HARBOUR SEALS AND HUMAN INTERACTIONS IN DANISH WATERS

PhD thesis

Signe May Andersen

2011

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DEPARTMENT OF BIOSCIENCE

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Data sheet

Title: Harbour seals and human interactions in Danish waters
Subtitle: PhD thesis

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Publisher: Aarhus University - Denmark
URL: http://www.dmu.au.dk

Year of publication: 2011
Editing completed: 9 September 2011

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Please cite as: Andersen, S.M. 2011. Harbour seals and human interactions in Danish waters. PhD thesis. Institute of Biology, University of Southern Denmark and Department of Bioscience, Aarhus University, Denmark. 130 pp.

Abstract: Since the protection of the Danish harbour seals in 1977 several seal reserves have been established, and the Danish harbour seal population has increased from around 2000 to approximately 16000 individuals. At the same time human activity in the marine environment has increased, both in terms of commercial and recreational use, and calls for a thorough evaluation of current management and its data basis is needed. Specifically, in order to manage the Danish harbour seals properly more detailed information on the current abundance and reproduction, as well as detailed information on harbour seal movements, and the importance of the interactions between harbour seals and human activities, such as fisheries and disturbance activities is needed.

The six papers included in the present PhD thesis starts out by providing an overview of the status of the Danish harbour seal populations (**Paper I**), where after examinations of management-related issues are addressed: the harbour seal – cormorant – fishery interactions in Limfjord (**Paper II**), the effects of constructional activity from an offshore wind farm on harbour seal haul-out numbers in the Rødsand seal reserve (**Paper III**), the effectiveness of current regulations in the Anholt seal reserve to protect harbour seals from disturbances (**Paper IV** and **V**), and the seasonal movements of harbour seal in Kattegat (**Paper VI**).

Based on the findings in the PhD, several suggestions to improve the current management of the Danish harbour seals are given.

Keywords: Anthropogenic disturbance; conservation; dietary overlap; harbour seal; harbour seal – cormorant – fishery interactions; Phoca vitulina; seal reserve; status; telemetry; wildlife-management

Layout: Tinna Christensen
Drawings: Signe May Andersen
Cover photo: Niels Martin Schmidt

ISBN: 978-87-92825-05-6

Number of pages: 130

Printed by: Rosendahls – Schultz Grafisk a/s

Circulation: 100

Supplementary notes: The thesis will be defended in public at The University of Southern Denmark, Odense, on 27 October 2011.

Content

PREFACE

This thesis has been submitted to the University of Southern Denmark, Odense, Denmark, in partial fulfilment of the requirements for the degree of *Philosophidae Doctor* (PhD).

The work has concentrated on harbour seals and their interaction with humans, in terms of fishery, recreational and constructional activity. The PhD project was motivated by the ongoing conflict of interest between human activities (commercial and recreational) and the interest of protection, and aims at contributing with information to management of the Danish seal reserves.

This PhD thesis consists of four introductory chapters and six scientific papers. The six papers included represent the results of the scientific work conducted during my PhD study. As this work relates directly to the Danish management of seals, the first introductory chapters introduce the current management of seals in Denmark (chapter I), the movements of harbour seals in Danish waters (chapter II), the interaction between harbour seals and humans (chapter III), while chapter IV summarises the conclusions from the previous chapters and puts them into the context of Danish management of seals.

During my PhD study I was enrolled in the PhD School *Sense organs, Nerve systems, Behaviour, and Communication* (SNAK). My PhD was conducted with financial support from SNAK, the Dean of the Faculty of Science, University of Southern Denmark, and the Department of Bioscience, Aarhus University. Additional financial support was kindly granted by the Aage V. Jensen Charity Foundation, the Danish Outdoor Council, the Danish Nature Agency, Gorenje and Knud Højgaards Fond.

ACKNOWLEDGEMENTS

I would like to thank my two supervisors, Lee A. Miller, University of Southern Denmark and Jonas Teilmann, Department of Bioscience, Aarhus University, for their help and support during my PhD study. Many thanks also to the co-authors of the included manuscripts for letting me use our joint papers in this thesis. I am very thankful to the former director of research Dr. Jesper Madsen who gave me the opportunity to work on this PhD-project, and put me on this track in the very beginning.

I would like to thank the staff at Greenland Institute of Natural Resources, Nuuk, Greenland, for making my stay there very exciting, especially thanks to Nannette, Philip and Aqqalu.

The following people have all been extremely helpful in connection with my PhD project and I thank them all: Morten Abildstrøm and Lotte Wissum for their invaluable help during my fieldwork and for their hospitality, Annette Bombosch, Theis Taarnby Nygaard, my colleagues at the Department of Bioscience, and the personnel from the Danish Maritime Safety Administration for their assistance in the field. Bernhard Fabricius and Kjeld Moser helped with the camera system, but without the help from Jan Nielsen during the many times the camera system posed problems, this setup would have been impossible. Bendt Nielsen has been very hospitable and I am thankful to him for letting me and my field assistants use the light house for observation and the gas house for staying at times when it was not possible to stay at the Fyrgården. I am grateful to Aréns for giving me the opportunity to stay at Fyrgården, a fantastic place to stay and a perfect place to match fieldwork with family.

And thanks to Erik Buchwald and Henrik Lykke Sørensen, Danish Nature Agency, for clarifying the Habitats Directive and the legislation regarding the Danish seal reserves.

I would also like to thank my other colleagues at the late Department of Arctic Environment (though you haven't seen much of me lately), especially my fellow PhD student Susi Edrén for company during the years, and Mikkel Tamstorf and Signe Sveegaard for patiently assisting me with GIS.

I am very grateful to Niels Martin Schmidt, Asbjørn, Kalle and Vilma, and the rest of my family, for their continuous support and assistance during my study. I am especially thankful to Asbjørn, Kalle and Vilma for your patience during the last couple of months, and for your company during the many trips to Anholt. Thank you for not accepting this PhD as equal to you, and for showing me the level of understanding appropriate for your age: Kalle and Vilma, now the ADHD and Åh-D, is over. And again, as it cannot be said to often, I am forever indebted to Niels for guiding me through this project.

DANSK RESUMÉ

Siden fredningen af spættet sæl i Danmark i 1977 er flere sælreservater blevet etableret. I de mellemliggende ca. 30 år er antallet af spættede sæler steget fra ca. 2.000 til omkring 16.000 individer i 2010. Sideløbende med denne populationstilvækst er der sket en stigning i den menneskelige udnyttelse af det marine miljø, både erhvervsmæssigt og rekreativt. Der må derfor forventes en tilsvarende stigning i antallet af interaktioner mellem spættede sæler og mennesker, hvilket medfører et behov for en grundig evaluering af den nuværende forvaltning og dens datagrundlag. En ordentlig forvaltning af den spættede sæl kræver, foruden detaljerede oplysninger om den aktuelle populationsstørrelse og -tilvækst, også detaljerede oplysninger om spættede sælers bevægelsesmønstre, og betydningen af samspillet mellem spættede sæler og menneskelige aktiviteter, såsom fiskeri og forstyrrelsesaktiviteter.

De seks artikler inkluderet i denne ph.d.-afhandling giver indledningsvis et statusoverblik for spættede sæler i Danmark (**Paper I**), hvorefter undersøgelser af forvaltnings-relaterede spørgsmål behandles: interaktioner mellem spættet sæl, skarv og fiskeri i Limfjorden (**Paper II**), konstruktionen af en havbaseret vindmølleparks effekt på antallet af spættede sæler i Rødsand sælreservat (**Paper III**), effektiviteten af Anholt sælreservat til beskyttelse af spættede sæler imod forstyrrelser (**Paper IV** og **V**), og den sæsonmæssige variation i spættede sælers bevægelsesmønstre i Kattegat (**Paper VI**).

Af de få fiskearter som spættet sæl og fiskeriet konkurrerer om i Limfjorden, tager den spættede sæl kun sild større end mindstemålet. Den direkte konkurrence mellem spættede sæler og fiskeriet er derfor ikke fremherskende i Limfjorden. Derimod er den direkte konkurrence mellem spættede sæler og skarver udtalt, undtagen om foråret hvor den spættede sæl hovedsageligt lever af sild. Større menneskeskabte konstruktioner, som havvindmølleparken ved Rødsand, synes ikke at have nogle længerevarende effekter på antallet af spættede sæler i Rødsand sælreservat, dog kan der i konstruktionsfasen forekomme en midlertidig fortrængning af de mest sensitive sæler til andre hvilepladser i yngletiden. Derimod reagerer spættede sæler kraftigt på forstyrrelser fra gående personer og fra både ved deres hvileplads i sælreservatet på Anholt. Reaktionen varierer med forstyrrelsestype og årstid. Spættede sæler udviser en stor tolerance overfor forstyrrelser i ynglesæsonen, en lignende tolerance ses dog hverken før eller efter yngleperioden, og er derfor ikke udtryk for en egentlig habituering.

Baseret på disse resultater gives en række forslag til forbedring af den nuværende forvaltning af spættede sæler i danske farvande.

SUMMARY

Since the protection of harbour seals in Denmark in 1977 several seal reserves have been established. In the intervening 30 years the Danish harbour seal population has increased from around 2000 to approximately 16000 individuals in 2010. Paralleling this population increase is an increase in human activity in the marine environment, both in terms of commercial and recreational use. Hence, the potential rise in number of interactions between harbour seals and humans demands a thorough evaluation of current management and its data basis. Specifically, in order to manage the Danish harbour seals properly more detailed information on the current abundance and reproduction, as well as detailed information on harbour seal movements, and the importance of the interactions between harbour seals and human activities, such as fisheries and disturbance activities is needed.

The six papers included in the present PhD thesis starts out by providing an overview of the status of the Danish harbour seal populations (**Paper I**), where after examinations of management-related issues are addressed: the harbour seal - cormorant - fishery interactions in Limfjord (**Paper II**), the effects of constructional activity from an offshore wind farm on harbour seal haul-out numbers in the Rødsand seal reserve (**Paper III**), the effectiveness of current regulations in the Anholt seal reserve to protect harbour seals from disturbances (**Paper IV** and **V**), and the seasonal movements of harbour seal in Kattegat (**Paper VI**).

Of the few fish species overlapping between harbour seal diet and the fishery in Limfjord, only Atlantic herring was taken by harbour seals in sizes larger than the minimum sizes of the fishery. Hence, direct competition between harbour seals and the fishery did not prevail. Harbour seals however, competed strongly with cormorants, except during spring when harbour seals switched to Atlantic herring. Constructional activities in the Rødsand area apparently had no negatively impact on harbour seal haul-out numbers, though a temporary displacement was observed during the breeding season. Conversely, harbour seals exhibited a strong response towards disturbances by pedestrians and boats at their haul-out site in the Anholt seal reserve. The response varied with disturber type and season, and harbour seals exhibited a high tolerance towards disturbing activities during the breeding season. This tolerance did, however, not exist before or after the breeding period, and therefore do not imply habituation.

Based on these findings, several suggestions to improve the current management of the Danish harbour seals are given.

LIST OF PAPERS INCLUDED

This thesis is based on the following six papers, which will be referred to in the introductory chapters by their roman numerals.

- **Paper I**. Olsen, M.T., Andersen, S.M., Teilmann, J., Dietz, R., Edrén, S.M.C., Linnet, A. and Härkönen, T. 2010. Status of the harbour seal (*Phoca vitulina*) in southern Scandinavia. NAMMCO Sci. Publ. 8:77-94.

- **Paper II**. Andersen, S.M., Teilmann, J., Harders, P.B., Hansen, E.H. and Hjøllund, D. 2007. Diet of harbour seals and great cormorants in Limfjord, Denmark: interspecific competition and interaction with fishery. ICES J. Mar. Sci. 64:1235-1245.

- **Paper III**. Edrén, S.M.C., Andersen, S.M., Teilmann, J., Carstensen, J., Harders, P.B., Dietz, R. and Miller, L.A. 2010. The effect of a large Danish offshore wind farm on harbor and gray seal haul-out behavior. Mar. Mammal. Sci. 26:614-634.

- **Paper IV**. Andersen, S.M., Teilmann, J., Dietz, R., Schmidt, N.M. and Miller, L.A. Behavioural responses of harbour seals to human-induced disturbances (resubmitted to Aquatic Conservation: Marine and Freshwater Ecosystems).

- **Paper V**. Andersen, S.M., Teilmann, J., Dietz, R., Schmidt, N.M. and Miller, L.A. Disturbance-induced responses of individual harbour seals (manuscript).

- **Paper VI**. Dietz, R., Teilmann, J., Andersen, S.M., Rigét, F. and Olsen, M.T. Movement patterns of harbour seals (*Phoca vitulina*) in Kattegat (manuscript).

1 Current status and conservation of harbour seals in danish waters

1.1 Protection of harbour seals

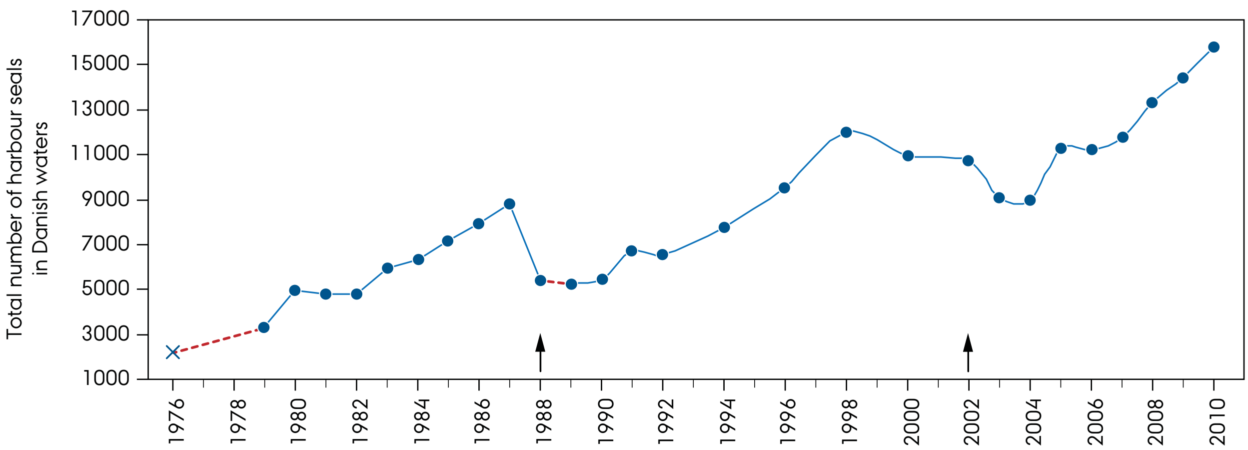
The protection of harbour seals (*Phoca vitulina*) in the 1970s in Denmark and Sweden represent a major shift in the population trajectory of the harbour seal populations in Southern Scandinavia. Prior to the protection the harbour seal populations in Scandinavian waters were constantly suppressed by hunting. The harbour seal has been hunted as a resource for skin and blubber and was since the early decades of the 20th century considered a pest, subjected to coordinated extermination campaigns in all of Scandinavia. These campaigns, which included a bounty system introduced in Denmark and Sweden in 1889 and 1902, respectively, almost succeeded in exterminating the harbour seal in Danish and Swedish waters, and by the 1920s the Danish harbour seal population was deprived to a number as low as approximately 2200 animals (Søndergaard *et al.*, 1976) (see **Paper I**). Concurrently, the grey seal was even closer to extinction in Danish waters, and ceased to breed there. The Danish bounty system was abolished in 1927 and the Swedish in 1965, and by 1977 and 1967 hunting bans were implemented and the harbour seal became totally protected in Denmark and Sweden, respectively. Except for two outbreaks of Phocine Distemper Virus (PDV) in 1988 and 2002 (Härkönen *et al.*, 2006), the Danish harbour seal population has increased since the protection, to the estimated number of 15800 animals in 2010 (Figure 1) (**Paper I**).

Following the protection of harbour seals and grey seals, the 11 most important seal localities in Danish waters were subjected to regulations to ensure safe haul-out sites to the seals primarily during breeding, nursing and moult. The reserves cover the haul-out sites themselves (reef, sandbank or island) and the majority of the reserves also include a sea-territory. Six of the reserves were established as actual seal reserves (Anholt, Ejerslev Røn, Livø, Møllegrunden and Rødsand), while the rest (Hesselø, Saltholm, Bosserne and three Wadden Sea areas: Lammelæger, Kore Sand and Langli Sand) were established as Nature and wildlife reserves (Jepsen, 2005; Danish Nature Agency, 2009) (See Figure 2).

1.1.1 The Habitats Directive and its implication for Danish harbour seals

In 1992 the European member states adopted the Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora, known as the Habitats Directive EC (European Commission, 1992). Harbour seals are covered by annex II of the Habitats Directive, which implies that all EU member states are

Figure 1. The estimated total number of harbour seals in Danish waters obtained from aerial surveys. During the period 1979–1989 surveys were only conducted in Kattegat and the Wadden Sea, and total numbers are therefore extrapolated from these. Total number in 1976 is based on estimations. Arrows indicate the two PDV outbreaks.



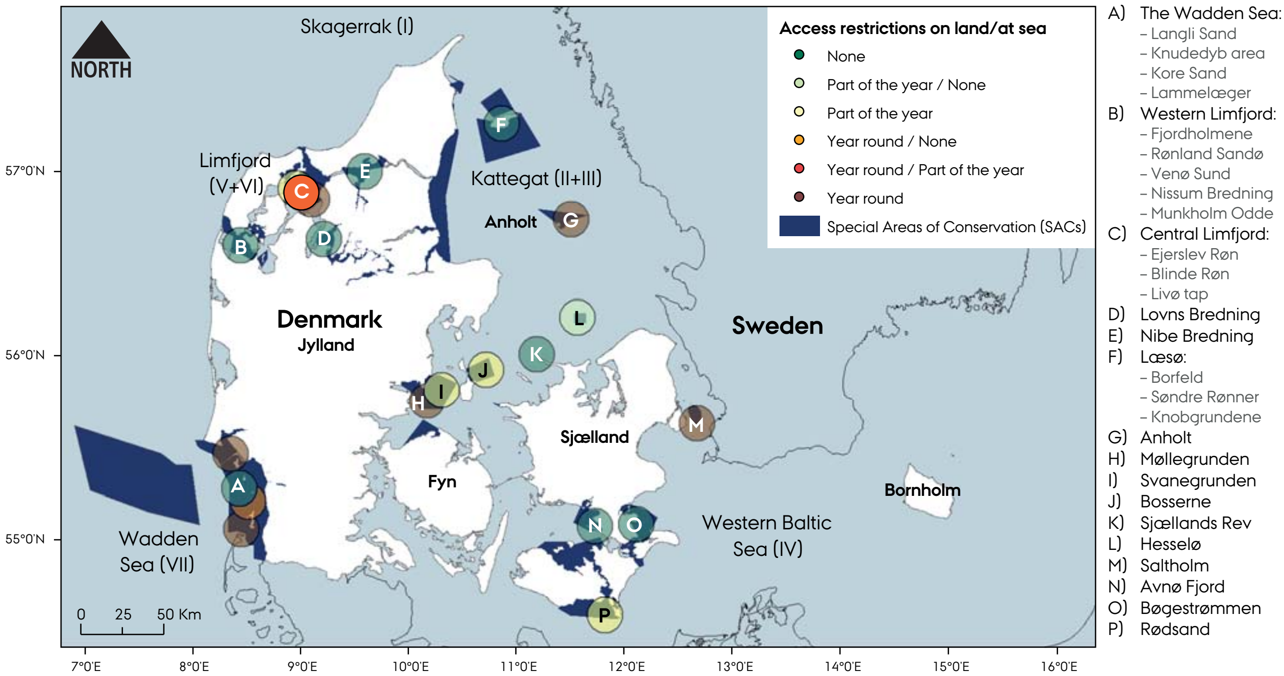


Figure 2. Current restrictions of the Danish harbour seal haul-out sites in Danish waters. The colours of the circles indicate the access restrictions at the individual haul-out sites and are explained in the insert and the letters refer to the place names given to the right (Jepsen, 2005; Danish Nature Agency, 2009). The blue areas show the 22 Danish SACs with harbour seal on the designation list (Danish Nature Agency, 2010a). Roman numbers refer to management areas.

obliged to designate special areas of conservation (SACs) and to implement a monitoring programme to maintain a favourable conservation status for the species, in terms of viability, population size, structure and distribution. As part of the coherent European ecological network NATURA 2000 Denmark has at the present time designated a total of 261 areas under the EEC Habitats Directive (=Special areas of conservation (SACs)) and 113 areas listed under the EEC Birds Directive, which together with 27 areas designated under the Ramsar Convention, are called International Protection Areas (Pihl *et al.*, 2001; Søgaard *et al.*, 2006; Danish Nature Agency, 2010b). Harbour seals exist on the designation list for 22 of the 261 Danish SACs (Danish Nature Agency, 2010a) (Figure 2). Harbour seals are furthermore covered by annex V of the Habitats Directive, which includes species that, if they are hunted or exploited, require management. Furthermore, Denmark has acceded several other conventions which help to ensure the best possible management of harbour seals in Danish and adjacent waters (see **Paper I**).

Despite that the harbour seal is on the designation list for 22 SACs in Denmark (Figure 2), and that all important haul-out places, but one (Sjællands Rev), used by harbour seals in Danish waters are included in a SAC, these areas do not share the same level of protection. Hence, the protection varies from year-round traffic prohibition on land and in the surrounding sea-territory (e.g. Anholt) to no restrictions at all (e.g. Læsø) (Figure 3). Common for all the areas is that the fishery is exempted all restrictions at all times (Danish Nature Agency, 2009).

1.2 Assessment of the conservation status of harbour seals in Denmark

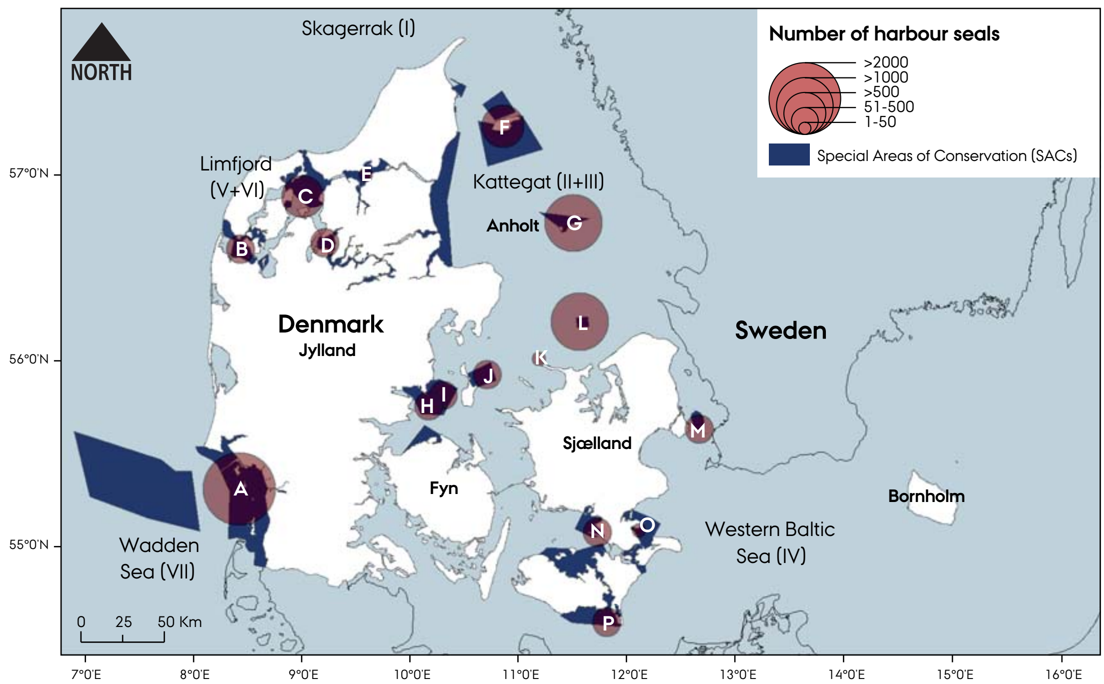
The protection of the harbour seal and the listing of it in connection with the designation of the SACs provide its statutory protection, but also mandate a systematic and continuously monitoring of the populations. Currently the abundance of harbour seals in Denmark is monitored by means of annual aerial surveys and the growth rate. The development of the populations is assessed from the information obtained from these surveys (see 1.2.1).

