified quality management system (certificate number: 124296-2012-AQ-NLD-RvA). This certificate is valid until 15 December 2015. The organisation has been certified since 27 February 2001. The certification was issued by DNV Certification B.V. Furthermore, the chemical laboratory of the Fish Division has NEN-EN-ISO/IEC 17025:2005 accreditation for test laboratories with number L097. This accreditation is valid until 1th of April 2017 and was first issued on 27 March 1997. Accreditation was granted by the Council for Accreditation.

9 Justification

Rapport number:	C090-14
Project Number:	BO-11-011.04-015

The scientific quality of this report has been peer reviewed by the a colleague scientist and the head of the department of IMARES.

Approved:	Dr Oscar Bos Researcher
Signature:	Bos
Date:	14/01/2015
Approved:	Drs Jakob Asjes Head of IMARES Ecosystems Department
Signature:	A
Date:	14/01/2015

Appendix A. Baltic grey seals

Box : Baltic grey seals

Halichoerus grypus macrorhynchus

In 1900, there were an estimated 80,000 to 100,000 grey seals in the Baltic Sea (Harding & Harkonen 1999). Then through most of the 1900s, the population declined. Grey seals in the Baltic Sea (and along the Norwegian coast) experienced on-going harvests and culls, which were supported by bounty systems. It is speculated that hunting was the main reason for much of the decline(Hook & Johnels 1972). Then in the 1960s, new problems emerged: pollution, disease and enhanced reproductive failure(Helle 1980, Bergman 1999, Bergman et al. 2001). By the 1970s, the population comprised 2000-4000 seals (Harding & Harkonen 1999). Hunting became prohibited in several Baltic Sea countries.

After the 1970s, a recovery of numbers commenced (Harding et al. 2007). Increases were greater in the north of the Baltic Sea, where growth was about 12% annually over the period 1982-97. In the south, the rate of increase was 5% annually. The reasons for the lower rate in the south are not known, but the residual effects of contaminants on reproduction could have been a factor. Another problem was high mortality rates among young grey seals who became entangled in fishing gear. To aid recovery in the south, grey seals from the north were reintroduced into the southern Baltic Sea along the German and Swedish coasts. By 2000, surveys indicated a total of approximately 15,000 Baltic grey seals in the whole of the Baltic Sea, mainly in Swedish, Finnish and Estonian waters(Harding et al. 2007, Hiby et al. 2007).

Legal hunting of grey seals in the Baltic Sea recommenced in 1999 in Finland and 2001 in Sweden. Currently, annual quotas are about 1000 in Finland (including Åland) and 180-230 in Sweden, and about 50% of quota is used (Anon. 2007). Drowning in fishing nets continues to be a significant human-related cause of death. Estimating the amount of by-catch is difficult because fishermen are not obliged to report by-catches. However, it is estimated that up to 1000 Baltic grey seals drown in fishing gear each year (Harding et al. 2007). A further issue for Baltic grey seals is that the sea-ice on which they pup is reducing in extent each year (Jussi et al. 2008). This may cause a change in pupping locations and/or reduced breeding success.

Appendix B. Grey seals and the Farne Islands, UK

It is valuable to review the status of seals at the Farne Islands, UK, due to the apparent strong link between activities at these islands and the re-establishment of grey seals in the Wadden Sea. The Farne Islands are located on the north-west coast of England, 2-5 km off the coast of Northumberland. They have experienced a unique conservation history. Grey seals have breed on the Farne Islands for several hundred years (Coulson & Hickling 1964). In 1861, the islands became privately owned, the inner Farne Islands by Archdeacon Charles Thorp and the outer Farne Islands by Lord Armstrong, and were run as an unofficial nature reserve (Lambert 2002). Then in 1925, when an estimated 100 seals were present, the islands were sold by the Thorp family to the National Trust. However, the islands continued to be managed by a local committee that was led by the former owner, Collingwood Thorp. Thorp adamantly prevented access to the islands by both fishing bodies wishing to cull the seals and scientific bodies wishing to research them. In 1950, though, a count was conducted and recorded 900 adults plus 454 pups (Lambert 2002).

Pressure to cull grey seals in the United Kingdom increased in the 1950s and following the death in 1955 of the former owner of the Farne Islands, culling commenced there in 1963 (Figure 23). Managers of the cull, the Ministry of Agriculture, Fisheries and Food, had the aim of reducing the population to 750 breeding females. Between 1963 and 1966, 325 pups were culled annually. Later culls took 1310 seals (pups and adult females) in 1972 and 1448 in 1975 (Harwood & Prime 1978, Summers 1978). They continued for several more years at a lower level. General public sentiment was against the culls and they did not reduce the number of seal interactions with fisheries in the area (Lambert 2002).

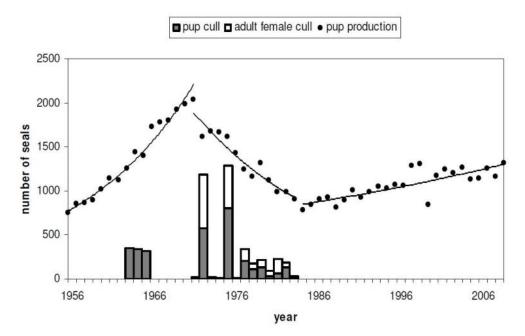


Figure 23. Pup production and number of adult females and pups killed during the population control program at the Farne Islands. Fitted lines are exponential curves – 7.4% per year between 1956 and 1971, -6.2% between 1972 and 1984 and 1.8% after 1984 (Thompson & Duck 2010).