1.2.1 Harbour seal population sizes in Danish waters

Following the protection, aerial surveys were initiated in the Wadden Sea and Kattegat. Since 1989 three surveys have been conducted each or every second year during the moulting period on all known haul-out sites in Denmark to gather information on the population size and haul-out use patterns, details that are decisive for the conservation and managing of harbour seals. The availability of this time series has enabled the assessment of long-term changes in the abundance and distribution of harbour seals in Denmark. From the protection in 1977 until the outbreak of the first PDV epidemic in 1988 the population increased by approximately 12% per year. During the 1988 PDV outbreak, the Danish population was approximately halved. Hereafter the population resumed increasing by averagely 10% per year, until the recurrence of PDV in 2002, which again almost halved the Danish population of harbour seals (Härkönen *et al.*, 2006; Teilmann *et al.*, 2010). The latest counting in 2010 revealed a Danish harbour seal population close to 15800 animals (Department of Bioscience, Aarhus University, unpublished data) (Figure 1).

1.2.2 Distribution of harbour seals

The harbour seal is the most widespread of all pinnipeds, with an area of distribution ranging from approximately 30°N–80°N, covering temperate, sub-arctic and arctic waters of the North Atlantic and North Pacific oceans (Perrin *et al.*, 2007). In Denmark harbour seals can be found in all waters, but are only rarely observed in the waters around Bornholm and Fyn. Based on aerial countings, the highest numbers of harbour seals are found on Hesselø and Anholt in Kattegat and at Knudedyb in the Wadden Sea (Figure 3).



A) The Wadden Sea:
- Langli Sand
- Knudedyb area
- Kore Sand
- Lammelæger

B) Western Limfjord:
- Fjordholmene
- Rønland Sandø
- Venø Sund
- Nissum Bredning
- Munkholm Odde

C) Central Limfjord:
- Ejerslev Røn
- Blinde Røn
- Livø tap

D) Lovns Bredning
E) Nibe Bredning
F) Læsø:
- Borfeld
- Søndre Rønner
- Knobgrundene

G) Anholt
H) Møllegrunden
I) Svanegrunden
J) Bosserne
K) Sjællands Rev
L) Hesselø
M) Saltholm
N) Avnø Fjord
O) Bøgestrømmen
P) Rødsand

Figure 3. Harbour seal haul-out sites and protected areas in Danish waters. The sizes of the circles refer to the number of harbour seals ashore during aerial surveys in late august 2010. As a fraction of the population (43%) will be at sea during survey, counted numbers are corrected with a factor of 1.75 to achieve total numbers (Härkönen and Harding, 2001). Letters refer to the place names given to the right (Jepsen, 2005; Danish Nature Agency, 2009). Roman numbers refer to management areas. The blue areas show the 22 Danish SACs with harbour seal on the designation list (Danish Nature Agency, 2010a). Modified from Paper I.

Traditionally the Danish waters have been divided into the following areas for the management of the seals: Skagerrak, Northern Kattegat, South-Western Kattegat, the Western Baltic Sea, central Limfjord, Western Limfjord and the Wadden Sea (see **Paper I**). Due to their genetic similarity, harbour seals in Kattegat N and Kattegat SV are managed together, but also Western Limfjord appear genetically to be a mix of the Wadden Sea and central Limfjord (Olsen *et al.* in prep.) (Figure 3).

1.2.3 The current conservation status is favourable

The official conservation status of the Danish harbour seal population is considered favourable, primarily due to the positive trend in total occurrence (Figure 1) and the apparently stable habitat conditions (Figure 3) (Pihl *et al.*, 2001). However, though the annual aerial surveys yield information about the general development in the harbour seal population, the increasing numbers of harbour seals observed on the haul-out sites is merely a yearly snapshot of the population. More detailed information on various aspects of harbour seal ecology, and how this varies temporally and spatially, is essential to support the information obtained from aerial surveys.

Whilst the positive population trajectory of the Danish harbour seal populations may make such detailed examinations irrelevant, it is important to keep in mind that, besides the legal obligations to secure undisturbed habitats (European Commission, 1992), management plans have to be prepared for future changes, such as another severe epidemic outbreak, additional human exploitation of the marine area, or climate changes, that might affect the current favourable status negatively. For instance, the very success of the Danish population may bring it closer to another outbreak of PDV, which is expected to occur with regular intervals at a certain population density (Härkönen *et al.*, 2006; Härkönen and Harding, 2010). Also, future climate changes may impact the seals in several ways, and for instance sea level rise may affect the number of suitable haul-out sites. Additionally, climate changes may affect fish distribution, thereby potentially affecting the inter-specific interactions between harbour seals and cormorants, but also humans (**Paper II**). This may further intensify the conflict between seals and the fishery and may generate an increase in the demands for licences to protective hunting and hunting as such (see 3.1). Finally, since the establishment of the reserves the human activities in the marine environment have increased substantially, both in terms of traffic at sea, offshore constructions and fisheries etc. In addition to such activities, nature-based tourism is escalating (see 3.2), and it is therefore of great importance to evaluate the effectiveness of the current regulations to provide adequate protection in the protected areas.

The following two chapters will first address harbour seal area-use on an annual basis (see 2), and secondly address some of the most common interactions between harbour seals and humans, namely in connection with the fishery (see 3.1), and in connection with harbour seal haul-out (see 3.2).

2 Harbour seal movement behaviour in Danish waters

Harbour seals are semi-aquatic mammals, foraging in the marine environment, while at the same time having an obligate requirement to haul-out on land, for instance during rest (Da Silva and Terhune, 1988), to escape aquatic predators (Terhune, 1985; Da Silva and Terhune, 1988), to moult (Reder *et al.*, 2003) and to give birth and rear their pups (Bigg, 1981; Thompson, 1989). The environmental conditions of the haul-out site are important, and harbour seals generally prefer isolated haul-out sites that minimize threats from terrestrial disturbers. Furthermore they prefer access to deep water, to permit an easy escape, a gentle slope and a plane surface and protection from wave action (Henry and Hammill, 2001).

Due to the difficulties of observing seals at sea, the methods of telemetry provide a powerful technique for tracking the movements of seals (Block *et al.*, 2011), and these methods constitute a central part in this PhD study, allowing for a detailed assessment of individual movement and space use patterns, and thus estimation of harbour seal space use in general. Using satellite and VHF telemetry we gathered data on harbour seal movements during the entire annual cycle from the Anholt seal reserve, to investigate the pattern and timing of sex and age specific movements in relation to different stages of the annual cycle (**Paper V** and **VI**).

On a yearly basis the harbour seals tagged on Anholt move over large areas, and make use of all available haul-out sites in Northern Kattegat, but exhibit a very strong site fidelity to Anholt during the pre-breeding, breeding and moult periods. Corresponding with this the size of home range and distances moved in Kattegat peaked in winter and decreased as the breeding period approached (**Paper V** and **VI**). Hence, our findings revealed harbour seal movement patterns in Kattegat to be similar to harbour seal movements in other areas (Thompson, 1989; Härkönen and Harding, 2001; Small *et al.*, 2005). Besides this seasonal change in haul-out site utilisation, harbour seals also show a seasonal pattern in their tendency to haul-out (frequency and haul-out duration) reflected in the seasonal changes in the demands of breeding and moult. During the most intense haul-out periods (breeding and moulting), they may, in many areas, come in close contact with humans, and hence, become more exposed to disturbances on land (**Paper IV** and **V**).

3 Interactions between harbour seals and humans

Given the increasing human utilisation of the marine environment, in terms of commercial (transport, marine constructions, and fisheries) (**Paper II** and **III**) and recreational use (**Paper IV** and **V**), an increase in interactions between seals and humans and a consequential possibility of significant unfavourable effects on the harbour seal habitats can be expected. Hence, a more thorough assessment of the current regulations concerning the Danish harbour seals is needed, including the assessment of the effects of interactions between seals and humans.

3.1 Harbour seals as competitors for fish

Harbour seals are relatively resident (Thompson *et al.*, 1998; Tollit *et al.*, 1998; Suryan and Harvey, 1998) and are therefore prone to interact with the local fisheries by foraging on fish in fishing gears and to compete for the same resources. To determine the correct management actions for harbour seals it is essential to document their diet and potential overlap with other species and the fishery.

In order to examine the competition between harbour seals and the fishery we conducted a dietary analysis of harbour seals in Limfjord, Denmark. Cormorants were included in the analysis, as harbour seals and cormorants potentially compete for the same food resources due to overlap in habitat use and that both forage on the seabed (Härkönen, 1988). We found harbour seal and cormorant diet to overlap substantially, but only in terms of prey species during summer and autumn, whereas they have different preferences for prey sizes. The competition between the two species is insignificant during spring, when the harbour seal switch to feeding almost exclusively on schooling Atlantic herring (**Paper II**). This opportunistic nature of the harbour seal is known in other parts of its range (e.g. Pierce *et al.*, 1991; Tollit and Thompson, 1996; Hall *et al.*, 1998).

In Limfjord the only direct competition is between the fishery and harbour seals for Atlantic herring, of which the fishery takes a significant larger share (**Paper II**). The other edible fish species consumed by harbour seals and cormorants (plaice, flounder, sprat and herring) is taken in sizes smaller than the allowed minimum sizes in the fishery, and this predation may remove only the “doomed surplus” (Friis *et al.*, 1994; Krebs, 2008). Apparently, the competition between harbour seals and cormorants in Limfjord is much more pronounced (**Paper II**). Both species are regarded as pests by the fishery (Engström, 2001), and ironically the competition between them may be an advance for the fishery. However, the interaction between harbour seals and the fishery includes other aspects.

There is an ongoing conflict between harbour seals and the fishery in Danish and adjacent waters, because harbour seals compete for the same resources and frequently destroy fishing gear in their search for food (Lunneryd, 2001; Königson *et al.*, 2006). This tension has intensified during the late 20th century owing to the growth of the harbour seal population and declining fish stocks (Hoffmann *et al.*, 2003). In certain areas in Denmark, fishermen are therefore allowed to regulate seals close to static fishing gear (Retsinformation.dk, 2011). Culling may be an efficient tool for mitigating such damages if targeted towards specialised individuals, as oppose to taking random measures against the whole population (Königson *et al.*, 2006); this however, is still debated (Boyd, 2001; Middlemas *et al.*, 2006; Butler *et al.*, 2008). The management of the seal-fishery interactions has been further complicated by the implementation of the Habitats Directive (European Commission, 1992), as the culling of seals to protect fisheries impinges upon the objectives of the Article 6.2 by killing and disturbing seals. Actually, on the basis of the Habitats Directive, the fishery in Scotland was denied permission to seal cull (Butler *et al.*, 2011). Hence, to balance the conflicting interests whilst fulfilling the conservation commitments, more effort should be put into the development of seal-safe fishing gear (see Westerberg *et al.*, 2008). Furthermore, a similar inconsistency with the Habitats Directive is the unrestricted access of fishing boats into the Danish seal reserves year-round, activities that are known to disturb harbour seals markedly (**Paper IV** and **V**).

3.2 Harbour seals and disturbing activities

In Denmark several seal reserves were established following the enforcement of the protection of harbour seals in 1977. The effectiveness of the reserves to protect the seals from human-induced disturbances, however, has not yet been evaluated, and the potential disturbance impacts have, hence, not yet been adequately addressed. The restrictions of the Danish seal reserves varies considerably (see 1.1.1), and are frequently violated, primarily during the prime months for tourism in Denmark, which coincides with the breeding period of harbour seals.

Due to the isolated location of most of the Danish harbour seal haul-out sites, the most common human disturbance is due to approaching boats, as the Danish waters are highly frequented by leisure boating during the summer. Only few areas, such as the Anholt seal reserve, are also accessible from land, and in the Anholt seal reserve the boundaries are often violated with the purpose to approach the seals. The number of trespassers seems to be escalating, especially during the prime months for tourism. Several Danish haul-out sites (e.g. Bosserne, Livø, Borfeld, and the Wadden Sea area) are visited frequently during the summer months (up to several times a day) by organised seal safaris. Moreover, the Danish waters hold a large number of bridges and offshore wind farms which may also impair the haul-out sites and cause disturbances of the seals (see **Paper III**). Within the near future an offshore wind farm is going to be built 15 km SW of Anholt and a bridge between Sjælland and Jylland, crossing SW Kattegat is under consideration.

Assessing the effects of disturbance has traditionally relied on proximate measures of short-term avoidance behaviour; and the level of these responses is often used as a measure of the relative sensitivity to disturbances; in that the strongest avoidance behaviour is often considered to imply the greatest need of protection from disturbances (Blumstein *et al.*, 2003; Taylor and Knight, 2003; Stankowich and Coss, 2007; Whitfield *et al.*, 2008). However, the observable behaviour is not always directly compatible to the internal state of the animal (Gill *et al.*, 2001; Stillman and Goss-Custard, 2002; Beale and Monaghan, 2004), and animals apparently tolerating approaches are not necessarily unaffected (Ellenberg *et al.*, 2006). As outlined by Bejder *et al.* (2009), tolerance has often been misinterpreted as habituation. Consequently, the assessment of harbour seal behavioural responses to disturbances is not straightforward and conclusions based on behavioural responses alone are therefore not always directly transferable into management.

We aimed at assessing the effects of disturbance on Danish harbour seals using two different approaches. The first approach was based on the surveillance of seals hauling out before, during, and after the construction of a large offshore wind farm near the Rødsand seal reserve (see Figure 3) (**Paper III**). The second approach was based on a series of experimentally controlled as well as un-planned disturbances occurring in the Anholt seal reserve (**Paper IV** and **V**). These three papers, hence, examine the disturbance response of harbour seals with an increasing level of detail from population (**Paper III**), to group (**Paper IV**), to individuals (**Paper V**).

The construction of the offshore wind farm app. 4 km from the Rødsand seal reserve seemingly had no long-term effects on the number of harbour seals hauled out (**Paper III**). Other studies also suggest that seals may exhibit a high degree of tolerance towards constructional activities (Moulton *et al*., 2003; Blackwell *et al*., 2004). It is however, important to notice the negative effect of the constructional activities during the breeding period observed in **Paper III**. During this period, the number of harbour seals decreased both in terms of the actual numbers, and relative to nearby haul-out sites. At the same time more pups than usually were observed at the nearest haul-out site (app. 16 km away) (**Paper III**). Given that this nearby haul-out site is frequently flooded and hence, may be regarded as a less optimal breeding site compared to Rødsand, this may indicate a temporary displacement of the less tolerant individuals (sensu Bejder *et al*., 2009), and also discussed for ringed seals by Blackwell *et al.* (2004). **Paper III**, thus, presents some general patterns in harbour seal population responses to human-induced disturbances. In the following, the results from the more detailed investigations on harbour seal – human interactions are presented.

In the Anholt reserve (see Figure 3), disturbances, such as human recreational activities, generally resulted in strong behavioural responses of the harbour seals (**Paper IV** and **V**). Across the three seasons examined, harbour seals responded to approaching boats at markedly longer distances compared to approaching pedestrians (**Paper IV**). Actually, harbour seals in most cases responded to boats when these were still well outside the reserve, whereas pedestrians did not inflict noticeable responses before having entered the reserve (**Paper IV**). Harbour seal response, however, also varied with season, and while harbour seals outside the breeding period responded to disturbances by fleeing, and not to return until the end of the day (**Paper IV** and **V**), harbour seals were reluctant to flee and returned immediately to the haul-out site during the breeding period (**Paper IV**). When comparing the characteristics of un-disturbed and post-disturbed trips during the pre-breeding period, we found that these characteristics were largely comparable, both in terms of trip extent, trip duration, area-use and return pattern (**Paper V**). Harbour seals in the Anholt reserve seemingly initiated foraging trips following a disturbance, and may, thus, be seen as exhibiting an adaptive behaviour in response to disturbances during this period (**Paper V**). In other periods, and in particular during the breeding season, this potentially adaptive behaviour is seemingly not prevalent as harbour seals here return to the haul-out site immediately after being disturbed (**Paper IV**), and instead exhibit a high degree of tolerance towards disturbances (**Paper IV**). This seasonal increase in tolerance may be attributable to the strong linkage to land during the breeding period (Thompson, 1989; Härkönen and Harding, 2001; Small *et al*., 2005). However, the remote location of the Anholt seal reserve with no alternative haul-out sites within approximately 50 km (**Paper IV**) is probably also a contributing factor, as displacement (Bejder *et al*., 2009) (see above and **Paper III**), may not be feasible. The strong site-fidelity observed during the pre-breeding and breeding periods (**Paper V** and **VI**) was replaced by an utilisation of multiple haul-out sites in other periods (**Paper VI**) (Thompson, 1989; Small *et al*., 2005).

Hence, the biological and ecological context in which disturbances occur is pivotal for the interpretation of the disturbance responses, and hence for the assessment of the effects (Stillman and Goss-Custard, 2002; Bejder *et al*., 2006; Lusseau and Bejder, 2007; Beale, 2007; Bejder *et al*., 2009). Disturbance responses may depend on parameters such as time of year (**Paper IV**), time of day (Suryan and Harvey, 1999), sex (Lusseau, 2003), as well as the cumulative effect of repeated disturbances (Bejder *et al*., 2009). Other species within the community may impact the disturbance response observed, and for instance the disturbance of birds may initiate a cascade that results in seals being disturbed, but not by the approaching disturber directly (**Paper IV**). Also, the distances between haul-out sites, may influence the response to disturbances (**Paper III**, **IV** and **V**). Last but not least, the history of the individuals or populations may be inflicting the disturbance responses observed. For instance, the observed tolerance (**Paper IV**) may be the result of a long-term process (Bejder *et al.*, 2009). The Danish seal populations are living in an anthropogenic environment, and have been interacting with humans through hunting, fisheries and recreational and constructional activities for centuries. Hence, the present distribution of harbour seals, the location of their haul-out sites, as well as their response to disturbances may still be inflicted by the "ghost of disturbance" (**Paper V**). Indeed, the haul-out sites currently in use are more or less the same as the ones used prior to the protection of harbour seals in Danish waters (see Søndergaard *et al.*, 1976), despite the 7-8 fold increase in the number of seals (Figure 1 and Figure 3) (Teilmann *et al.*, 2010).

4 Management implications

Based on results presented in this thesis and in the literature, the following suggestions to improve management regulations are proposed. These suggestions serve mainly to help harmonising current Danish seal management and the imperatives of the Habitats Directives, but also to stress important aspects of management.

4.1 Access restrictions in Danish seals reserves

- In order to provide year-round protection of harbour seals from disturbances in the Anholt seal reserve, reserve borders must on land be positioned at least 425 m from the haul-out area and the sea-territory must extent at least 850 m from the haul-out area (**Paper IV**). While these distances can be taken as a rule of thumb, examinations on the various haul-out sites are needed in order to gain site-specific knowledge.
- Protection in the Danish seal reserves must as a minimum cover harbour seal breeding and moulting periods (**Paper IV**). Additionally, as the grey seal makes tentative attempts to breed in Danish waters, and is on the designation list for nine of the Danish SACs, protection should also include grey seal breeding and moulting periods.
- The level of protection in the Danish seal reserves varies considerably. Some localities are totally unprotected (e.g. Læsø), whereas others have no restrictions for boating (e.g. Hesselø). Several seal reserves within the Danish SACs are not fulfilling the commitments as outlined by the Habitats Directive. Furthermore, the protection of the areas vary in terms of buoying, duration of protected periods, the existence of and the size of the sea-territory, and whether boating is subjected speed limitations.
- Border marking of the reserves must be clear and unified, to ascertaining that the legislation is actually respected.

4.2 Constructional work

- While the constructional work examined here apparently resulted in only short-term responses by harbour seals (**Paper III**), other types of constructions may result in different responses. General conclusions are, thus, hard to draw. However, as a minimum a proper analytic design (i.e. before-after-control-impact design) must be applied to each environmental impact assessment in order to gain the best evaluation of the constructional activity in question.

4.3 Fisheries

- Direct competition between harbour seals and the fishery is low in Limfjord (**Paper II**), and may not be widespread in Danish waters. More effort should be put into the development of seal-safe fishing gear.
- The exemptions currently given to the fishery to regulate seals, but also to enter the Danish reserves, should be revoked as they impinge upon the Habitats Directive.

Additionally, some general recommendations emerge from examinations conducted during the present PhD study. Firstly, as harbour seals in Danish waters interact with other species in their immediate environment, either through competitive interactions (**Paper II**) or through cascading disturbance responses (**Paper IV**), harbour seal management must take into account such co-inhabiting species. Secondly, as harbour seals in Kattegat during the year move between Danish and Swedish haul-out sites (**Paper VI**), stresses the importance of coordinated management efforts from both countries. Finally, it is very important that reserve regulations are regularly evaluated in order to keep up with changes in the patterns of human-induced disturbances, as well as changes in the physical parameters, such as shape and size of sandbanks and beaches on which the harbour seals haul-out (**Paper IV**), to ensure a proper level of protection for the Danish harbour seals.

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PAPER I

STATUS OF THE HARBOUR SEAL (*PHOCA VITULINA*) IN SOUTHERN SCANDINAVIA

Olsen, M.T., Andersen, S.M., Teilmann, J., Dietz, R., Edrén, S.M.C., Linnet, A. and Härkönen, T. 2010.

NAMMCO Scientific Publications 8:77-94.
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Status of the harbour seal *(Phoca vitulina)* in Southern Scandinavia

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ABSTRACT

The harbour seal population in Southern Scandinavia has experienced repeated declines caused by hunting and epizootics. These events have shaped the current distribution and abundance of the population. This paper assesses the current status of the population. We estimate trends in abundance of harbour seals from long term survey data, compare these with historic trends inferred from previously published material, and discuss past and potential threats to the harbour seal population of Southern Scandinavia. It is evident that harbour seals have disappeared from haulout areas along the Danish shores of Kattegat and in the westernmost part of the Baltic Sea, where they were previously numerous. In the 1920-30s, when abundance was at its lowest, the population is estimated to have been only a fraction of its original size. Following 30 years of protection the population is currently approaching historic abundance and might have reached the carrying capacity in some areas. Further development depends largely on effects of future epizootics, anthropogenic disturbance, and availability of suitable haulout sites.

Olsen, M.T., Andersen, S.M., Teilmann, J., Dietz, R., Edrén, S.M.C., Linnet, A., Härkönen, T. 2010. Status of the harbour seal *(Phoca vitulina)* in Southern Scandinavia. *NAMMCO Sci. Publ.* 8:77-94.

INTRODUCTION

The harbour seals *(Phoca vitulina)* in Southern Scandinavia have experienced a turbulent history. Persisting in low numbers since the end of the last glaciation, harbour seals likely became abundant in the region only a few centuries ago (Härkönen *et al.* 2005). Once established, harbour seals were subject to hunting; first due to the value of skin and blubber and later because of conflicts with the commercial fisheries (Søndergaard *et al.* 1976, Heide-Jørgensen and Härkönen 1988). The decline during the first decades of the 20th century was driven by a coordinated Scandinavian campaign, with the objective to exterminate the seals. The population was at its lowest during the 1920s. After protection measures were taken in the 1960-70s the population started to recover, but was struck by two severe epizootics in 1988 and 2002 caused by the Phocine Distemper Virus (PDV), killing approximately half the population on each occasion (Dietz *et al.* 1989a; b, Härkönen *et al.* 2006). These events have had significant impacts on the distribution and abundance of harbour seals in Southern Scandinavia.

This paper summarizes published and unpublished data to assess the current status of the Southern Scandinavian population. Specifically, we present previously published material to account for the historic trends, and apply survey data covering the past 30 years to estimate population size and recent development. We evaluate the possible risks to the harbour seal population in Southern Scandinavian waters and provide a perspective for the future development of the population.

MATERIALS AND METHODS

Study population

The harbour seal is currently the most common seal species in Southern Scandinavia. It is a coastal, relatively sedentary seal, which - although observed in most parts of the region - is mainly found around haulout sites on undisturbed coasts, reefs, and islands, where it breeds, moults, and rests (Fig. 1). Haulout habitats vary greatly among regions, ranging from rocky shores in the Skagerrak and along most of the Swedish Kattegat coast to sandbanks, stone reefs, and single large stones in the Danish Kattegat, the Limfjord, and the western Baltic Sea. The harbour seal also occurs on the rocky shores of Kalmarsund in the Baltic proper and at the sand banks in the Wadden Sea. The harbour seals in Kalmarsund carry a unique genetic signature and appear isolated from stocks in the western Baltic and Kattegat-Skagerrak (Goodman 1998). Some genetic exchange occurs between the Limfjord and the

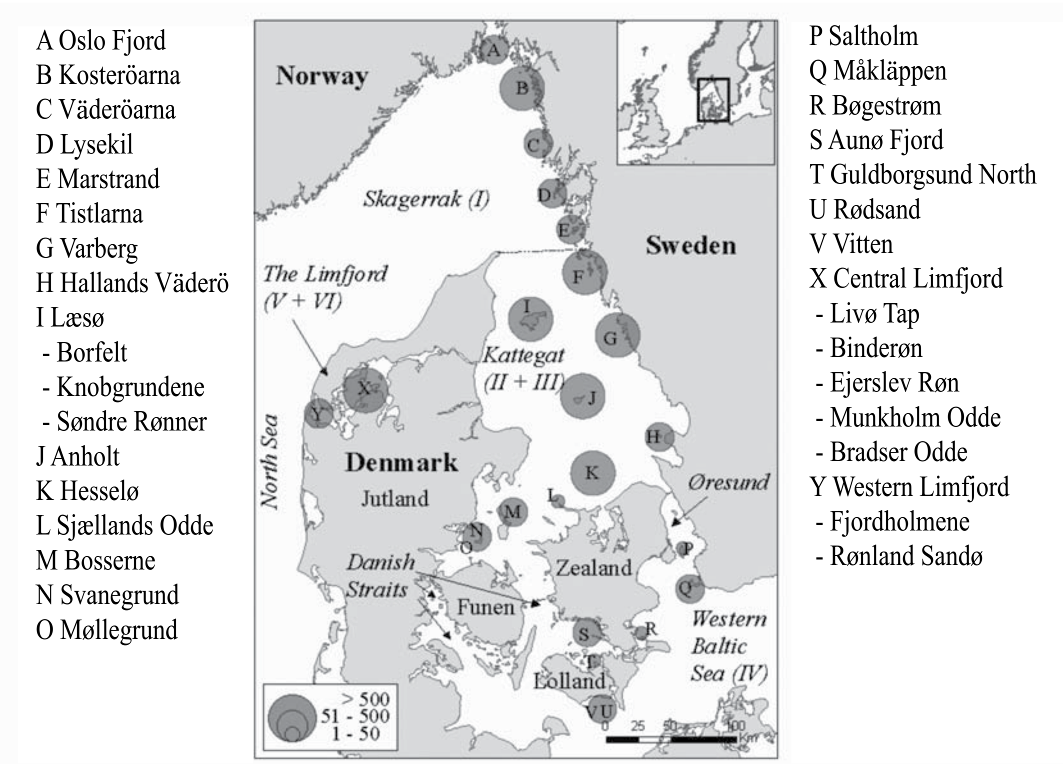

Fig. 1. *Harbour seal haul-out sites in Southern Scandinavia. Subpopulations treated in this review are Skagerrak (I), Kattegat (II and III), western Baltic (IV), and Limfjorden (V and VI). Roman numerals refer to sub-units used for management and aerial surveys.*

Wadden Sea (Olsen *et al.* in prep.), but we assume that this is not of a magnitude to affect local population trends. Both the Kalmarsund and the Wadden Sea harbour seals are discussed elsewhere in this volume and not included here.

Within the study area, harbour seals have traditionally been divided into a number of units for management and conservation purposes, including the Skagerrak, central Kattegat, southwestern Kattegat, western Baltic, the central Limfjord, and the western Limfjord (Fig. 1) (Heide-Jørgensen and Härkönen 1988, Teilmann and Heide-Jørgensen 2001). Recent genetic studies, however, documented genetic exchange between some of these units (Olsen *et al.* in prep.), suggesting the existence of 4 subpopulations within the study area: the Skagerrak, the Kattegat, the western Baltic, and the Limfjord. Although genetic studies indicate restricted historic gene flow between the central and western part of the Limfjord, there is evidence that the differentiation is in process of breaking down (Olsen *et al.* in prep.). Consequently, we treat the Limfjord as a single subpopulation.

Historic material

Information on the abundance and distribution of harbour seals in Southern Scandinavia until the 1970s was mainly obtained from reviews by Søndergaard *et al.* (1976) and Härkönen *et al.* (2005) who comprehensively gathered the information available from archaeological findings, historical scripts, and old fisheries bulletins. These reviews provide insights to the distribution of harbour seals but does not allow for estimates of abundance. The earliest detailed quantitative accounts of harbour seals stem from the hunting statistics introduced with the bounty systems in the 1890s. From 1940, information mainly originates from hunting statistics, questionnaires to hunters and fishermen issued since the 1960s, and sporadic boat or aerial based surveys initiated in the early 1960s and 1970s in Denmark and Sweden, respectively. Given the inaccessibility of much of the historic material we mainly refer to Søndergaard *et al.* (1976) and Härkönen *et al.* (2005) for references of older date.

Recent survey methods

Systematic aerial surveys were initiated in 1979 in the Skagerrak-Kattegat region to monitor the population development following the legal protection of harbour seals (Heide-Jørgensen and Härkönen 1988). In the Limfjord and the western Baltic similar surveys have been conducted since 1988. The aim was to conduct 3 surveys during the moulting season in the latter half of August each or alternate year. Survey hours were between 0900-1500 hours and under conditions standardized such that surveys were only carried out when wind speed was less than 10m/s and precipitation was absent (Heide-Jørgensen and Härkönen 1988). Timing to tidal cycle was only needed in the western Limfjord since the influence of tides is negligible in other study areas.

The seals were photographed from a single engine high-winged Cessna 172 aircraft, from an altitude of 300-500 feet (90-150 m), flying at 70-80 knots (ca 130-150 km/hr). Two observers on the same side of the aircraft took photos of haulout sites using hand held cameras equipped with 135-200 mm lenses. Afterwards the number of seals was counted on high quality photos. On the few localities where haulouts consist of single stones, seals were counted during overflight.

Statistical methods

To visualize the trend of the population index we plotted the estimated number of seals against survey year for the 4 subpopulations; Skagerrak, Kattegat, western Baltic, and the Limfjord, respectively. The number of seals in each subpopulation was estimated by applying a correction factor of 1.75, since merely 57% of the seals are estimated to haul out during surveys (Härkönen and Harding 2001). In addition to the graphic point presentation of the temporal trend of the population estimates Lowess smoother curves were applied to the 4 regions using a 25% smoothing factor. These graphics were carried out in StatView (V 5.0.1).

The average yearly growth of the subpopulations in the period before the first epizootic in 1988, between the two epizootics (1989-2001), and in the period after the second epizootic was estimated assuming an exponential growth model. Counts from both 1988 and 2002 were

Table 1. Number of seals from aerial surveys in the 4 subpopulations of Southern Scandinavia during the period 1979-2008, where Count denotes the average number of seals observed on land (for n larger than 2 the average was calculated by a trimmed mean), n is the number of surveys carried out that year, SD is the standard deviation of the counts, and Estim is the estimated number of seals in the sub-population corrected for seals in the water at the time of the survey. Note that some data in this table differs from Teilmann *et al* 2010 because of differences in data treatment. * From year 2000 it includes data from Oslo fjord.

Year	Skagerrak*				Kattegat				Western Baltic				Limfjord			
	Count	n	SD	Estim	Count	n	SD	Estim	Count	n	SD	Estim	Count	n	SD	Estim
1979	568	1	-	996	1776	1	-	3116	-	-	-	-	-	-	-	-
1980	674	1	-	1182	2096	1	-	3677	-	-	-	-	-	-	-	-
1981	709	1	-	1244	2386	1	-	4186	-	-	-	-	-	-	-	-
1982	696	1	-	1221	1491	1	-	2616	-	-	-	-	-	-	-	-
1983	1062	1	-	1863	2482	1	-	4354	-	-	-	-	-	-	-	-
1984	1127	1	-	1977	2570	2	-	4509	-	-	-	-	-	-	-	-
1985	1336	1	-	2344	3960	1	-	6947	-	-	-	-	-	-	-	-
1986	1333	1	-	2339	4458	1	-	7821	-	-	-	-	-	-	-	-
1987	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
1988	748	6	24	1312	2247	3	16	3942	96	3	4	168	345	2	6	604
1989	1057	3	43	1854	2178	3	43	3820	98	1	-	172	546	3	59	958
1990	775	3	56	1359	2153	3	119	3777	175	5	11	307	510	3	29	894
1991	1180	3	28	2070	2888	3	216	5067	180	3	48	316	682	3	91	1196
1992	1036	2	325	1818	2839	3	403	5195	182	3	13	319	586	3	233	1027
1993	1910	3	115	3351	-	-	-	-	-	-	-	-	-	-	-	-
1994	2102	3	81	3687	3761	3	680	6598	181	3	32	317	650	3	194	1140
1995	2533	3	148	4444	-	-	-	-	-		-	-	-	-	-	-
1996	2338	3	47	4101	4326	3	141	7589	271	3	42	475	727	3	68	1275
1997	-	-	-	-	-	-	-	-	-	-	-	-	956	2	119	1677
1998	3201	3	414	5615	6189	3	82	10858	290	3	1	508	1044	4	316	1832
1999	2704	3	47	4743	-	-	-	-	-	-	-	-	1444	2	264	2533
2000	3979	2	239	6981	5941	3	185	10422	389	3	16	682	713	5	153	1251
2001	5981	3	406	10493	-	-	-	-	-	-	-	-	855	2	408	1499
2002	-	-	-	-	-	-	-	-	260	3	20	456	1159	3	60	2032
2003	2702	3	117	4740	4895	3	37	8587	401	3	52	704	802	2	92	1407
2004	2692	2	138	4723	4759	1	-	8349	494	3	87	866	965	1	-	1693
2005	3605	3	78	6325	5425	3	144	9518	560	3	30	982	781	3	46	1369
2006	2754	2	473	4832	5440	2	6	9544	448	2	43	785	853	3	165	1496
2007	2553	3	192	4479	5484	2	49	9620	511	3	23	896	772	2	151	1354
2008	4427	3	462	7767	-	-	-	-	737	3	21	1293	1048	3	30	1839

excluded since it is suspected that an ongoing decrease will affect the number of seals resting on land. Counts were included for 2002 for the Limfjord as surveys were carried out prior to the first observed occurrence of the disease in this area (Härkönen *et al.* 2006). The number of seals counted was $\log_e$-transformed prior to the analyses. The average annual growth rate was derived by linear regression of each subpopulation, based on a trimmed mean where the lowest count in each year was deleted. This reduce the variation in number of hauled out seals caused by disturbances during surveys and gives considerably better estimates compared to having all counts included (Teilmann *et al.* 2010). If only two surveys were conducted a given year we calculated the regular (untrimmed) mean rather than the trimmed mean, contrary to Teilmann *et al.* 2010 where the lowest of the two or three counts was deleted for trimmed mean. In years when only one survey was conducted we simply used this single observation to represent the average annual count.

TRENDS IN HISTORIC TIMES (PREHISTORY - 1970s)

The pristine abundance and distribution of harbour seals in Southern Scandinavia is uncertain. Skeletal remains in natural deposits and archaeological excavations of cultural sites in the Kattegat area suggest that seals were present in parts of Southern Scandinavia at least 8,000 years ago (Søndergaard *et al.* 1976, Aaris-Sørensen 1998, Härkönen *et al.* 2005). The abundant record of grey seal (*Halichoerus grypus*) and harp seal (*Pagophilus groenlandicus*) remains suggest that these species were previously abundant in the area. Contrastingly, harbour seal remains are scarce and totally absent for prolonged periods, suggesting that harbour seals may have colonised the area several times and subsequently become extinct (Härkönen *et al.* 2005).

The first information on the occurrence of seals in the region stem from the 16-18th century, but little information regarding species, abundance, and distribution is at hand from this period

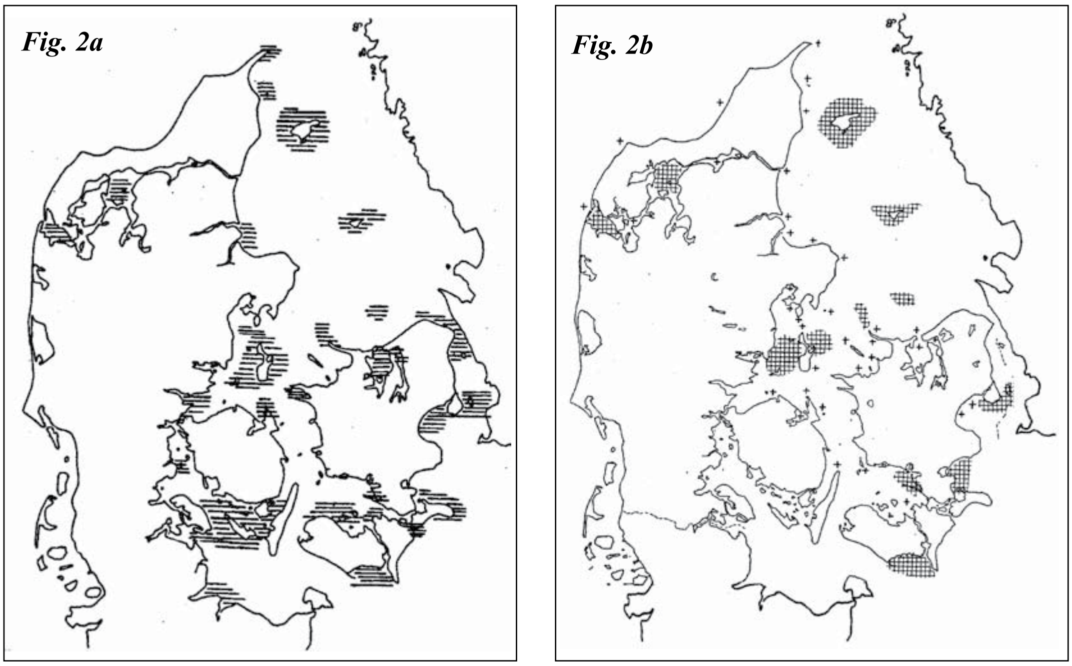

Fig. 2. *Estimated distribution of harbour seals in Denmark prior to the onset of the bounty system in 1890 (a) and in the 1970s (b). Highligted areas designate distribution of breeding sites. + designates occasional haul-out observations. Figures modified from Søndergaard et al. (1976).*

(Søndergaard *et al.* 1976). From the mid 18th century, seals were increasingly hunted, and written records describe their presence in most Scandinavian waters; often, however, without distinguishing between species of seals. Harbour seals probably colonised the region only after severe depletion of the formerly abundant grey seals during the 18th and 19th centuries (Härkönen *et al.*2005).

Increasing demands on governments were raised from commercial fisheries to control the seal population due to its presumed influence on fish stocks and damage to fishing gear. In 1889 and 1902 the Danish and Swedish governments, respectively, introduced a bounty system for hunting seals (Harding and Härkönen 1999). The number of harbour seals killed in Kattegat and Skagerrak alone during the period 1889 to 1976 is estimated to 35,300 (Heide-Jørgensen and Härkönen 1988). The effect of the campaign was unquestionable; the harbour seal population declined to a minimum in the 1920s (Søndergaard *et al.* 1976). Notably, while grey seals previously appeared to be the most abundant seal species, the proportion of harbour seals killed during the bounty system suggests that in the late 19th century the grey seal was almost extinct and the harbour seal had replaced the grey seal as the most abundant seal species in Denmark and Sweden (Härkönen *et al.* 2005). Although the bounty system was abandoned in 1927 in Denmark, the Danish government continued to provide economical support for seal harvest in some areas. In Sweden the bounty system was abandoned in 1965, and hunting bans on harbour seals were implemented in 1967 and 1977 in Sweden and Denmark, respectively (Heide-Jørgensen and Härkönen 1988, Bøgebjerg *et al.*1991). Currently, licenses can be issued at specific locations to shoot seals close to fishing gear (Dietz *et al.* 2000, Härkönen pers. comm.).

Regional trends

Skagerrak

Extrapolating from the hunting statistics of the bounty period, Heide-Jørgensen and Härkönen (1988) estimated the 1890 Skagerrak-Kattegat harbour seal population to 16,500, assuming growth rates of 5% per year in the very beginning of the 20th century, and 12% per year after 1920. According to the 1979-2006 counts given in Table 1, the Skagerrak subpopulation is about 30% (SD 4.9%) of the total size of the Skagerrak-Kattegat population. Applying this ratio to the estimate from 1890, the number of harbour seals in Skagerrak was approximately 5,500. By 1979, the Skagerrak subpopulation was estimated to about 1,000 seals *i.e.* 18% of its original size. These figures rely on a number of assumptions concerning the accuracy of the hunting statistics, the proportion of the stock killed, the ratio between the number of seals in the Kattegat and Skagerrak, and harbour seal population growth rates and are merely crude approximations. Nevertheless they serve as a guideline to the abundance of harbour seals in Skagerrak prior to the initiation of systematic hunting.

Kattegat

Records from the 18th century suggest an extensive distribution of harbour seals in Kattegat. (Søndergaard *et al.* 1976). Due to their accessibility from land and/or threat to salmon fisheries in the inlets, harbour seals were hunted and became rare at the majority of these sites by the end of the 19th century, but still abundant in areas such as Samsø, where "thousands" of seals could be observed in the 1880s (Søndergaard *et al.*1976).

The 20th century witnessed steady declines at most sites throughout the region and by the 1930s seals were more or less restricted to haulout sites on Hesselø, Læsø, Anholt, in the Samsø area, Hallands Väderö, Varberg, and Onsala. In the following period harbour seal numbers continued to decrease in the Samsø area, and is at the same time considered to have been stable at Læsø, Hesselø, and Anholt. From the 1950s numbers were increasing at the two latter sites (Søndergaard *et al.* 1976). Information on the population development at Hallands Väderö, Varberg, and Onsala during the period is limited. In 1979 the total Kattegat population was estimated to about 3,100 animals (Fig. 3b) or approximately 25% of its estimated 1890 size of 11,550 seals (see above).

Western Baltic

The single most important seal locality in the western Baltic region is the sand bar Rødsand

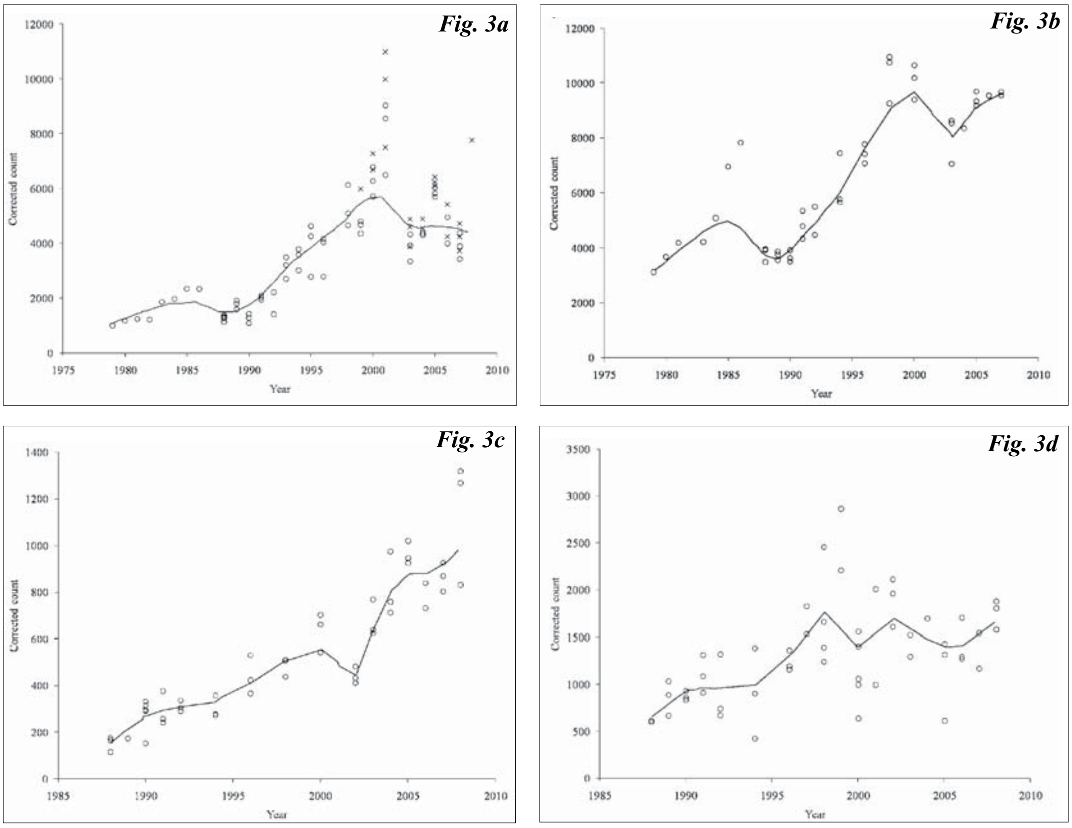

Fig. 3. *Trends in number of seals in the 4 subpopulations; Skagerak (a), Kattegat (b), western Baltic (c), and the Limfjord (d). X-axis shows year of survey and Y-axis the estimated population size corrected for the proportion of seals in the water. In addition to the graphic point presentation of the temporal trend of the population estimates Lowess smoother curves were applied to the four regions using a 25% smoothing factor. Crosses in Figure 3a is abundance including Oslo Fjord, Norway.*

in the shallow lagoon-like area south of Lolland (Fig. 1) where harbour seals and also grey seals hauled out in large numbers. Both species were subject to intensive harvest with up to 900 seals killed on single days in the spring of 1801 (Søndergaard *et al.* 1976). The intense hunting pressure gradually deprived the grey seals from the area, but harbour seals appear to have occurred in numbers as high as 200-300 seals in some years up to the 1950s. However, the repeated harvest ultimately resulted in a decline in this harbour seal population as well, with only about of 30-40 animals remaining.