In the 1970s at the Farne Islands, it was speculated that grey seals were trampling vegetation which might hasten erosion and threaten burrowing seabirds (Bonner & Hickling 1971). Along with culling, a policy developed to frequently disturb breeding seals and encourage them to move elsewhere. This

'moving-on' of the seals potentially contributed to the establishment of breeding colonies elsewhere in the UK, including 80 km to the north at the Isle of May, in the Firth of Forth, Scotland (Harwood 1978).

By 1983, the number of breeding females at the Farne Islands had dropped to the designated target of around 750: culling ceased. Since then, the number of pups born has gradually increased, but at a slower rate than elsewhere in the UK (Thompson & Duck 2010). The disturbance program potentially retarded growth at this site.

The disturbance program at the Farne Islands which has been linked to the establishment of other colonies may also have stimulated the relocation of some grey seals to the Wadden Sea. Establishment and rapid growth of grey seal breeding in the Netherlands coincided with the disturbance program at the Farne Islands. Furthermore, over the years, a number of tagged, branded and paint-marked seals from the Farne Islands have been re-sighted in the Netherlands, providing a strong link between the two breeding areas.

Appendix C. Potential for antagonism between seal species?

The ranges of grey seals and harbour seals overlap considerably. In fact the entire range of grey seals is contained within the range of harbour seals, which spread further north than grey seals. There is some overlap in the habitats utilised on land and in water, and in diet of the two seals (Thompson et al. 1996). Since species with overlapping requirements for habitat and food must, by definition, compete with each other, especially when resources are in short supply (Gause 1934, Tilman 1982), some level of competition is likely to exist between grey and harbour seals. Over time, though, species that have coevolved under pressure of competition, diverge from each other so that each occupies a different niche within a habitat (May 1974, Schoener 1974).

In water, the greatest potential for competition between grey and harbour seals is with prey (Thompson et al. 1996). One separating factor could be that there is a marked distinction between the seals' body size - grey seals are larger - and size is an important habitat-defining characteristic that influences prey availability (fast swimming, too manoeuvrable, benthic/ cryptic, too deeper, too big or too small etc.) and amounts of prey required. In seals, the larger the size, the more food required, and also the longer individuals can fast and the longer they can breath-hold, so the deeper they can forage (Kooyman et al. 1981, Mori 2002). Large size imparts additional qualities that influence diet, such as higher speed and larger gape, but reduced manoeuvrability – adding to dietary niche separation. Nonetheless, there is some overlap in size. For instance, juvenile and young female grey seals are equivalent in size to adult male and female harbour seals. If foraging in the same habitat, there is the chance for overlap in available prey and thus for competition. In the Wadden Sea and adjacent North Sea waters, there are insufficient data on habitat specialisation and dietary overlap between distinct age/size classes of grey and harbour seals to elucidate local levels of dietary competition.

On land, the greatest potential for competition is with breeding space. Body size influences dominance in grey seals, with larger individuals outcompeting smaller individuals for optimal breeding positions (Anderson & Fedak 1985). If breeding together, larger grey seals may be expected to outcompete smaller harbour seals for optimal land habitats. However, grey and harbour seals breed at different times of year and have different habitat requirements during pup support, which reduces the chance for such competition. Grey seals have their pups during winter in relatively dense and well-formed colonies, they select surfaces that are not usually flooded, and typically mate on land or in very shallow water. Harbour seals, on the other hand, have their pups during summer in loosely spaced colonies (such as along the edge of tidal channels), they select habitats that are submerged by high tides and mate in the water (Boness & James 1979, Boness et al. 2006). Harbour seal pups can swim at birth whereas grey seal pups cannot swim without maternal support until they are about 10 days old.

During the grey seal breeding period, because of aggressive, territorial and mating behaviours of grey seals, there is the potential for harbour seals to be excluded from preferred haul-out locations. Grey seal females aggressively exclude other seals from their vicinity during pupping (Boness et al. 1982), and perhaps of greater effect could be that subordinate grey seal males can be unselective when seeking partners (Boness et al. 1995) and may seek to mate with resting harbour seals (Wilson 1975). An instance of a young (~6 year old) male grey seal playing with and killing harbour seals has also recently been recorded on the island of Helgoland, Germany (van Neer et al. 2014). These behaviours could force harbour seals to shift to alternative haul-outs away from grey seals, leading to range shifts.

On land throughout the year, there is also the potential for competition for space. Grey seals tend to be more gregarious, lying closer to one another, whereas harbour seals are more spaced apart when resting ashore. The gregarious behaviour of grey seals might intimidate some harbour seal, causing them to haul-out in areas adjacent to the grey seals rather than mixed within them. Such separation is unlikely to

lead to exclusion from an area, however, because harbour seals tolerate more ephemeral rest sites, that are going to flood with rising tides, than grey seals, which prefer rest sites that remain dry at most high tides.

Surprisingly little is known about the potential for competition between these two seals. At Sable Island during the past 20 years, increasing grey seal numbers coincided with reducing harbour seal numbers, but the two trends had a range of potentially separate causes (Bowen et al. 2003a, Bowen et al. 2003b). Similarly in the northern UK there have been increases in grey seal numbers and declines in harbour seals, but alternative reasons than competition could explain the apparent negative correlation (Lonergan et al. 2007, Bolt et al. 2009). The potential dynamics of harbour and Baltic grey seal populations in the Kattegat-Skagerrak region of Sweden were modelled and results suggested harbour seals were resilient to regulation by the grey seals unless harbour seal populations were dramatically reduced, such as by viral epidemics (Svensson 2012).

At present, it is not possible to predict if the growing numbers of grey seals in the Wadden Sea could have an impact on the numbers of harbour seals present. This may become evident through future monitoring.