Seal haulouts also existed in other parts of the Baltic. Harbour seals were abundant and widely distributed on the many islands, reefs, and islets south of Funen in the most western part of the Baltic and in the Danish Straits (Fig. 2a), but were already severely depleted by the end of the 19th century, being close to absent from the area today. Harbour seals were also abundant in Øresund between Denmark and Sweden where they, according to 18-19th century fisheries bulletins, caused significant disturbance to the fisheries and consequently were hunted intensively (Søndergaard *et al.* 1976). By the end of the 19th century, seals had disappeared from much of the area and were only relatively abundant on Saltholm in the middle of Øresund and at Måkläppen off Falsterbo in Sweden. By the 1970s, this stock had declined as well, numbering only 10-15 animals at both sites (Fig. 2b). Although estimates are associated with much uncertainty the decline in this region up until the 1970s appears to have been in the order of 80-90%, perhaps more.

Table 2. Estimated annual growth rates in the 4 subpopulations based on the exponential growth model for periods corresponding to before, between, and after the two PDV epidemics. Note that some data in this table differs from Teilmann *et al* 2010 because of differences in data treatment.
* Includes data from Oslo Fjord, Norway.

Area	Period	Growth rate (%)
Skagerrak	1979-1986	13.3
	1989-2001	13.6
	2003-2008*	6.1
Kattegat	1979-1986	12.1
	1989-2000	10.2
	2003-2007	2.9
W. Baltic	1989-2000	9.8
	2003-2008	8.5
Limfjord	1989-1999	7.9
	2000-2002	25.1
	2003-2008	2.1
Overall	1979-1986	12.4
	1989-2000	10.6
	2003-2007	2.2

The Limfjord
Harbour seals were rarely reported in the Limfjord prior to 1825, when this, hitherto largely isolated brackish water system, became connected to the North Sea. Subsequently, the harbour seal stock experienced a marked increase in abundance, becoming relatively numerous in particularly the western part of the inlet by the turn of the previous century. Although minor fluctuations likely occurred, the population is believed to have been stable at approximately 200 animals from the early 20th century to the 1970s (Søndergaard *et al.* 1976).

TRENDS IN RECENT TIMES (1970s - PRESENT)

Following the protection of the harbour seal in 1967 and 1976, the subpopulations in all areas where seals were surveyed increased exponentially by an average of 12.4% per year until the outbreak of the first PDV epizootic in 1988 (Tables 1, 2 and Fig. 3a, b). Reliable data does not exist for all areas, but the Skagerrak and Kattegat counts suggest a mortality of 7,000 seals representing a 55% decline from the years 1986 to 1989 (Dietz *et al.* 1989a, Härkönen *et al.* 2006). One year after the epizootic the total population was estimated at 6,804 seals, after correcting for seals in water at the time of the survey. Thereafter the population growth resumed increasing exponentially, reaching an estimated total of 18,886 seals for the whole study area in 2000. However, in May 2002 the PDV again appeared on Anholt in central Kattegat, from where it spread to the other subpopulations. The 2003 survey data indicate that approximately 11,300 harbour seals died during the second epizootic. However, although a greater number of seals were killed, the percentage decimation of the population was less compared to the first epizootic in 1988. On average, subpopulations declined by 20%, although more than 50% were killed in Skagerrak (Härkönen *et al.* 2006). Also this time the population started to recover, but at a much slower rate than after the first event (Table 2). In 2007, the population of the study area amounted to approximately 16,000 seals; approximately four times the size of the 1979 population and very close to the estimated pre-hunting population estimate.

Regional trends

Skagerrak
From the first surveys in 1979 to 1986, the harbour seal abundance in Skagerrak increased with an annual growth rate of 13.3% (Tables 1, 2 and Fig. 3a). In populations of true seals with even sex ratios and stable age structures the intrinsic rate of increase cannot exceed 13% per year. Larger values indicate a non-stable population structure or populations affected by migration (Härkönen *et al.* 2002). Consequently, we assume that the Skagerrak subpopulation had reached a stable age structure at the time of the first PDV outbreak. The epizootic in 1988 resulted in a population decline of 43.9%. Afterwards the subpopulation increased exponentially by 13.6% until 2002 when the second epizootic caused a decline by 53.1%. The growth has henceforth been at 6.1%

for the period 2003-2008, a rate that is influenced by a decline in 2007 caused by an as yet unidentified pathogen (Harkönën *et al.* 2008). In 2008, 4,427 harbour seals were counted in the Skagerrak. Correcting for the number of seals in the water at the time of the survey suggests a population size of 7,767 animals for the subpopulation: less than prior to the second epizootic, but about 30% more than estimated for its pre-hunting (*i.e.* 1890) size.

Kattegat

From an estimated total of 3,116 seals in 1979 the Kattegat subpopulation increased by 12.1% per year up to 1986 and 10.2% from 1989 to 2000 (Tables 1, 2 and Fig 3b). Both these rates are close to the intrinsic growth rate of harbour seals. In the period 1998-2000 the Kattegat subpopulation ceased increasing and might have reached its carrying capacity. The decline during the first epizootic was 51.1%, much more pronounced than the 17.6% observed under the second epizootic in 2002. Since then, growth has been a mere 2.9% per year in the Kattegat subpopulation and by 2007 its abundance was estimated at 9,620 seals. This estimate is close to the level observed immediately prior to the second epizootic, indicating that the Kattegat subpopulation is again approaching its current carrying capacity. Reaching an abundance of 11,500 seals as estimated for the 1890 subpopulation probably requires availability of additional suitable haulout sites.

Western Baltic

Systematic surveys of the seals in western Baltic were first initiated in 1988. Hence information on the effects of the first PDV epizootic is limited. However, 50% of seals died at the Måkläppen locality in 1988 (Dietz *et al.* 1989a; Härkönen *et al.* 2006). Until year 2000, the population grew with 9.8% per year, and hereafter declined with 33.1% as a consequence of the 2002 epizootic (Tables 1, 2 and Fig. 3c). The PDV epizootic in 2002 struck this site prior to the annual count; hence the estimated decline might be slightly higher compared to the actual mortality (Härkönen *et al.* 2006). The subpopulation increased exponentially during the first years following the epizootic, but growth appears to have ceased over the last couple of years. During 2003-2008 the annual growth rate was 8.5%, approaching 1,300 seals in 2008, substantially more than the 50-70 seals in the 1950s subpopulation. It is uncertain how the size of the current subpopulation relates to the pre-hunting size, but at those haulout sites inhabited by harbour seals today, abundance is probably similar to the abundance prior to hunting.

The Limfjord

The Limfjord subpopulation increased by 7.9% from 1989 to 1999, and was thereafter reduced by 50.6% in 2000 compared to the year before (Tables 1, 2 and Fig. 3d). The reduction was most prominent in the central part of the Limfjord. The low number of seals was confirmed by 4 additional surveys that year and neither new haulout sites nor unusual numbers of dead seals were reported. Similar declines were observed in the fisheries and in the local black cormorant population *(Phalacrocorax carbo)* (Anton Linnet, pers. comm.), which has dietary overlap with harbour seals during summer and autumn (Andersen *et al.* 2007). This indicates that food limitation might have forced the seals out of the fjord system, which was also supported by the lack of suitable seal prey in their diet during some months (Andersen *et al.* 2007). From 2000 to 2001, seal numbers increased by 25.1% indicating strong migration back into the central part of the Limfjord. Although seemingly rare, such migration supports the view that the Limfjord should be considered as a single unit when assessing harbour seal population dynamics. The epizootic in 2002 caused a 30.8% mortality from which the subpopulation has not recovered yet. The subpopulation has exhibited low growth rate (2.1%) since 2003 and amounted to 1,839 seals in 2008, which is considerably larger than the subpopulation of roughly 200 seals inhabiting the area up until the 1970s.

THREATS TO THE POPULATION

Interactions with fisheries

The conflict between fisheries and harbour seals is not new. Hunting to control seals as a competitor to fisheries was previously of major importance to seal mortality in Southern Scandinavia, but basically ceased with the legal protection of the harbour seals in the 1960s and 1970s in Sweden and Denmark, respectively. In some areas of Sweden fishermen are allowed to kill single seals in order to protect their fishing gear (Harding and Härkönen 1999). This practice is also followed in Denmark, where dispensation to commercial fishermen can be granted to shoot a limited number of seals close to fishing gear in some regions (*e.g.* Rødsand) if serious damage to their nets or catch can be documented (Jepsen 2005). This amounts to about 10 (up to 18) seals shot per year (Dietz *et al.* 2000, Danish Forest and Nature Agency, pers. comm.), which should not be of significance for the status of the population. Also, incidental by-catch occurs, but although information is scarce this appears to have limited consequences for harbour seal abundance (Jepsen 2005).

Over the past decades high fishing pressure has resulted in depletion of fish populations and caused local changes in marine community structure (Ducrotoy and Elliott 2008). Several studies have documented the dramatic influence of these changes on mammals and birds relying on fish as food resource (Hamre 1994, Hjermann *et al.* 2004, Matthiopoulos *et al.* 2008). However, very little is known about the potential impact of fisheries in the form of reduced carrying capacity of harbour seal habitats in Southern Scandinavia. Assessing such relationship requires quantitative information on the intensity of competition, that is, whether harbour seal predation overlaps in space and time with commercial fishing. Harbour seals are opportunistic feeders showing significant regional and seasonal variation in their diet, presumably relating to prey abundance (Härkönen 1987, Brown and Pierce 1998, Andersen *et al.* 2007). Furthermore, total seal predation is often small compared to the amount taken by fisheries and many fish consumed by harbour seals are either not targeted by fishery or are under the legal minimum landing sizes (Brown and Pierce 1998, Hansen and Harding 2006, Andersen *et al.* 2007, Matthiopoulos *et al.* 2008). These observations suggest that the competitive overlap is minimal. Alternatively, it could be a consequence of adaptations by harbour seals to limited food supplies, indicating high competition pressure from the fisheries. More research is needed to address these questions.

Eutrophication

Eutrophication and seasonal oxygen deficiency can have devastating effects on benthic animals and commercial fish species (Islam and Tanaka 2004), some of which has already been observed in the North Sea-Baltic Sea region (Karlson *et al.* 2002). Feeding mainly on benthic fish species, changes in the benthic macrofauna are likely to affect the harbour seal. In 2000, large numbers of seals migrated out of the central Limfjord in what might have been a response to a collapse of the fish stock in this semi-enclosed water body (see above). The cause of the 2000 collapse is currently unknown, but eutrophication and oxygen deficiency is a frequent issue in the Limfjord system (Jensen 1990, Karlson *et al.* 2002). Eutrophication also occurs in open waters like the Kattegat, where seasonal oxygen deficiency and negative effects on the benthic macrofauna have been observed most years since the 1980s. Similarly, several fjords along the Swedish Skagerrak coast have shown declining oxygen concentrations and a seasonal lack of benthic fauna in the deeper parts (Karlson *et al.* 2002). Thus, although active management strategies in Denmark have reduced phosphorus and nitrogen levels in coastal waters by 22-57% and 44%, respectively, over the past 15 years (Carstensen *et al.* 2006), eutrophication might pose a threat to harbour seal abundance in Southern Scandinavia, at least on a local scale.

Contaminants

Several studies discuss the role of bioaccumulation and biomagnification of contaminants in relation to harbour seal health. Seals in the Dutch Wadden Sea and in the Baltic Sea have previously experienced low reproduction rates due to elevated levels of polychlorinated biphenyls (PCBs) in their diet (Rejinders 1980, Bergman and Olsson 1985, Rejnders 1986), and experimental studies have shown that levels of PCBs measured among harbour seals (20 ppm) cause impaired immunity functions (DeSwart *et al.* 1996). Harbour seals in Southern Scandinavia generally exhibit high fertility rates (Table 2) (Härkönen and Heide-Jørgensen 1990) and toxicological analyses for PCBs have revealed decreasing trends in north-eastern Atlantic marine mammals (Aguilar *et al.* 2002, Reijnders and Simmonds 2003), suggesting that these compounds might no longer be a serious issue for harbour seal health. Still, the apparent susceptibility to epizootics exhibited by the Southern Scandinavian harbour seal population (Härkönen *et al.* 2006), the regular observation of seals with wounds (Authors pers. obs.), and the continuous prevalence of bone lesions in form of alveolar exostosis (Mortensen *et al.* 1992, Härkönen pers. comm.), suggest that other compounds might be affecting the immunological response of harbour seals. Although frequencies of wounds have decreased along with the decline of some conventional POPs other compounds in the POP group could affect the immune function of harbour seals. Similarly could organohalogens as discussed in the case of alveolar exostosis (Mortensen *et al.* 1992). The role of OHC contamination, through impeding immune system function, could potentially have had an effect on the severity of the 1988 and 2002 epizootic, but no causal relation have so far been established (*e.g.* Hall *et al.* 1992a; b, Reijnders and Aguilar 2002, Härkönen *et al.* 2006, Dietz 2008).

Offshore constructions

Offshore wind farms have been established in both Denmark and Sweden as part of the national strategy for increasing the production of renewable energy. Effects of these activities on the habitat use and haulout behaviour of harbour seals were studied between 1999 and 2005 during the construction and operation of the Horns Reef and Nysted offshore wind farms in Denmark (Dietz *et al.* 2003, Teilmann *et al.* 2006, Edrén *et al.* 2010). No general change in behaviour at sea could be linked to the Horns Reef offshore wind farms. On land, the only effect detected was a short-termed alteration in seal haulout behaviour during pile drivings, which took place about 10 km from the seal locality at Rødsand in the western Baltic. However, pile driving is of limited duration and should not cause significant threats to harbour seals. The effect of wind farms on feeding behaviour of seals is still unknown.

Human disturbance

Human disturbance in the form of urban development, sea-, land- and air-based traffic, and recreational activities (*e.g.* seabird hunting and leisure crafts during winter and summer, respectively) affect harbour seal distribution and abundance (Allen *et al.* 1984, Watts 1996, Montgomery *et al.* 2007). In the densely populated Southern Scandinavia, harbour seals have disappeared from haulout sites close to human developments and are currently restricted to undisturbed coasts in sanctuaries or relatively remote areas. It is therefore of outmost importance to harbour seal viability that haulout sites are protected and disturbance kept to a minimum to allow the population to increase or remain stable. Detailed studies evaluating the effects of human disturbance on harbour seal haulout patterns in central Kattegat are in progress (Andersen *et al.* in prep).

Interspecific competition

Interspecific competition might be another factor that affects the distribution and abundance of harbour seals in Southern Scandinavia. Grey seals and harbour seals have overlapping habitats and might also be competitors for food sources (Bowen *et al.* 2003). Both species have been subject to severe anthropogenic impacts, but responded very differently (Søndergaard *et al.* 1976, Wolff 2000, Härkönen *et al.* 2005). The previously dominating grey seal population suffered severe declines whereas harbour seals gradually increased in abundance and distribution. Contrary to harbour seals, grey seal pups are immobile for the first weeks after birth and are easily hunted. Thus, grey seals appear more vulnerable to disturbances at breeding sites, providing an advantage to harbour seals in periods of disturbance. As a consequence of conservation and management efforts during the past decades, the grey seal stock in Southern Scandinavia is currently growing and might become a competitor to harbour seals. The declines observed recently in British harbour seals might result from competition with the grey seal (Lonergan *et al.* 2007). Moreover, seeming to be more or less unaffected by PDV, the grey seal might act as an indirect competitor to harbour seals by carrying the PDV-like viruses affecting harbour seal populations

(Härkönen *et al.* 2006). Locally, competition might also occur with the great cormorant. Andersen *et al.* (2007) studied the interactions between cormorants and harbour seals in Limfjorden and observed dietary overlap of the two species during summer and autumn. Diet overlap has also been documented for the Southern Kattegat area (Härkönen 1988). However, it is unknown if this overlap results in competition. Although not studied in details the habitat selection and diet composition of harbour seals and harbour porpoises *(Phocoena phocoena)* are quite similar and may also result in interspecific competition (*e.g.* Aarefjord *et al.* 1995, Teilmann *et al.* 2007).

Genetic effects
Population declines and fragmentation might influence individual fitness through loss of genetic diversity, inbreeding depression, and reduction of the adaptive potential of individuals (Nei *et al.*1975, Hoelzel *et al.* 2001, Acevedo-Whitehouse *et al.* 2003). As discussed in the contaminant paragraph a number of observations indicate that the Southern Scandinavian harbour seal population experience reduced immunological response. This could be due to contaminants but it might result from low levels of genetic diversity. Valsecchi *et al.* (2004) found that inbred dolphins were less resistant to morbillivirus infections. So far no such correlation has been documented in harbour seals (Härkönen *et al.* 2006) and levels of genetic diversity in the Southern Scandinavian population appear similar to those observed in other populations (Goodman 1998, Olsen *et al.* in prep). However, detecting a relationship between inbreeding and immunity might require larger genetic resolution than the 7 and 15 microsatellite loci applied in the two studies, respectively. Recently Rijks *et al.* (2008) used 27 microsatellite loci to document a correlation between low genetic diversity (*i.e.* heterozygosity) and lung worm burdens in Wadden Sea harbour seals, suggesting that although remaining to be tested thoroughly, genetic diversity might also influence immune response in Southern Scandinavian harbour seals. In theory, such effects should be most prominent in harbour seals at apparently isolated localities like Rødsand (Dietz *et al.*2003) and less so in *e.g.* the Skagerrak-Kattegat area where movements among haul-out sites are more frequent (Olsen *et al.* in prep, Dietz *et al.* unpubl.).

Epizootics
Within the past 20 years the largest cause of harbour seal mortality in the region – and most of Europe – was the two outbreaks of PDV (Dietz *et al.* 1989a, b, Heide-Jørgensen *et al.* 1992, Jensen *et al.* 2002, Härkönen *et al.* 2006). Harding and co-authors (2002, 2003) investigated the sensitivity of projected populations under different future scenarios and found that populations with low growth rates and/or large annual variability in rates were the most vulnerable to future mass mortality events. In fast growing populations, like those in Southern Scandinavia, projections are more complicated, but there is an indication that the risk of extinction (*i.e.* declining to 10% of original size within 100 years) increase from 9% to 56% in the presence of epizootics (Harding *et al.* 2003).

In summer 2007, increased mortality among seals in central Kattegat caused the concern of a third PDV outbreak (Härkönen *et al.* 2008). By December approximately 300 dead seals had washed ashore in the Skagerrak-Kattegat region but as many as 2,300 seals were estimated to have died based on expected and observed aerial counts. Although it is now clear that the deaths were caused by an as yet unidentified pathogen and not PDV, the repeated occurrence of epizootics among the harbour seals of Southern Scandinavia indicate that epizootics might be the factor posing the greatest risk to the population and must be included in future conservation and management plans.

CONSERVATION AND MANAGEMENT

On a national level several Danish and Swedish seal sanctuaries have been established to ensure undisturbed haulout sites; some throughout the year and others only during the breeding and moulting period. Internationally, Denmark and Sweden have ratified the Bern Convention of 1979, aiming to conserve wild plants and animals including their habitats and protect them against threats (Jong *et al.* 1997). Both countries are also members of the Helsinki Commission (HELCOM) and have signed the Helsinki Convention of 1974 and 1992 working to protect the marine environment of the Baltic Sea. Also, all Baltic seals, including those in the Kattegat are listed under the EU Habitat Directive Annex II, and member countries are obliged to carry out monitoring of the status of seal populations and to establish special areas of conservation.

Denmark and Sweden have also ratified the 2006 HELCOM Seal Recommendation, where the following long-term management principles are accepted: all species and populations should have natural distribution and abundance and a health status that ensures their future persistence in the ecosystem. In practice this means that seal populations are allowed to reach their natural carrying capacities and former distributions. Furthermore, Denmark, The Netherlands, and Germany have established the Trilateral Governmental Cooperation in order to develop an overall conservation and management plan for the Wadden sea area (Kuiper and Enemark 2003).

The guidelines set by HELCOM and the Trilateral Government Cooperation were to a large extent implemented in the Danish seal management plan developed by the Danish Forest and Nature Agency (Jepsen 2005). In brief, the objectives of the plan are to i) preserve the seal population and its habitat; ii) evaluate existing seal reserves and assess the need for additional protected areas; iii) identify and solve conflicts with fisheries; iv) maintain or improve the possibility for the general public to observe seals; and v) promote exchange of information with neighbouring countries to ensure the best possible management of harbour seals in the region (Jepsen 2005). A management plan for harbour seals in Sweden is underway.

CONCLUSION

Compared to some centuries ago, the distribution of harbour seal breeding sites in Southern Scandinavia is now reduced. Harbour seals were previously widespread in the most western part of the Baltic Sea and the Danish Straits where they are now nearly absent. They have also disappeared from the western and Southern mainland shores of the Kattegat, and experienced significant declines in the Øresund. At its lowest in the 1920s, the total number of harbour seals in Southern Scandinavia probably did not exceed 2,000 animals; about 8x lower than the estimated abundance in 1890. Following their legal protection in the 1960s-70s conservation efforts have resulted in exponential growth in the harbour seal population, only interrupted by declines during the epizootics. Growth was close to the intrinsic rate in the Skagerrak and Kattegat subpopulations and a little lower in the western Baltic and Limfjord subpopulations. The population as a whole is now approaching pre-hunting abundance and appear healthy in terms of reproduction. However, the recurrent outbreak of epizootics indicates that the Southern Scandinavian population is having some fitness issues, the causes of which are poorly understood. Further, harbour seals are in large part restricted to the same haulout areas as 30 years ago and might have reached the current carrying capacity in some areas, as suggested by the slower or negative growth rates observed over the past couple of years. As several of the adverse factors observed to influence harbour seal fitness appear to be density dependent, further increases in the population will be determined by the availability of suitable harbour seal habitats and adequate food resources.

ACKNOWLEDGEMENTS

This study was jointly funded by the Danish Forest and Nature Agency and the Swedish Environmental Protection Agency. We greatly thank our skilled pilots and observers participating in aerial seal surveys since 1979. Frank Rigét provided kind advice on the statistical treatment of data. Mads Peter Heide-Jørgensen and an anonymous referee provided valuable comments to the manuscript, and their help is gratefully acknowledged.

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PAPER II

DIET OF HARBOUR SEALS AND GREAT CORMORANTS IN LIMFJORD, DENMARK: INTERSPECIFIC COMPETITION AND INTERACTION WITH FISHERY

Andersen, S.M., Teilmann, J., Harders, P.B., Hansen, E.H. and Hjøllund, D.

ICES Journal of Marine Science 64:1235-1245.
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Diet of harbour seals and great cormorants in Limfjord, Denmark: interspecific competition and interaction with fishery

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Andersen, S. M., Teilmann, J., Harders, P. B., Hansen, E. H., and Hjøllund, D. 2007. Diet of harbour seals and great cormorants in Limfjord, Denmark: interspecific competition and interaction with fishery. – ICES Journal of Marine Science, 64: 1235–1245.

Comparative studies on seasonal and regional variation in the diet of harbour seals and great cormorants were conducted in Limfjord, a semi-closed water system in northwest Denmark. To compare harbour seal diet from an open water system containing similar prey species, a small diet analysis from the western Baltic is included. Seal diet during spring reflected the abundance of Atlantic herring entering Limfjord to spawn (90% of the weight consumed), whereas during summer and autumn, seal diet was rather more mixed. The diet of seals in the Rødsand area and cormorants in Limfjord showed no marked seasonal trends. During spring, there was little overlap between seal and cormorant diets in Limfjord because seals fed almost exclusively on Atlantic herring, and they consumed significantly larger herring than did the cormorants. During summer and autumn, seal and cormorant diets overlapped markedly, although the fish items consumed by seals were generally larger. Few commercially targeted species were found in the stomachs and scats of seals and casts of great cormorants, but Atlantic herring were taken by the seals at a size greater than that allowed by the fishery.

Keywords: diet, dietary overlap, faecal samples, fishery, great cormorants, harbour seals, interspecific competition, *Phalacrocorax carbo sinensis*, *Phoca vitulina vitulina*, seal/fisheries interactions.

Received 18 August 2006; accepted 25 May 2007; advance access publication 3 July 2007.

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Introduction

Harbour seals (*Phoca vitulina*) are generalists that feed on a wide range of fish species (Härkönen, 1987; Härkönen and Heide-Jørgensen, 1991; Andersen *et al.*, 2004), yet their diet is often dominated by a few key species (Härkönen and Heide-Jørgensen, 1991; Tollit and Thompson, 1996). Several studies have noted that the importance of the key species varies both seasonally (Brown and Mate, 1983; Härkönen, 1987; Pierce *et al.*, 1991; Olesiuk, 1993; Tollit and Thompson, 1996; Hall *et al.*, 1998) and regionally (Härkönen, 1987; Olesiuk *et al.*, 1990; Olsen and Bjørge, 1995). Similarly, great cormorants (*Phalacrocorax carbo*) are described as generalist foragers (Warke *et al.*, 1994), with a diet varying between regions (Hald-Mortensen, 1995) and seasons (Madsen and Spärck, 1950). Hence, harbour seals and great cormorants are mainly piscivorous and, because they often share the same habitats, they potentially compete for the same food resources. In the relatively shallow Limfjord in northwest Denmark, the dietary overlap between these two top predators is expected to be of particular relevance.

Harbour seals and great cormorants are found throughout Danish waters. From an aerial survey in 1997, the Danish population of harbour seals was estimated to be ~11 000 strong, of which 1400 inhabited Limfjord (NERI, unpublished data). Following the total extermination of great cormorants in Denmark in the 1860s, the species took until 1938 to nest again (Madsen and Spärck, 1950). For the past 10 years, there has been a constant 40 000 cormorant nests in Denmark, of which some 6000 were in Limfjord (Eskildsen, 2001, 2005). Up to that point, the populations of harbour seals and great cormorants increased substantially in Denmark, a consequence of their protection from hunting in 1977 and 1980, respectively, and the establishment of several reserves in the late 1970s (Danish Forest and Nature Agency, 2002, 2005). The increases in population size of both combined with declining fish stocks have prompted concern by fishers (Hoffmann *et al.*, 2003). Both have, however, been regulated by epidemics of phocine distemper virus (PDV) in 1988 and 2002, causing the death of up to 50% of the Danish harbour seals then (Härkönen *et al.*, 2006), and a law promulgated in 1994 allowing new cormorant colonies to be removed (Danish Forest and Nature Agency, 2002).

In both Limfjord and the Rødsand area, seal damage to fishing equipment is especially severe. Since 2003 the number of conflicts between fishers and seals has decreased in Limfjord (Danish Forest and Nature Agency, 2005), but conflicts between cormorants and fishers have become more severe. Here, we present data on the diet of harbour seals and great cormorants in Limfjord and analyse trophic interactions between them, and also look at the diet of harbour seals in the western Baltic to compare diets of seals between a semi-closed and an open water system. Finally, we assess potential competition between fishers and these two predators in Limfjord using fish survey results, adapted from Hoffmann (2000).

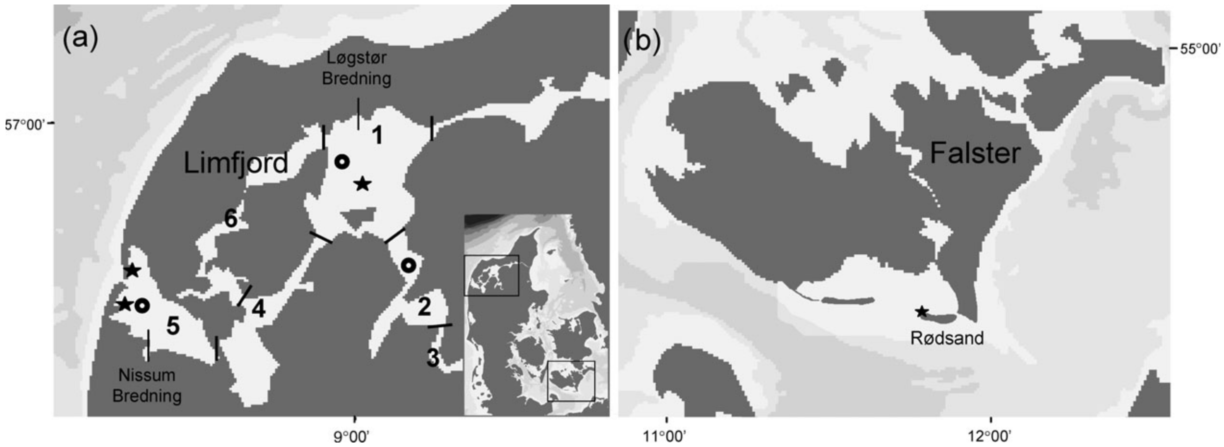

Figure 1. The study area in (a) Limfjord, and (b) Rødsand, showing haul-out sites where harbour seal scats and digestive tracts (stars) were collected, and resting sites where great cormorant casts (circles) were collected. Trawl areas are designated by numbers.

Material and methods

During spring, summer, and autumn of 1997, and spring 1998, 106 harbour seal scats and 198 great cormorant casts were collected from haul-out sites and resting places, respectively, in two different parts of Limfjord, Løgstør Bredning and Nissum Bredning (Figure 1), to allow for examination of the geographic variation in diet of harbour seals and great cormorants in Limfjord. Nissum Bredning, in western Limfjord, is influenced by the North Sea, so the water is supplied with various species from the North Sea and the salinity is higher than that in Løgstør Bredning, in the inner Limfjord.

Material from the Rødsand reserve, south of Falster Island in southern Denmark, consisted of 13 harbour seal scats collected during the period March–November of 2001–2005 and 17 digestive tracts from harbour seals shot by fishers with permission of the Danish Ministry of Environment. These healthy seals were shot in the vicinity of fishing gear, within a few kilometres of the haul-out sites. Because of the limited number of samples from Rødsand, these are used only in discussing the conclusions from the Limfjord samples.

Processing and identifying prey remains

All scats, casts, and digestive tracts were stored frozen (-20°C) in individual polythene bags until processing. Before analysis in the laboratory, scats, casts, and digestive tracts were left to thaw for ~24 h in water, after addition of a few drops of household detergent to emulsify the soft constituents. Scats and digestive tract contents were then washed through three stacked interlocking test sieves with mesh sizes of 300 μm, 750 μm, and 2.0 mm (Endocott). Otoliths were recovered and stored dry until identification. One decilitre of water and 4–5 tablets of sodium hydroxide (NaOH) were added to the casts, and the mixture was stirred until the tablets were dissolved. The mixture was left until the next day for the detergent and NaOH to dissolve the mucous membrane. The mixture was then thoroughly washed through a sieve with mesh size of 180 μm, and otoliths were recovered and stored dry until identification.

Otoliths were identified to the lowest taxon possible, using a reference collection and the otolith identification guide of Härkönen (1986). Otoliths were sorted into right- and left-sided otoliths, and the more numerous side was used to determine the number of fish consumed; if this was not possible because of degrading, the number of fish was estimated by dividing the total number of otoliths by two. Otolith length was measured (accuracy 10^{-2} mm) parallel to the sulcus, from the anterior tip of the rostrum to the posterior edge, and otolith maximum width was measured perpendicular to the length under a dissecting microscope (Cambridge Instruments) with a binocular micrometer ($\times$6.5 and $\times$40). The weight of the individual fish consumed was estimated from the otolith length and width, using the otolith size : fish weight formulae for each species in Härkönen (1986). From the Rødsand area, some flatfish otoliths were identifiable only to family, i.e. Pleuronectidae, and regressions based on combined data from the two most likely species (plaice, *Pleuronectes platessa*, and flounder, *Platichthys flesus*) were used.

Studies from captive feeding experiments found that correction factors can be applied to obtain a more accurate estimate of prey size (Harvey, 1989; Tollit *et al.*, 1997b), but it is still unknown if these correction factors apply to free-ranging pinnipeds; inactivity is likely to have an impact on the digestion and hence on the condition of the otoliths recovered. Grellier and Hammond (2005) showed that only digestion coefficients derived from *in situ* experiments can be used to estimate fish size accurately, whereas digestion coefficients derived from carrier experiments yield larger digestion coefficients, which tend to overestimate fish size. Correction factors derived from *in situ* experiments were not available for all prey species relevant to this study, so we did not use them to preclude introducing further bias when comparing interspecies fish weight.

Diet competition between harbour seals and great cormorants

Diet was considered to overlap between harbour seals and great cormorants when a prey species constituted >5% of both seal and cormorant diet, and when each sample consisted of ≥5 specimens of a particular prey species. The estimated length frequency distributions of prey for which seals and cormorants potentially competed were compared using Kolmogorov–Smirnov two-sample tests.

Biomass estimates and length frequency distributions of fish species in Limfjord were produced on research trawl surveys in September 1997 (Hoffmann, 2000). Prey sizes in the seal and cormorant autumn diet were compared with these trawl samples using Kolmogorov–Smirnov two-sample tests to determine whether the range of fish sizes in the diet was consistent with the range of prey sizes in the fjord. Finally, the estimated length frequency distributions of seal and cormorant prey were compared with fishery minimum size limits (Ministry of Food, Agriculture and Fisheries, 2003). The proportion of the various prey species (by mass) in harbour seal and great cormorant diet was compared with their relative abundance in Limfjord.

Seasonal differences in mean number of fish and mean total weight per scat sample were examined using analysis of variance (ANOVA) on log-transformed data, with Tukey–Kramer as the *post hoc* test ($p < 0.05$). This analysis was carried out solely on scat samples. All statistical tests were conducted in S-plus 6 (Insightful Corporation).

Results

In Limfjord and the Rødsand area, harbour seals fed on a minimum of 17 and 20 species, respectively, and 22 fish species were found in the cormorant casts from Limfjord (Tables 1–3).

Seasonal and regional variation in diet

Harbour seals fed almost exclusively on marine fish. However, bones and otoliths from the brackish roach were identified in one harbour seal digestive tract from Rødsand. Roach have been

Table 1. Estimated number and percentage by weight of prey species found in harbour seal *Phoca vitulina* scats collected in Limfjord during 1997 and spring 1998.

Prey species	Løgstør Bredning						Nissum Bredning	
	May 1997, and March and April 1998 (n = 30)		June, July, and August 1997 (n = 30)		September, October, and November 1997 (n = 30)		July and August 1997 (n = 16)	
	Estimated number of individuals	Weight (%)	Estimated number of individuals	Weight (%)	Estimated number of individuals	Weight (%)	Estimated number of individuals	Weight (%)
Clupea harengus Atlantic herring	156 (=54.2%)	89.9	43 (=2.9%)	3.9	12 (=0.4%)	6.0	1 (=0.5%)	0.1
Sprattus sprattus Sprat	121 (=42.0%)	7.0	289 (=19.4%)	11.4	249 (=7.9%)	4.5	–	–
Anguilla anguilla Eel	1 (=0.3%)	2.0	17 (=1.1%)	6.2	3 (=0.1%)	2.9	–	–
Gadus morhua Atlantic cod	–	–	1 (=0.1%)	0.4	–	–	–	–
Merlangius merlangus Whiting	–	–	–	–	–	–	1 (=0.5%)	0.1
Ammodytes tobianus Lesser sandeel	–	–	205 (=13.7%)	12.2	1 (≤0.1%)	0.1	–	–
Hyperoplus lanceolatus Greater sandeel	2 (=0.7%)	0.1	91 (=6.1%)	5.2	22 (=0.7%)	2.0	60 (=29.7%)	5.0
Gobius niger Black goby	3 (=1.0%)	0.1	219 (=14.7%)	6.4	988 (=31.2%)	20.5	1 (=0.5%)	<0.1
Pomatoschistus minutus Sand goby	2 (=0.7%)	<0.1	11 (=0.7%)	0.1	1 798 (=56.8%)	15.9	–	–
Pholis gunnellus Butterfish	–	–	5 (=0.3%)	0.1	–	–	–	–
Zoarthes viviparus Eelpout	2 (=0.7%)	0.3	446 (=29.9%)	23.2	15 (=0.5%)	2.1	8 (=4.0%)	2.0
Myoxocephalus scorpius Bullrout	–	–	43 (=1.5%)	8.0	3 (=0.1%)	1.4	–	–
Taurulus bubalis Long-spined sea scorpion	–	–	5 (=0.3%)	0.4	1 (≤0.1%)	0.1	–	–
Limanda limanda Dab	–	–	–	–	–	–	8 (=4.0%)	14.1
Platichthys flesus Flounder	1 (=0.3%)	0.6	5 (=0.3%)	1.9	27 (=0.9%)	30.7	53 (=26.2%)	65.0
Pleuronectes platessa Plaice	–	–	129 (=8.6%)	17.7	44 (=1.4%)	13.9	70 (=34.7%)	13.7
Solea solea Sole	–	–	3 (=0.2%)	3.1	–	–	–	–
Total	288	100.0	1492	100.0	3163	100.0	202	100.0

Bones from three-spined and 15-spined stickleback were found, but weight was not estimated and the data are therefore not used in calculations.

Table 2. Estimated number and percentage by weight of prey species found in great cormorant *Phalacrocorax carbo sinensis* casts collected in Limfjord during 1997.

Prey species	Løgstør Bredning						Nissum Bredning			
	April and May 1997 ($n = 75$)		June, July, and August 1997 ($n = 50$)		September 1997 ($n = 18$)		May 1997 ($n = 49$)		June 1997 ($n = 6$)	
	Estimated number of individuals	Weight (%)	Estimated number of individuals	Weight (%)	Estimated number of individuals	Weight (%)	Estimated number of individuals	Weight (%)	Estimated number of individuals	Weight (%)
Clupea harengus Atlantic herring	26 (=1.6%)	6.9	2 (=0.3%)	0.1	–	–	14 (=2.3%)	1.8	–	–
Sprattus sprattus Sprat	46 =(2.7%)	1.3	27 =(3.7%)	1.8	–	–	1 (=0.2%)	0.1	–	–
Salmo trutta Trout	2 (=0.1%)	0.3	–	–	–	–	–	–	–	–
Osmerus eperlanus Smelt	–	–	14 (=1.9%)	0.7	–	–	–	–	1 (=1.4%)	0.4
Anguilla anguilla Eel	5 (=0.3%)	1.4	2 (=0.3%)	1.2	4 (=1.1%)	4.7	1 (=0.2%)	0.4	–	–
Gadus morhua Atlantic cod	2 (=0.1%)	6.2	–	–	–	–	16 (=2.6%)	9.9	8 (=11.6%)	43.9
Melanogrammus aeglefinus Haddock	–	–	–	–	–	–	1 (=0.2%)	0.3	–	–
Ammodytes tobianus Lesser sandeel	6 (=0.4%)	0.3	1 (=0.1%)	0.1	–	–	30 (=4.9%)	2.6	–	–
Hyperoplus lanceolatus Greater sandeel	3 (=0.2%)	0.2	8 (=1.1%)	1.1	–	–	58 (=9.5%)	4.3	–	–
Gobius niger Black goby	425 (=25.4%)	16.1	186 (=25.5%)	12.6	164 (=45.2%)	33.8	18 (=2.9%)	1.8	3 (=4.3%)	0.5
Pomatoschistus minutus Sand goby	752 (=44.9%)	5.2	186 (=25.5%)	2.3	161 (=44.4%)	5.7	11 (=1.8%)	0.1	–	–
Pholis gunnellus Butterfish	2 (=0.1%)	0.1	3 (=0.4%)	0.2	–	–	1 (=0.2%)	<0.1	–	–
Zoarthes viviparus Eelpout	136 (=8.1%)	12.1	191 (=26.2%)	36.9	4 (=1.1%)	1.2	72 (=11.8%)	7.6	4 (=5.8%)	2.5
Eutrigla gurnardus Grey gurnard	–	–	–	–	–	–	1 (=0.2%)	0.1		
Myoxocephalus scorpius Bullrout	191 (=11.4%)	35.2	59 (=8.1%)	27.5	20 (=5.5%)	35.7	34 (=5.6%)	6.1	2 (=2.9%)	2.6
Taurulus bubalis Long-spined sea scorpion	75 (=4.5%)	14.3	23 (=3.2%)	6.3	5 (=1.4%)	5.3	1 (=0.2%)	0.1	–	–
Scophthalmus rhombus Brill	–	–	–	–	–	–	1 (=0.2%)	0.3	–	–
Hippoglossoides platessoides Long rough dab	–	–	–	–	–	–	1 (=0.2%)	0.1	–	–
Limanda limanda Dab	1 (=0.1%)	0.1	–	–	–	–	99 (=16.2%)	15.2	–	–
Platichthys flesus Flounder	–	–	–	–	1 (=0.3%)	4.9	16 (=2.6%)	10.4	1 (=1.4%)	1.7
Pleuronectes platessa Plaice	3 (=0.2%)	0.2	26 (=3.6%)	9.5	3 (=0.8%)	6.7	233 (=38.1%)	36.0	49 (=71.0%)	42.6
Solea solea Sole	–	–	–	–	1 (=0.3%)	2.0	3 (=0.5%)	2.9	1 (=1.4%)	5.9
Total	1675	100.0	729	100.0	364	100.0	612	100.0	69	100.0

Note: Bones from garfish, roach, and three-spined stickleback were found, but weight was not estimated and the data are therefore not used in the calculations.

Table 3. Estimated number of prey species and percentage by weight of prey species found in harbour seal *Phoca vitulina* scats and digestive tracts collected in the Rødsand area during the period 2001–2005.

Prey species	March and April (Four scats, three digestive tracts)		June, July, and August (Three scats, two digestive tracts)		September, October, and November (Six scats, eight digestive tracts)	
	Estimated number of individuals	Weight (%)	Estimated number of individuals	Weight (%)	Estimated number of individuals	Weight (%)
Clupea harengus Atlantic herring	15 (=11.0%)	15.4	–	–	25 (=4.8%)	5.5
Sprattus sprattus Sprat	1 (=0.7%)	0.3	–	–	14 (=2.7%)	1.3
Belone belone Garfish	2 whole fish (=1.5%)	4.7	–	–	5 whole fish (=1.0%)	6.0
Gadus morhua Atlantic cod	16 (=11.8%)	42.3	6 (=7.7%)	22.0	57 (=11.0%)	42.7
Ammodytes tobianus Lesser sandeel	64 (=47.1%)	13.6	2 (=2.6%)	0.3	263 (=51.0%)	15.7
Hyperoplus lanceolatus Greater sandeel	1 (=0.7%)	0.8	1 (=1.3%)	0.2	–	–
Gobius niger Black goby	14 (=10.3%)	0.7	12 (=15.4%)	0.1	86 (=16.7%)	0.3
Pomatoschistus minutus Sand goby	–	–	1 (=1.3%)	<0.1	–	–
Pholis gunnellus Butterfish	3 (=2.2%)	0.5	–	–	–	–
Zoarthes viviparus Eelpout	3 (=2.2%)	1.1	10 (=12.8%)	3.7	13 (=2.5%)	2.4
Taurulus bubalis Long-spined sea scorpion	–	–	–	–	2 (=0.4%)	0.2
Ctenolabrus rupestris Goldsinny wrasse	6 (=4.4%)	1.0	1 (=1.3%)	0.1	5 (=1.0%)	1.1
Limanda limanda Dab	4 (=2.9%)	10.1	5 (=6.4%)	9.2	38 (=7.4%)	21.0
Platichthys flesus Flounder	2 (=1.5%)	3.1	15 (=19.2%)	24.3	2 (=0.4%)	1.2
Pleuronectidae spp. (*Pleuronectes platessa* and *Platichthys flesus*)	–	–	20 (=25.6%)	24.3	–	–
Pleuronectes platessa Plaice	5 (=3.7%)	6.4	1 (=1.3%)	3.8	4 (=0.8%)	2.6
Enchelyopus cimbrius Four-bearded rockling	–	–	1 (=1.3%)	<0.1	2 (=0.4%)	<0.1
Gymnocephalus cernus Ruffe	–	–	1 (=1.3%)	0.1	–	–
Solea solea Sole	–	–	1 (=1.3%)	1.9	–	–
Rutilus rutilis Roach	–	–	1 (=1.3%)	10.1	–	–
Total	136	100.0	78	100.0	516	100.0

Note: Bones from haddock and garfish were found, but weight was not estimated and the data are therefore not used in in the calculations.

caught several times in pound nets by local fishers on the south coast of Lolland (M. Schjelde, pers. comm., 2005).

Atlantic herring was the principal prey item of the seal diet during spring in Løgstør Bredning, accounting for 90% of the weight consumed (Table 1). The importance of Atlantic herring in seal diet there declined in summer and autumn, then increased again in spring the following year. In summer and autumn, seals fed on a wide variety of prey, although their diet was dominated by a few key species. Eelpouts and plaice were important in summer, accounting for 23% and 18% of the weight consumed, respectively (Table 1), whereas flounders and gobies dominated in autumn, 31% and 36% of the weight consumed, respectively. In contrast to these findings, flounder dominated seal summer diet (65%) in Nissum Bredning (Table 1). In Løgstør Bredning, the mean number of fish recovered in harbour seal scats and the mean total weight per scat varied with season ($r^2 = 0.14$, $F_{2,82} = 6.75$, $p = 0.002$, and $r^2 = 0.11$, $F_{2,82} = 5.33$, $p = 0.007$, for mean fish number and mean total weight, respectively). Hence, there were significantly fewer fish per scat in spring than in summer or autumn, although there was a significantly higher mean total weight per scat in spring than in autumn (Figure 2a).

There were no seasonal differences in the mean number of fish recovered and the mean total weight per scat in the harbour seal material from the Rødsand area ($r^2 = 0.00$, $F_{2,10} = 0.01$, $p = 0.986$, and $r^2 = 0.07$, $F_{2,10} = 0.40$, $p = 0.681$, for mean fish number and mean total weight, respectively) (Figure 2b). In the Rødsand area, cod (*Gadus morhua*) dominated both spring and autumn seal diet (42% and 43%, respectively, of the weight consumed) (Table 3). Cod were less common in summer (22%), when flounder and plaice together made up 52% of the weight consumed. In all, seven newly ingested garfish lacking their heads were recovered in two seal digestive tracts from Rødsand.

In contrast to the diet of seals, cormorant diet showed no marked seasonal trends ($r^2 = 0.02$, $F_{2,138} = 1.06$, $p = 0.348$, and $r^2 = 0.002$, $F_{2,138} = 0.14$, $p = 0.873$, for mean fish number and mean total weight, respectively) (Table 2). Bullrout, black goby, and eelpout were the most important prey species in Løgstør Bredning. Bullrout accounted for ~30% in all seasons. Summer diet was dominated by eelpout (37%), whereas the diet in autumn was dominated by black goby (34%). In contrast to these findings, the cormorant diet composition in Nissum Bredning was dominated by plaice (36%) in spring. Plaice and cod together dominated the summer diet, constituting 43% and 44% of the weight consumed, respectively.

Diet competition between harbour seals and great cormorants

In Løgstør Bredning, the spring diet of seals consisted of eight species, in contrast to the 15 prey species in great cormorant spring diet. Seven prey species were preyed on by both, of which only Atlantic herring constituted >5% in the diet of both. Seals fed almost exclusively on Atlantic herring (90% of the weight consumed) in spring, but that species was of minor importance to cormorants in spring (7% of the weight consumed). Hence, the competition in spring between cormorants and seals in Løgstør Bredning seems to be minimal (Figure 3a). Seal and cormorant summer diet consisted of 15 and 13 prey species, respectively, of which 12 were preyed on by both, but only plaice, eelpout, bullrout, and black goby constituted >5% in the diet of both. These prey items constituted 55% of seals' summer diet compared with 87% of cormorants' summer diet (Figure 3b). In autumn, seals took 12 prey species and cormorants 9, of which eight were taken by both predators, although only sand goby and black goby constituted >5% of the diet of both predators. Combined, these prey species in autumn made up 50% of the harbour seal diet and 46% of the cormorant diet (Figure 3c). Competition for black goby is particularly evident, because this species constituted >20% of the diet of both.

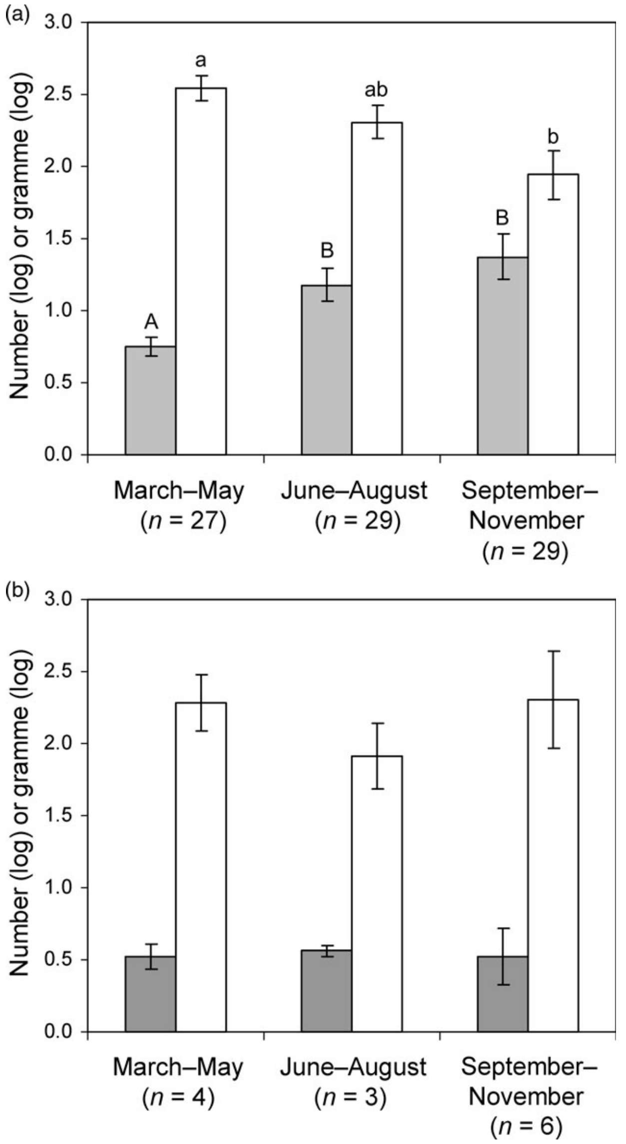

Figure 2. Seasonal variation in the mean number of fish (grey histograms) and mean total weight per scat (white histograms) in harbour seal scats from (a) Løgstør Bredning during 1997 and 1998, and (b) Rødsand during the period 2001–2005. *n* is the number of scats, and the bars indicate s.e. Shared letters denote non-significant differences ($p > 0.05$), and vice versa.

Estimated length frequency distributions of the fish species eaten by both seals and cormorants in Løgstør Bredning are given in Figure 3d–f. Generally, seals preyed on larger fish than cormorants, but the difference was only significant for Atlantic herring in spring. At that time, seals consumed herring of mean length 21.5 ($\pm$5.5) cm, whereas the length of herring consumed by cormorants was 10.2 ($\pm$6.9) cm ($D = 0.3846$, $p = 0.042$) (Figure 3d).

Estimated length distributions of seal and cormorant prey were compared with those derived from trawl catches. The sizes of prey eaten by seals and cormorants reflected the sizes available in Limfjord, so we conclude that seals and cormorants do not seem to select particular prey sizes. Because trawl surveys were carried out in September, this comparison was made only with autumn data (Kolmogorov–Smirnov two-sample tests, $p > 0.24$ for all tests) (Figure 4). Harbour seals in Limfjord tend to select larger fish (Figure 4). Moreover, the size of herring in the harbour seal diet does not seem to reflect the availability of various sizes of herring in Limfjord (as revealed by the autumn survey trawl) (Figure 5).

In spring, harbour seals consumed Atlantic herring larger than the allowed minimum size in the fishery, so in spring at least, seals were in direct competition with the fishery (Figure 3d). This was not the case in summer and autumn. All other fish species were consumed at sizes smaller than allowed fishery minimum sizes, so competition was only indirect in that small fish grow to commercial size some years later (Figures 3e and 4).

Discussion

The results of this study confirmed the polyphagous nature of both harbour seals and great cormorants documented in previous studies (Härkönen and Heide-Jørgensen, 1991; Bowen and Harrison, 1996; Tollit and Thompson, 1996; Andersen *et al.*, 2004), and also that both species are generalist feeders (Bigg, 1981; Härkönen, 1987; Tollit *et al.*, 1997a). The changes in diet between seasons documented here should be seen in the light of varying prey availability. Specifically, Atlantic herring enter Limfjord in spring to spawn (Pedersen, 1996), and it was at that time that herring constituted the bulk of harbour seal diet in Løgstør Bredning. Thompson *et al.* (1991) noted that Scottish harbour seals similarly preyed on clupeids when they were particularly available. This may be due to Atlantic herring being a high-energy food source, generating some degree of prey selection by harbour seals (Thompson *et al.*, 1997). Harbour seals in this study clearly relied on resident fish species, such as eelpouts, black gobies, and flounders in summer and autumn, perhaps related to a lesser availability of Atlantic herring then. Further, in a previous study by Friis *et al.* (1994), black gobies dominated harbour seal autumn diet in Løgstør Bredning, and the authors

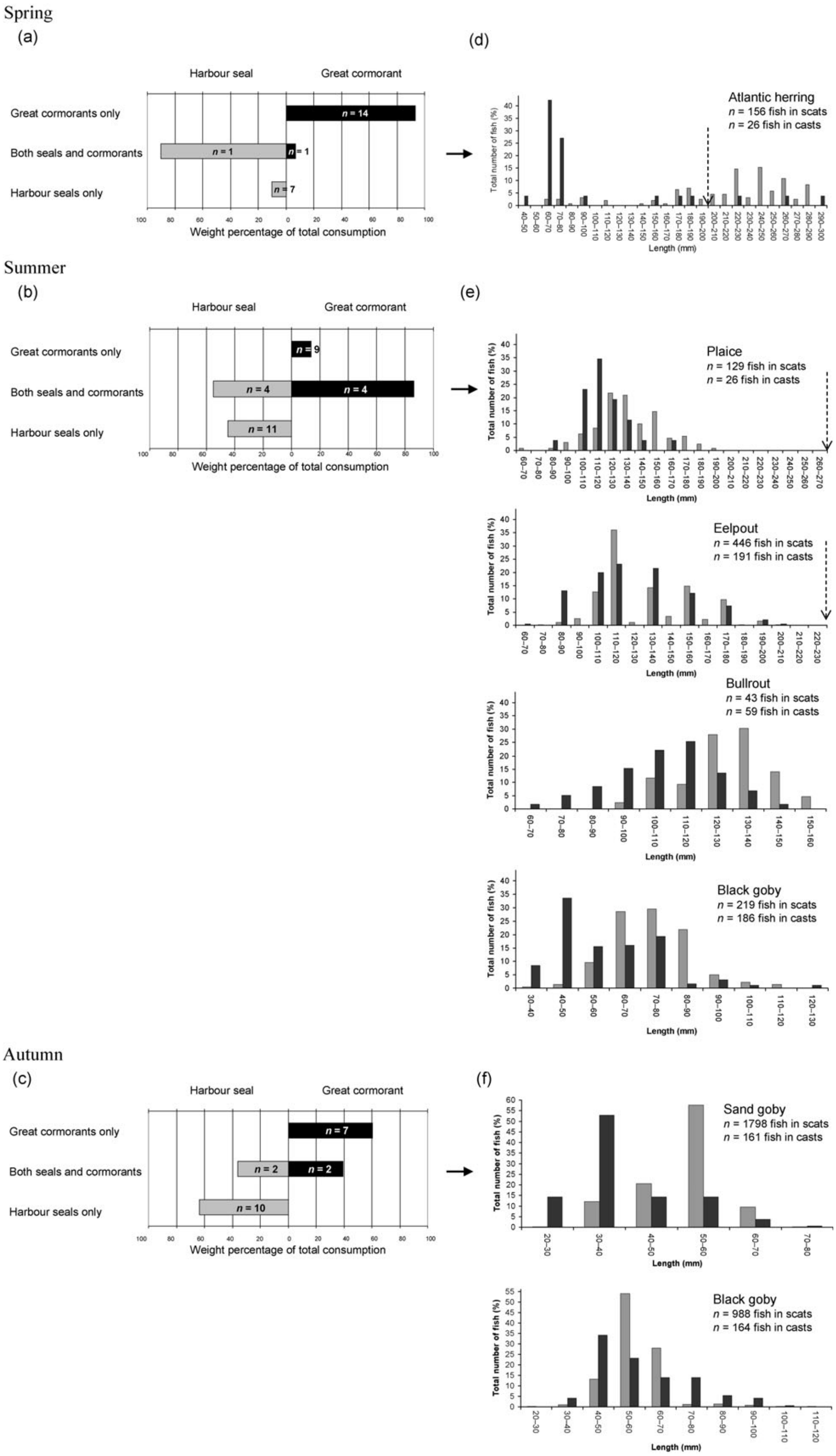

Figure 3. Diet overlap between harbour seals and great cormorants in Løgstør Bredning during (a) spring, (b) summer, and (c) autumn. Only species accounting for >5% of the total biomass in both seal and cormorant diet were compared. *n* is the number of prey species. Comparisons of the length frequency distributions of the species overlapping in the diet of harbour seals (grey histograms) and great cormorants (black histograms) in Løgstør Bredning are shown for (d) spring, (e) summer, and (f) autumn. The dotted lines indicate fishery minimum sizes.

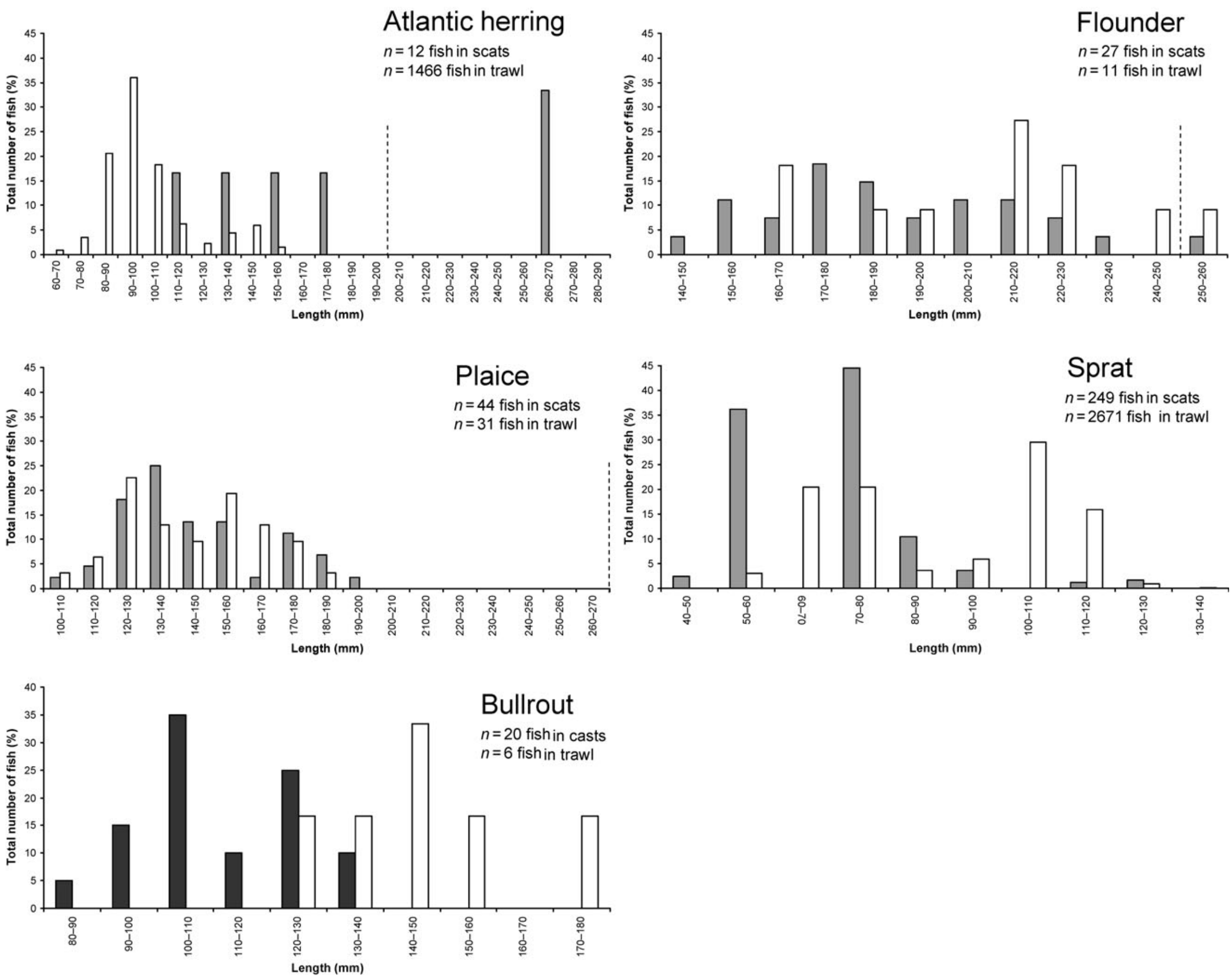

Figure 4. Comparisons of length frequency distributions of key species in the diet of harbour seals (grey histograms) and great cormorants (black histograms) with length frequency distributions of the same fish measured during fish trawl surveys in Limfjord during September 1997 (white histograms). The vertical dotted lines indicate fishery minimum sizes. *n* is the number of individuals found in harbour seal scats and great cormorant casts, and in survey trawls.

suggested that this reflected a marked increase in the population of black gobies after the mid-1980s. Hence, harbour seals are perhaps specialist feeders or maybe specialists and generalists, as suggested by Grellier and Hammond (2006). Our results from Limfjord suggest that seals may prefer to eat herring when the latter are available in spring, whereas they seem to be generalist feeders during the rest of the year when herring have migrated out of the area, so no particular species is preferred.

In contrast to the diet of harbour seals, that of great cormorants did not vary markedly across season, because great cormorants generally relied on bullrouts as prey throughout the year. In an earlier study (Madsen and Spärck, 1950), Danish cormorants responded to increased herring availability, so it was unexpected that Atlantic herring constituted $<7\%$ of the great cormorant spring diet during this study.

Both harbour seal and great cormorant diets varied among localities in Limfjord. Harbour seals generally forage up to 30–50 km from their haul-out sites (Thompson and Miller, 1990; Thompson *et al.*, 1991; Tollit *et al.*, 1998), so it is likely that harbour seals hauling out in Limfjord forage in all parts of Limfjord and also in the North Sea. It is, however, worth noting that all prey species recovered from harbour seal scats are found regularly in Limfjord (Hoffmann, 2000). Most prey species consumed by harbour seals in Nissum Bredning are found in (sandeels) or live on (flatfish) the seabed. No samples were collected during spring in this area, so similar dominance of herring then could not be concluded.

Great cormorants in Nissum Bredning had a broader diet spectrum than cormorants in Løgstør Bredning. Grey gurnard, long rough dab, and haddock are not generally present in Limfjord (Hoffmann, 2000), but they were found in the diet of cormorants at Nissum Bredning, indicating probably that great cormorants also forage in the North Sea. Moreover, there are indications of a marked decline in overall prey availability in Limfjord (Hoffmann, 2000), which may have forced both harbour seals and great cormorants to make longer foraging trips, perhaps out of Limfjord.

Harbour seal diet was apparently limited during autumn. To maintain their energy intake then, they were compelled to consume a large number of small fish that were available.

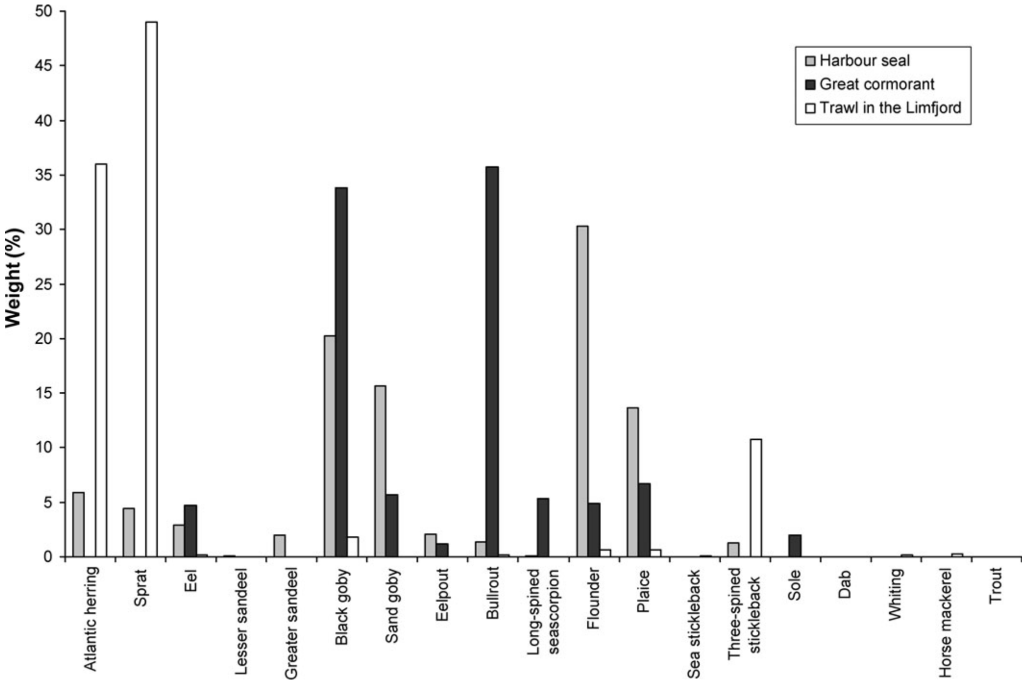

Figure 5. Relative abundance of fish species in Limfjord (white histograms), and their proportion (by weight) in the diet of harbour seals (grey histograms) and great cormorants (black histograms).

In spring, they could manage with a smaller number of the much larger herring available then. Comparing this result with harbour seal diet in the Rødsand area, it is obvious that harbour seals there consume fish of a much more uniform size through the year, and that they are apparently not as limited in diet. The Rødsand data were pooled across 5 years, and may cover between-year differences (Middlemas *et al.*, 2006).

The fact that harbour seals might have limited diet during some time of the year may increase the importance of possible competition between harbour seals and great cormorants in Limfjord. Both harbour seals and great cormorants feed on the seabed (Härkönen, 1988). Cormorants generally forage in shallow water, whereas harbour seals prefer to feed on plain seabeds down to 30 m (Härkönen, 1988). Hence, in Limfjord, which has an average depth of 5 m (maximum 28 m) (Lissner *et al.*, 2004), dietary overlap between harbour seals and great cormorants would be expected. Competition between harbour seals and great cormorants was minimal in spring, because herring were of only minor importance to cormorants. Moreover, the herring consumed by cormorants were significantly smaller than those taken by seals. In summer and autumn, the extent of dietary overlap increased. In summer, competition seemed to have the greatest impact on cormorants, because the overlapping prey species constituted a larger portion of the diet of great cormorants. Although not significantly, the fish consumed by seals were larger than those consumed by cormorants. Competition eases in autumn, because most of the Danish cormorant population leaves Denmark between August and October only to return in March (Bregnballe *et al.*, 1997).

Some 50 years ago, Madsen and Spärck (1950) argued that herring were so abundant in Danish waters that the ~300 Danish breeding pairs of cormorants at that time could feed on them without having any effect on the fishery. In 1997, the total Danish population of cormorants had become 40 000 pairs, the total Danish harbour seal population had increased from ~2000 in 1977 to some 11 000 in 1997 (NERI, unpublished data) (1400 in Limfjord), and the fish populations in Limfjord had declined markedly. This scenario caused an increase in interactions between the fishery and cormorants and seals during the 1990s, in terms of both interference around static fishing gear and competition for the same fish resources. Hence, harbour seals and great cormorants are often viewed now as having a negative impact on commercial fish species. However, in this study, only a few commercial species (and sizes) were included in their diet. Flounder, plaice, eelpout, cod, and Atlantic herring are exploited by seals, cormorants, and the fishery. Of these, only Atlantic herring were consumed by harbour seals in sizes larger than the allowed minimum size in the fishery; all other prey species taken by harbour seals and great cormorants were smaller than the minimum allowed sizes. Hence, Atlantic herring was the only prey species on which harbour seal could have had a direct impact. Harbour seals and great cormorants preyed on other prey species at sizes smaller than the allowed minimum sizes in the fishery, which might indicate indirect competition, but this predation might compensate for other mortalities. Moreover, such predation might, through a reduction in intraspecific competition among prey species, give the survivors an increased chance to attain the size required by the commercial fishery size (Friis *et al.*, 1994). However, not applying correction factors in our study has inevitably biased the size distribution towards smaller sizes, and this fact must be kept in mind when comparing fish size distribution in harbour seal and great cormorant diets, and the fishery.

The harbour seal population in Limfjord (1400 animals) consumed some 424 t (based on a daily consumption of 5 kg per seal (Bonner, 1982) of herring during 1997 compared with the

2680 t of herring landed by the commercial fishery. Hence, seals do compete with the fishery, because they consume herring of size larger than the allowed minimum size in the fishery. However, the amount taken is still six times less than that taken by the fishery (without any correction factors being applied). Other prey species were caught at sizes smaller than the minimum fishery sizes, by both harbour seals and great cormorants. If it is assumed that there are sufficient small fish to sustain the stocks of fish at commercial size, the impact on the fishery in Limfjord will be minor. However, if the seals and cormorants are limiting recruitment to commercial size, there will be competition.

By not applying correction factors in our study, we underestimated fish sizes and therefore our values are minimum estimates, but unfortunately the otoliths from the various prey species do not reduce in size by the same amount. Grellier and Hammond (2005, 2006) showed, in a controlled study with captive grey seals, that larger otoliths had greater digestion coefficients, which leads to even greater underestimation of prey size in the case of larger otoliths. Moreover, Grellier and Hammond (2005) demonstrated that otoliths from larger fish have a greater possibility of being recovered (greater recovery rates) in samples, which results in overestimation of their number as well. However, we believe that the extent of competition between harbour seals, great cormorants, and the fishery, as well as the limited values calculated for the food resources for harbour seals in Limfjord, will persist even if correction factors were applied.

Acknowledgements

We thank E. Hoffmann for supplying raw trawl data from the Limfjord fish trawls, P. H. Mortensen for assistance with otolith identification, and A. Linnet for help in the field. M. Schjelde, a Rødsand fisher, supplied valuable information about the fish stocks in the Rødsand area. The contributions by EHH and DH were used for partial fulfilment of Masters of Science degrees at the University of Southern Denmark. Carol Bang-Christensen is thanked for comments on an earlier draft of this manuscript.

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doi:10.1093/icesjms/fsm092

PAPER III

THE EFFECT OF A LARGE DANISH OFFSHORE WIND FARM ON HARBOR AND GRAY SEAL HAUL-OUT BEHAVIOR

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Marine Mammal Science 26:614-634.
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Marine Mammal Science

MARINE MAMMAL SCIENCE, 26(3): 614–634 (July 2010)

DOI: 10.1111/j.1748-7692.2009.00364.x

The effect of a large Danish offshore wind farm on harbor and gray seal haul-out behavior

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ABSTRACT

This study investigates the effects of the construction and operation of a large Danish offshore wind farm on harbor and gray seal haul-out behavior within a nearby (4 km) seal sanctuary. Time-lapse photography, visual monitoring, and aerial surveys were used to monitor the number of seals on land in daylight hours. Seals were monitored during two preconstruction periods (19 June–31 August 2001 and April–August 2002), a construction period of the wind farm (August 2002–December 2003), and a period of operation of the wind farm (December 2003–December 2004). Monthly aerial surveys were conducted to estimate the proportion of seals in the sanctuary relative to neighboring haul-out sites. From preconstruction to construction and through the first year of operation the number of harbor seals in the sanctuary increased at the same rate as the number of seals at the neighboring haul-out sites. No long-term effects on haul-out behavior were found due to construction and operation of the wind farm. However, a significant short-term decrease was seen in the number of seals present on land during sheet pile driving in or near the wind farm. Acoustic deterrents were utilized simultaneously to avoid hearing damage.

Key words: offshore wind farm, human disturbances, gray seal (*Halichoerus grypus*), harbor seal (*Phoca vitulina*), haul-out behavior, aerial surveys, time-lapse photography.

During the last decade, marine areas have been increasingly exploited by humans (Renouf *et al.* 1981, Allen *et al.* 1984, Suryan and Harvey 1999, Harris *et al.* 2001, Seuront and Prinzivalli 2005, Johnson and Acevedo-Gutiérrez 2007). Recently, offshore wind farms have been constructed to cover the increasing demand for non-fossil energy supplies. Limited information is available on the effect of offshore wind farms on seals.

Seals may be very tolerant to recurring disturbances that do not pose a threat. For example, the Øresund Bridge, constructed in 1997–1999 between Sweden and Denmark, only about 1 km from a seal haul-out site, had no apparent permanent effect on the seals. The number of seals hauling out close to the construction site decreased during construction but after construction the seals returned to their favorite haul-out sites close to the bridge (Teilmann *et al.* 2006*b*).

Though hauling out is important to both harbor and gray seals for resting, molting, parturition, and nursing their young (Boulva and McLaren 1979, Watts 1996, Stevick *et al.* 2002), they spend most of their time in the water. Harbor seals haul out more frequently during the summer months, particularly during molting and parturition when they are reported to spend about half of their time on land (Heide-Jørgensen and Härkönen 1988, Härkönen *et al.* 1999). Gray seals are more frequent during their molting season in June. The Baltic gray seals breed on the ice in late February and beginning of March (Hook and Johnels 1972), but only a few gray seals are born annually on Danish localities (Edrén *et al.* 2005). The gray seals are therefore not expected to be more frequent on land in Denmark during parturition.

Between 2002 and 2003 the world's largest offshore wind farm at the time, Nysted Offshore Wind Farm, consisting of 72 2.3 MW wind turbines, was constructed 4 km from the Rødsand Seal Sanctuary. It is possible that some of the activities involved in construction and operation of the wind farm could have a negative impact on the seals. The most likely sources of possible effects are the physical presence and noise from ships going to and from the wind farm during construction and operation and the temporary or permanent loss of habitats near the wind farm. Both harbor and gray seals use the sanctuary for resting and breeding. The study area may be more important to the harbor seal as they remain within approximately 50 km of the seal sanctuary year-round (Dietz *et al.* 2003). Gray seals appear to have alternative feeding and haul-out sites as they move between sites in Sweden, Estonia, and Denmark (Dietz *et al.* 2003). Fewer gray seals than harbor seals use the Rødsand Seal Sanctuary. Thus, this study focuses primarily on harbor seals.

The seals in the area of Rødsand Seal Sanctuary are familiar with human activities. Passenger ferries pass the area every few hours at a distance of 7 km and the waters 13 km south of the sanctuary comprise one of the world's busiest shipping routes. From September to March, when the seal sanctuary is open for access, the sand bank is used for hunting birds, and small boats are regularly seen in the area. Moreover, a few hunting permits are issued every year allowing local fishermen to shoot harbor seals near their fishing gear outside the sanctuary.

This study investigates how construction of the Nysted Offshore Wind Farm influenced short- and long-term haul-out behavior of harbor seals (*Phoca vitulina*) and gray seals (*Halichoerus grypus*) on a sanctuary sand bank 4 km from the Wind Farm.

Materials and Methods

Study Area

Nysted Offshore Wind Farm was constructed in the southwestern Baltic Sea in 2002–2003, 7 km west of Gedser, the southernmost city of Denmark (Fig. 1). The water depth within the area of the wind farm ranges from 5.5 to 9.5 m. The area has no significant tide but the water level fluctuates irregularly with strong westerly winds in the North Sea forcing water masses into the Kattegat, Belt, and Baltic Sea. Amplitudes rarely exceed 1 m. About 2 km north of the wind farm, a shallow (<8 m deep) lagoon-like area is formed by a 10-km-long isolated sand bank. The western part of the sand bank is a favorite harbor seal haul-out site. The sand bank also serves as a resting area for gray seals. This part of the sand bank is within the 450 ha Rødsand Seal Sanctuary, which was established in 1978. The sand bank is situated 4 km northeast of the wind farm (Fig. 1). A closed zone with a radius of about 500 m is enforced around the tip of the sandbank from 1 March to 30 September to avoid any disturbance from boat activity during breeding and molting of the harbor seals. The closest alternative haul-out site (Vitten) is located 16 km west of the seal sanctuary (Fig. 1).

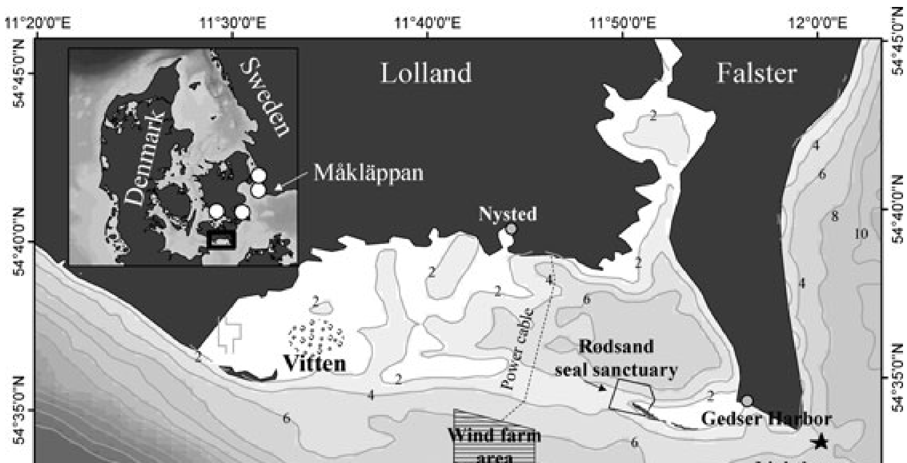

Figure 1. Map of study area in southeastern Denmark, showing the wind farm, Rødsand Seal Sanctuary, and Vitten, another haul-out site in the vicinity. Pile driving occurred in the wind farm area, Gedser harbor, and at Gedser lighthouse. Four other haul-out sites in the vicinity of the seal sanctuary with possible exchange of seals are located outside the large map and marked with white circles on the inserted map.

Table 1. Study conditions for the effects on Danish harbor and gray seals during and after construction of an offshore wind farm (Nysted).

Study periods	Time period	Monthly aerial surveys	Visual observations	Time-lapse photography (still images)	Average wind speed
First preconstruction	June–August 2001		On-site (650 h) (bird tower)		
Second preconstruction	April–16 August 2002	4 surveys		1,798	6.8 m/s
Construction	17 August 2002–November 2003	6 surveys		3,403	6.1 m/s
Operation	December 2003–December 2004	9 surveys	Online (342 h) (video camera)	2,550	6.6 m/s

Construction Work

Activities associated with construction of the wind farm took place from early February 2002 and concluded in December 2003 when the wind farm began normal operation. During the first 6 mo, some ship activity related to construction occurred about 10 km from the seal sanctuary. This activity was considered minor in comparison with the ship activity from ferries and cargo ships in the area (13 km from the seals). The actual construction of the wind farm began on 17 August 2002 with the digging of a trench for the 132 kV cable from the wind farm to land (passing 5 km west of the seal sanctuary). Table 1 shows the various stages of construction and operation during the study. A detailed schedule of the construction work can be found in Figure S1.

Pile Driving

Each of the 72 2.3 MW turbines was placed on a concrete foundation laid on a bed of stone chippings. At one location the seabed was too soft and steel sheets were driven into the seabed to support the foundation using vibration pile drivers. Construction of this foundation occurred in the southwestern end of the wind farm, approximately 10 km from the seal sanctuary (26 August–20 November 2002). During the study, three other pile driving periods occurred outside the wind farm: (1) during the mounting of four meteorological poles east and west of the wind farm area (5–11 km from the sanctuary, 26–28 September 2003), (2) during construction of a new sea wall by pile driving corrugated steel sheets in Gedser harbor (7 km east of the seal sanctuary, 5–12 September 2002), and (3) during construction of a new lighthouse outside Gedser harbor (28 July 2003) (Fig. 1).

Underwater noise from the pile driving was not measured during this study. Measurements from other pile driving activities showed a source level of 235–272 dB re 1 μPa at 1 m (Nedwell *et al.* 2005, Tougaard *et al.* 2009), intensities that are likely to affect the behavior of marine mammals and induce hearing impairment at close range (Southall *et al.* 2007). At Nysted, a seal deterrent (189 dB re 1 μPa at 10–15 kHz) and porpoise pingers (145 dB re 1 μPa at 20–160 kHz) were therefore deployed from the pile driving platform and activated 30 min prior to pile driving at the turbine foundation and meteorological poles to limit the number of seals and porpoises exposed to physically damaging noise (see Discussion). No mitigation measures were employed prior to the work at Gedser harbor or Gedser lighthouse. Thus, the data analysis of pile driving had three different levels: no pile driving, pile driving without deterrents, and pile driving with deterrents.

There was a 20% overlap between the pile driving at the wind farm and Gedser lighthouse. However, because the wind farm is closer to the Rødsand seal haul-out site, Gedser contribution to pile driving was ignored.

Sampling Methods

Three different sampling methods were used to collect data: aerial surveys, visual monitoring, and time-lapse photography (Table 1). All seals on land in the sanctuary were sampled. The different types of sampling methods were analyzed assuming generic sources of variation: (1) differences between the three periods, (2) seasonal variation, (3) diurnal variation, and (4) effect of wind speed and direction. Wind speed and direction were measured at two locations in the vicinity of the wind farm. Wind conditions were different during the three periods, and therefore it was important to include wind as a potential explanatory factor.

The two seal species are combined in the analysis of aerial survey data because gray seals were difficult to identify from the air at some of the localities except for the Swedish locality Måkläppan where the two species formed separate groups. For this locality, only the harbor seals were included (see inserted map in Fig. 1). The two seal species were pooled in the analysis of time-lapse photography at the sanctuary as distinction was not possible. However, seal species were distinguished during visual monitoring and were therefore analyzed separately in this data set.

Aerial Surveys

The seasonal haul-out pattern and number of seals in the sanctuary in relation to five other nearby haul-out sites (Fig. 1) were studied by monthly aerial surveys during 2002–2005 (except for November and December, when no seals rested on land. These six sites in the southwestern Baltic Sea constitute one population unit of harbor seals with limited exchange to other harbor seal populations in the Baltic proper and the Kattegat Sea between Sweden and Denmark (Dietz *et al.* 2003, Olsen *et al.* in press). The monthly surveys were supplemented by yearly aerial surveys from 1990 to 2005 by the Danish environmental monitoring program conducted during the molting season in late August.

The plane used was a Cessna 172 Skyhawk flying at low speed (135 km/h) at an altitude of 150–200 m above the seal haul-out sites. Seals were counted visually and pictures were taken for verification of groups larger than 10 individuals. A total of 64 aerial surveys were conducted. To reduce variation across different types of weather and time of day, surveys were conducted at the same time of day (before noon) and during similar weather conditions (*e.g.*, avoiding rain and wind speeds >10 m/s).

Statistical Analysis of Aerial Surveys

The number of seals counted at Rødsand was considered to be distributed binomially, with a parameter (p) denoting the proportion of seals at Rødsand relative to the total number of seals at all localities surveyed. The proportion of seals at Rødsand was modeled by yearly and monthly factors as well as factors describing the periods of second preconstruction, construction, and operation and the interaction of period with month. The yearly factor was nested within the three periods (second preconstruction, construction, and operation). There was no replication of the monthly variation within periods and consequently, the interaction month × period represented a combination of changes in the seasonal pattern due to periods and interannual variation, *i.e.*, the effect of periods could not be separated from interannual variation. Data were analyzed using generalized linear models (GLMs) using a logistic link function in SAS (Version 9.1.3; PROC GENMOD).

Generally, the models tended to over disperse; however, this was accounted for in the test statistics by calculating the scaled deviance (see *e.g.*, McCullagh and Nelder 1989). The number of seals counted at Rødsand was similarly analyzed as a log-normal distributed variable subject to the same sources of variation. The significance of the different factors was tested using the Likelihood Ratio test at 5% significance level, eliminating the least significant factor ($P > 0.05$) one at a time. *Post hoc* tests were carried out by calculating contrasts, *i.e.*, differences between means of the model.

Visual Monitoring

In summer 2001, during the first preconstruction period, on-site seal monitoring was conducted from a 7 m high bird observation tower located just outside Rødsand, at a distance of 1.1 km from the seals' most preferred haul-out site. A total of 43 days of monitoring was completed in eight periods of 3–7 d duration. Monitoring was performed with a 10 × 50 binocular and a 20× monocular telescope. The total number of harbor and gray seals on land was noted hourly from 0600 to 2100 (see Table 1 for details on sample size and period).

In April 2002, 4 mo before construction activity began, a remotely controlled camera system (SeeMore Wildlife System Inc., Hommer, AK) with two video cameras was mounted on a 6 m tower, 300–400 m from the seals inside the sanctuary. The video cameras were powered by 12V DC batteries charged by two solar panels and a wind generator placed on the top of the tower. Each camera had a 300× zoom lens. By use of microwave transmission the live video images were transmitted to a transformer station in Gedser (11 km from the cameras) where a computer, connected to the Internet, received the signals. The cameras were controlled remotely by a VHF link, and a custom-made software program provided real-time views and control of the cameras (pan, tilt, zoom, and wipe). The images from the cameras were either (1) viewed in real time (visual monitoring) or (2) stored on a computer as time-lapse pictures. Because of the low angle (1°) from the seals to the cameras 300–400 m away, it was not possible to count the exact number of seals in the time-lapse images when the number of seals exceeded 20. However, the total number of seals could be counted online in real time with the use of the zoom function because the seals frequently lift their head to scan their surroundings. It was possible to make distinctions between harbor and gray seals with the use of the zoom function.

From June through August 2004, the total number of seals on land was counted online hourly in real time from 0600 to 2100 (see Table 1 for details on sample size). These counts were compared with those from the observation tower in 2001 (first preconstruction period). For intercalibration of the two methods, an additional

72 hourly simultaneous observations were conducted from the observation tower and the online video camera during four 2-day sessions in June, July, and September 2004. No visual monitoring was conducted during the construction period.

Statistical Analyses of Visual Monitoring

The variance of count data is commonly assumed proportional to the count (McCullagh and Nelder 1989), and therefore, a weighting factor for each observation of $1/\sqrt{n+1}$ was employed (+1 to account for zero observations), where n is the count. All analyses were carried out separately for the number of harbor seals and the number of gray seals.

First, visual monitoring (both online and onsite) was intercalibrated by calculating the difference between the two corresponding counts. The weighting factor for the difference was as above with n equal to the average of the two counts. The difference was investigated for systematic deviations from 0 in general, with respect to time (trend) and with respect to the hour (diurnal) of observation. Following this analysis, a combined time series for the two methods of counting was obtained.

The potential impact of the wind farm on the seal counts at the sanctuary was investigated by examining changes with respect to the two periods in the seasonal variation (period × month), in the diurnal variation (period × hour), in the response to wind speed (period × wind_speed and period × wind_speed^2), and in the response to wind directions (period × wind_direction). These different interactions were analyzed separately.

Secondly, the seasonal variation in seal counts was modeled by means of a locally weighted regression (LOWESS, Cleveland *et al.* 1988) common to both periods (summer of 2001 and 2004), and residuals from this regression were analyzed with a general linear model assuming systematic variations to stem from the following factors: (1) Diurnal variation by hourly values (hour), (2) baseline *vs.* operation period (period), (3) linear response to wind speed (wind_speed), (4) wind direction dependent response (wind_direction), and (5) quadratic response to wind speed (wind_speed^2). It was hypothesized that there would be an optimum wind speed for seals hauling out and therefore, the effect of wind speed was modeled as a quadratic response.

The potential impact of the wind farm on the seal counts at the seal sanctuary was investigated by examining changes with respect to the two periods in the seasonal variation (period × month), in the diurnal variation (period × hour), in the response to wind speed (period × wind_speed and period × wind_speed^2), and in the response to wind directions (period × wind_direction). These different interactions were analyzed separately.

Third, marginal means were computed from these models to describe the different sources adding negatively or positively to the overall seasonal variation described by the LOWESS regression.

Time-lapse Photography

In addition to the visual monitoring, still images were stored (JPEG format) every 5 s during daylight hours from April 2002 to December 2004 (during the second preconstruction, construction and operation periods). The two methods could not be compared since the exact number of seals in the time-lapse images was difficult to determine due to the low resolution from the wide angle pictures, which was necessary to make sure that all seals were included in the images. Therefore, the images were categorized into six group size classes: 0 seals, 1–5 seals, 6–10 seals, 11–15 seals, 16–20 seals, and >20 seals. Only hourly counts of seals from the images were analyzed. Seal group size was categorized into 20 levels by hour (0400–2300), 12 levels by month (January–December), three levels by period (second preconstruction, construction, operation), and eight levels by wind direction (N, NE, E, SE, S, SW, W, NW). Hourly counts within the six group size classes were computed and the percent of time when seals hauled out over the course of the day was calculated.

The potential impact of the wind farm on the seals hauling out at the sanctuary was investigated by examining changes in the seasonal variation (period × month), in the diurnal variation (period × hour), in the response to wind speed (period × wind_speed and period × wind_speed^2), and in the response to wind directions (period × wind_direction). These different interactions could not be analyzed simultaneously in all models, due to over-parameterization, and were therefore analyzed separately.

After the overall sources of variation were determined, we investigated the potential influence of the pile driving activity on seal behavior by identifying the seal group size classes associated with the time of pile driving and included that as an additional factor in the model.

Statistical Analysis of Time-lapse Photography

The six group size classes obtained from the stored images and used to describe the number of seals on land were modeled using the multinomial distribution. This model is an ordinal model since the six group size classes represent a natural order of increasing number of seals. These data were analyzed within the framework of generalized linear models using a logistic link function (McCullagh and Nelder 1989), assuming that shifts between the group size class probabilities were affected by different factors: (1) Seasonal variation by monthly values (month), (2) diurnal variation by hourly values (hour), (3) baseline *vs.* construction and operation (period), (4) changes in the seasonal pattern between periods (period × month), (5) linear response to wind speed (wind_speed), (6) quadratic response to wind speed (wind_speed^2), and (7) wind direction dependent response (wind_direction). Thus, these factors would describe a shift towards higher or lower seal group size classes by increasing or decreasing the cumulative category probabilities. This model was then modified to examine changes in the wind dependency between periods by replacing period × month with the interactions of period and the three wind terms.

The model parameters were estimated by maximum likelihood regression, and the significance of the difference factors was tested by means of a likelihood ratio test (chi-square distributed with degrees of freedom equal to the number of free parameters reduced with this factor). Differences between the different qualitative factors were calculated as contrasts between parameter estimates. Marginal means of the category probabilities were calculated from the parameter estimates for the different factors using the inverse logistic function for back-transformation. Marginal means describe typical responses of the different factors in the model that are not affected by lack of balance in the data (differences in the number of observations for different months and times of the day).

We acknowledge the lack of true controls in this study for some of the analyses and with replication for time in this study as the study periods are confounded with changes in time and cannot be separated, but the results will be discussed in light of these statistical concerns.

Results

Results of Aerial Surveys

The aerial surveys conducted in August at Rødsand Seal Sanctuary and at the adjacent haul-out sites showed a gradually increasing trend in the number of seals (harbor and gray seals combined) from 1990 to 2005, though declining in 1994 and 2002 (Fig. 2a). The highest number of seals at Rødsand to date was recorded in 2005 (mean = 173) compared to a mean of 154 seals in 2004 and approximately 100 seals in 2002 and 2003 (construction period). The number of seals in the sanctuary increased

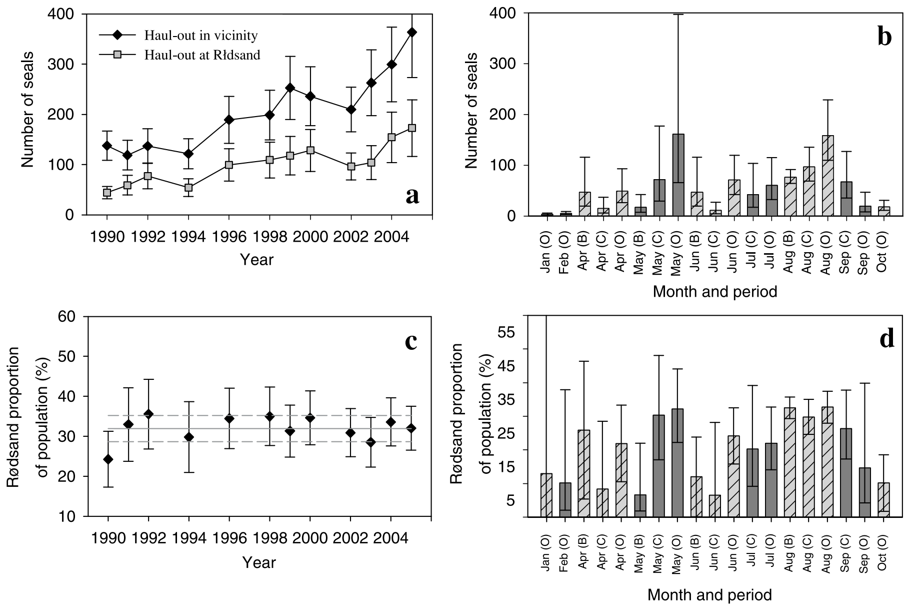

Figure 2. Aerial surveys. Number of both harbor and gray seals combined on land counted from aerial surveys at Rødsand Seal Sanctuary and the five other haul-out sites in the vicinity, shown in Figure 1. Mean number of seals during late August (a) at Rødsand Seal Sanctuary (gray squares) and at all the other haul-out sites in the vicinity (black diamonds) and the Rødsand proportion (%) of the population relative to all other localities in the vicinity during late August (c) from 1990 to 2005 ($n = 3$ for each year). Mean number at Rødsand (b) and proportion (%, d) of Rødsand population from monthly surveys during the investigated periods: preconstruction (B, August 2001–June 2002), construction (C, August 2002–September 2003), operation (O, January 2004–October 2004). Not all months were surveyed during the periods. The error bars show the 95% confidence limits of the mean estimate. The striped and solid bars in (b) and (d) are to make it easier for the reader to distinguish between the months.

Table 2. Variations in count of seals (harbor and gray) from aerial surveys at Rødsand ($n = 64$) and the proportion of seals at Rødsand relative to all haul-out sites in the region ($n = 63$) analyzed within the framework of generalized linear models using lognormal and binomial distributions, respectively. The interaction period[a] × month was further partitioned into changes between periods for specific months and differences between periods within each month. Significant variations ($P < 0.05$) are in bold.

	Count of seals at Rødsand			Proportion of seals at Rødsand		
Source of variation	df	χ^2	*P*	df	χ^2	*P*
Period[a]	2	17.14	**0.0002**	2	4.38	0.1117
Year (nested in period)[b]	9	26.13	**0.0019**	9	7.33	0.6033
Month	8	298.04	**<0.0001**	8	32.58	**<0.0001**
Period[a] × month[c]	8	39.26	**<0.0001**	7[d]	13.13	0.0690
April (B, C, O)[e]	2	5.06	0.0797	2	3.15	0.2068
B *vs.* C	1	3.21	0.0731	1	2.40	0.1210
B *vs.* O	1	0.01	0.9401	1	0.16	0.6862
C *vs.* O	1	4.66	**0.0320**	1	2.02	0.1553
May (B, C, O)	2	12.78	**0.0017**	2	10.19	**0.0061**
B *vs.* C	1	5.13	**0.0235**	1	5.33	**0.0216**
B *vs.* O	1	12.45	**0.0004**	1	6.67	**0.0098**
C *vs.* O	1	1.59	0.2067	1	0.03	0.8546
June (B, C, O)	2	12.86	**0.0016**	2	6.84	**0.0328**
B *vs.* C	1	5.19	**0.0227**	1	0.49	0.4834
B *vs.* O	1	0.63	0.4276	1	3.33	0.0679
C *vs.* O	1	12.85	**0.0003**	1	2.92	0.0873
July (C *vs.* O)	1	0.44	0.5061	1	0.04	0.8471
August (B, C, O)	2	12.95	**0.0015**	2	0.95	0.6211
B *vs.* C	1	1.47	0.2297	1	0.80	0.3701
B *vs.* O	1	12.71	**0.0004**	1	0.01	0.9207
C *vs.* O	1	3.92	**0.0223**	1	1.02	0.3131
September (C *vs.* O)	1	5.22	**0.0223**	1	1.02	0.3131

[a]Period: Baseline (B), Construction (C), and Operation (O).
[b]12 yr of aerial surveys nested in three periods = 9 df.
[c]10 combinations minus 2 df for periods = 8 df.
[d]8 surveys of all localities = 7 df.
[e]Of the 9 mo with aerial surveys only those with significant differences are listed here.

with a growth rate of approximately 8% per year prior to 2002 and approximately 17% from 2002 to 2005. A maximum of 23 gray seals were observed in the area (June 2005), compared to approximately five in 1990, and four newborn pups were observed, two in each year in late February 2003 and 2004.

In general, the number of seals hauling out varied significantly with the three periods ($\chi^2_2 = 17.14, P = 0.0002$), years within periods ($\chi^2_9 = 26.13, P = 0.0019$), month ($\chi^2_8 = 298.04, P < 0.0001$), and month within periods ($\chi^2_8 = 39.26, P < 0.0001$, see Table 2 for details on variation within each month). The number of seals peaked in May 2002 and in May and August 2003 and 2004 (Fig. 2b), whereas only a few seals were observed from October to February. Significant variation in number of seals was observed between periods in May, June, August, and September (Table 2). In May and August, the Rødsand seal stock increased significantly from the second preconstruction to the operation period. A significantly lower number of seals were observed in June during the construction compared to the second preconstruction and the operation period, whereas no difference between second preconstruction and operation was detected. Finally, in September there was a significant decrease in the number of seals at Rødsand in the operation period compared to the construction period.

In August, the seals' preference for Rødsand compared to all seal sites in the area was relatively constant, around 33% (±3, Fig. 2c) with the exception of 1990 where only 24% of the seals were found at Rødsand (see Teilmann *et al.* 2006*a* for individual data from each seal site).

The seasonal proportion of seals at Rødsand relative to all haul-out sites in the region varied significantly over the months ($\chi^2_8 = 32.58$, $P < 0.0001$), and changes in the seasonal pattern between periods were not seen (Table 2). May and June did, however, display significant changes in the proportion of seals at Rødsand with significant increases from second preconstruction to construction and operation periods in May and relatively few seals in June during the construction period (Fig. 2d).

Results of Visual Monitoring

In general, no systematic differences were found between the tallies from the bird tower and those made with the online video camera, neither for harbor seals ($F_{1,67} = 0.79$, $P = 0.3773$) nor gray seals ($F_{1,67} = 0.82$, $P = 0.3693$) with respect to number and time of day. Furthermore, a few aerial surveys conducted simultaneously with an online count showed no differences in number of seals on land between the three counting methods.

The number of both harbor and gray seals increased significantly from first preconstruction (2001) to the operation period (2004) ($F_{1,916} = 23.56$, $F_{1,916} = 25.54$, respectively, $P < 0.0001$ for both) during the periods of observation (June–August). The mean number (June–August, 9–22) of harbor seals increased by 6.9 seals (±1.4, $t_1 = 4.85$, $P < 0.0001$), while the less abundant gray seal increased by 1.4 seals (±0.3, $t_1 = 5.05$, $P < 0.0001$), when differences in time of observation and wind conditions were accounted for.

Gray seals were more abundant on land during June–July in the first preconstruction and operation periods, whereas harbor seals were most abundant on land in August (Fig. 3). The variation around the estimated mean count increased with increasing number of seals.

In addition to the sources of variation and increase in number of seals described above, the potential effect from operation of the offshore wind farm was investigated. This was done by analyzing changes in the seasonal and diurnal pattern, wind speed, and wind direction between the first preconstruction and operation periods by introducing interactions between the factor period and another source of variation (*e.g.*, month). The interaction between period × month was significant for both harbor and gray seals ($P < 0.0001$ for both, Table 2), although the month-specific changes were not the same for the two species. For harbor seals, there was a significant decline of 4.3 (±2.0, $t_1 = -2.19$, $P = 0.0291$) seals in June (see also Fig. 3), a significant increase of 7.0 (±1.9, $t_1 = 3.74$, $P = 0.0003$) seals in July, and a significant increase of 18.0 (±3.2, $t_1 = 5.64$, $P < 0.0001$) seals in August from first preconstruction to operation period. For gray seals, there was a significant increase of 2.4 (±0.5, $t_1 = 4.92$, $P < 0.0001$) seals in June, a significant increase of 2.9 (±0.5, $P < 0.0002$) seals

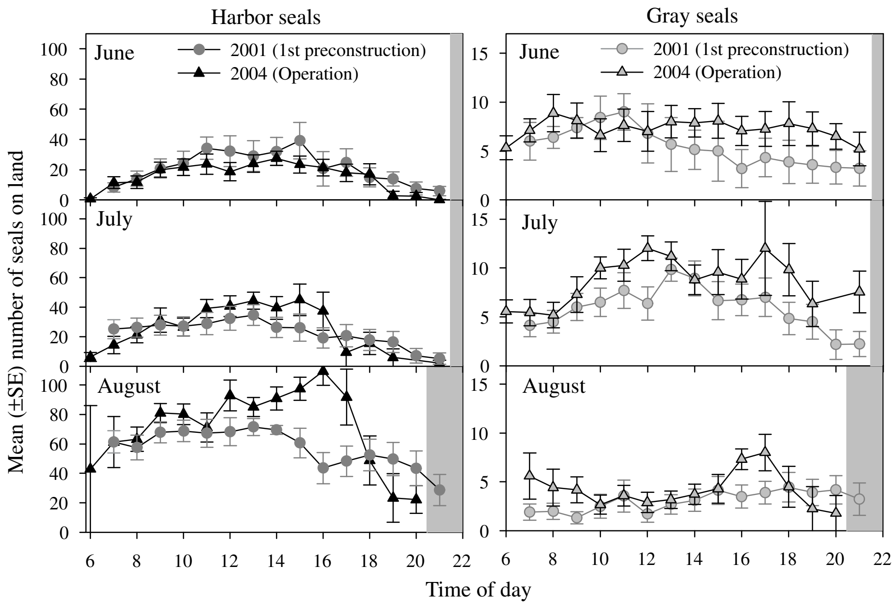

Figure 3. Visual monitoring. The mean (± SE) diurnal variation in number of seals on land in Rødsand seal sanctuary in June, July, and August. In 2001 (first preconstruction period, circles), seals were counted from the observation tower and in 2004 (operation period of the wind farm, triangles) seals were counted online using a video camera. Shaded areas represent hours when the number of seals could not be counted due to darkness.

in July, and a significant decrease of 1.0 (±0.5, $t_1 = -2.28$, $P = 0.0230$) in August. These significant variations were due to a combination of interannual differences in the seasonal pattern and differences in human activities between the two periods. The change in the wind speed sensitivity between the first preconstruction and operation was relatively small and did not indicate any systematic change.

The residuals from the LOWESS regression showed significant variations for time of monitoring of harbor and gray seals (hour, $F_{13,916} = 14.31$ and $F_{13,916} = 4.58$ for harbor seals and gray seals, respectively, $P < 0.0001$ for both species), wind speed (quadratic term, $F_{1,916} = 3.89$, $P = 0.05$ for harbor seals and $F_{1,916} = 6.29$, $P = 0.01$ for gray seals), and wind direction ($F_{7,916} = 11.26$ and $F_{7,916} = 31.81$ for harbor and gray seals, respectively, $P < 0.0001$ for both species). Wind speed for linear terms was not significant ($F_{1,916} = 2.06$, $P = 0.15$ for harbor seals and $F_{1,916} = 0.50$, $P = 0.48$ for gray seals).

Results of Time-lapse Photography Analysis

The first time-lapse images of the seals at Rødsand Seal Sanctuary were recorded on 12 April 2002 (the second preconstruction period) and the two cameras were in operation until the end of 2004 (the operation period). The cameras were operational for 66% of the time (656 of 995 d) resulting in 1,798, 3,403, and 2,550 hourly observations from time-lapse images from the three periods, second preconstruction, construction, and operation, respectively (Table 1).

The wind speed was included as a quantitative factor with data ranging from 0.1 to 20.9 m/s. All factors included in the model were highly significant (χ^2 test, all $P < 0.0001$). This, of course, should be seen in the light of the many observations that allowed identification of even small differences. Seasonal and diurnal variations were taken into account when investigating differences due to the construction and operation of the wind farm, since the observations collected during the three distinct periods did arise from different months, times of day, and wind regimes.

There was a pronounced seasonal variation, common to all three periods, in the seal group size classes with lower probability of seals hauling out during winter months and a relatively higher probability of seals hauling out during summer months (Fig. 4). In general, the annual pattern was very similar for the three periods.

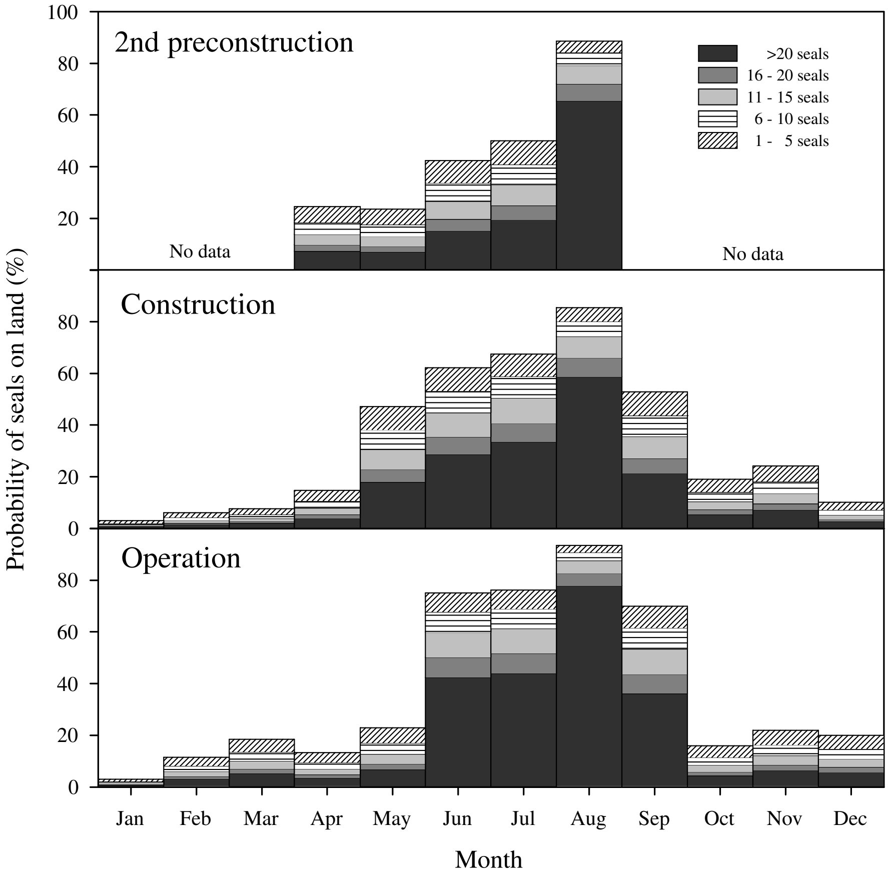

Figure 4. Time-lapse photography. Estimated annual distributions for probability of observing each of the six group size classes during the second preconstruction (April–16 August 2002), construction (17 August 2002–November 2003), and operation (December 2003–December 2004) periods of the wind farm. These were calculated for an average wind speed of 6.1 m/s, an average of all eight wind directions and an average of all hours recorded (04:00–23:00). The probabilities (%) were calculated as marginal means from a multinomial model. The legends for the second preconstruction apply to all three graphs. Distinction between species was not possible from the images.

Monthly mean occurrence of seals on land ranged from 5% of the light hours in January to 90% in August. The seal group size classes of >20 seals occurred more frequently in August as well. There was a general increase in the probability of seals on land during the three periods, particularly for the group size class >20 seals. The annual probabilities for seals hauling out, estimated from the period-specific probability distributions given by the statistical model, were 25% during second preconstruction, 26% during construction, and 34% during operation. The change from second preconstruction to construction was insignificant ($z = 1.73$, $P = 0.08$), whereas the changes from second preconstruction to operation and from construction to operation were both highly significant ($z = 6.92$, $P < 0.0001$; $z = 6.33$, $P < 0.0001$, respectively). Thus, there has been a general increase in the number of hours with seals present on land during the investigated periods. This increase was not equal for all months (the interaction of period × month was significant). April and May deviated from the general pattern by having a higher probability of seals on land in the second preconstruction period in April and in the construction period in May.

The relationship between occurrence of seals on land and wind speed changed between the three periods for both the linear term ($\chi^2_2 = 7.43$, $P = 0.02$) and the quadratic term ($\chi^2_2 = 8.40$, $P = 0.02$). For all three periods, the estimated optimum for seals on land was obtained at wind speeds between 5.6 and 6.0 m/s (Fig. 5). The shapes of wind speed dependent probabilities were quite similar for the second preconstruction and the operation periods, differing by a scaling factor of about 2, whereas the construction period had a relatively high probability of seals during high wind speeds. However, the differences in the functional relationship were relatively small and the association to wind speed between periods did not change fundamentally. Figure 5 though shows an increase in the probability of seals on land for all wind speeds during the study period from second preconstruction to construction and operation period.

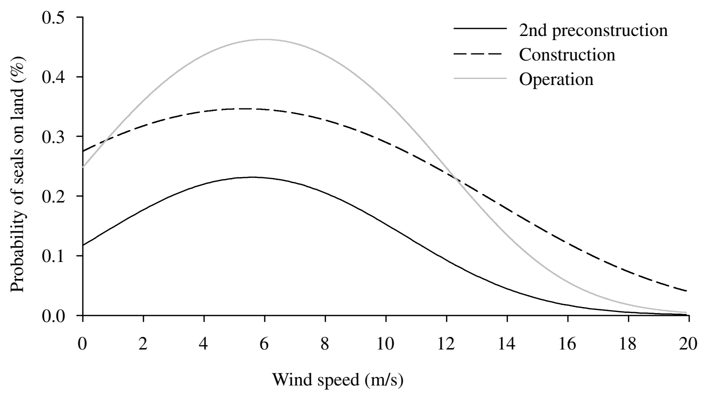

Figure 5. Time-lapse photography. Estimated probability for seals on land in Rødsand Seal Sanctuary in the three periods (second preconstruction, construction, and operation) during different wind speed conditions. The probabilities were calculated as marginal means from a multinomial model. The difference between periods was significant (see text). Note that the marginal means represent hours between 05:00 and 21:00. Distinction between species was not possible from the images.

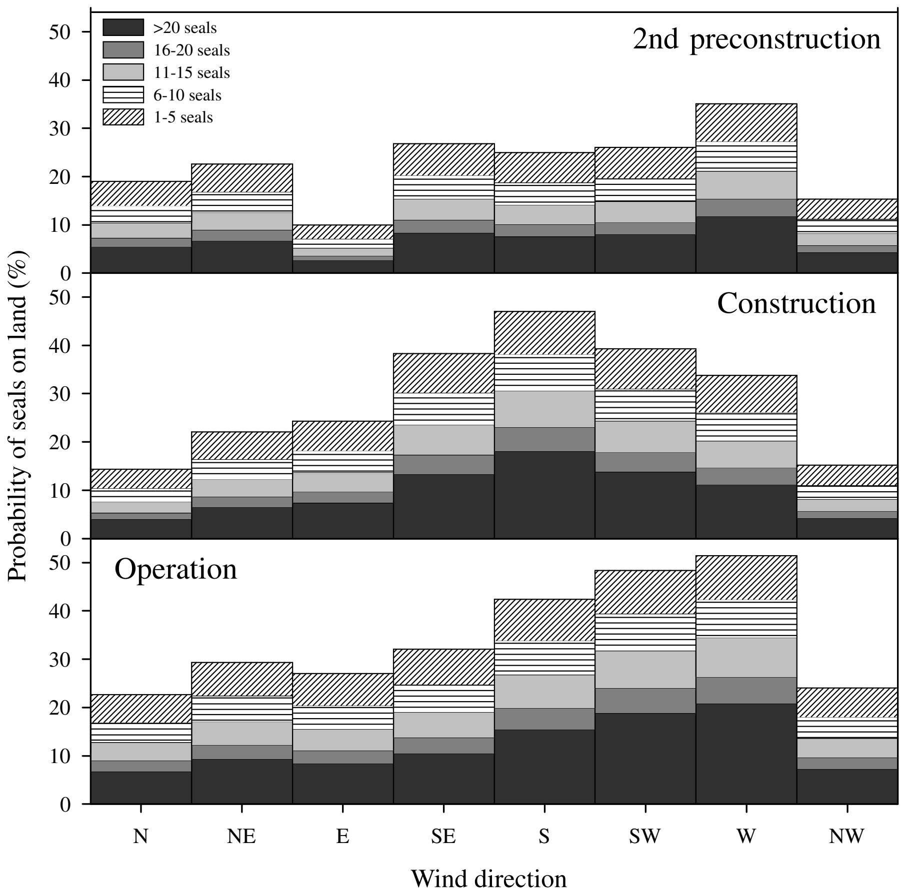

Figure 6. Time-lapse photography. Estimated distributions for probability of observing each of the six seal group size classes at the sanctuary for different wind directions during the three periods at the wind farm site. The probability for each size class was calculated as a marginal mean from a multinomial model. There was a significant difference between the periods. The legends for the second preconstruction apply to all three graphs. Distinction between species was not possible from the images.

The differences in the probability of seals on land during the three periods with different wind conditions were also analyzed by introducing the interaction term period × wind_direction. The purpose was to investigate whether the noise from the construction activity or the operating turbines in air would affect seals hauling out. The term period × wind_direction was significant ($\chi^2_{14} = 83.76$, $P < 0.0001$), indicating that differences existed between the periods depending on the wind direction (Fig. 6). During the second preconstruction and operation periods, the probability of seals on land during the day was highest for westerly winds, while southeastern to southwestern winds increased the probability of seals on land in the construction period. In general, southerly and westerly winds increased the likelihood for seals on land for all periods, whereas northwestern wind in general decreased the likelihood of seals on land.

Effect of Pile Driving

Analysis of time-lapse images showed no sudden reaction in the behavior of seals hauling out in the Rødsand Seal Sanctuary as the pile driving in the wind farm began or when the seal deterrent was turned on. Seals both entered and left the haul-out site during these pile driving periods. There was, however, a significant effect ($\chi^2_2 = 34.09$, $P < 0.0001$) of pile driving activities on seal haul-out behavior when taking wind, month, and time of day into account. Pile driving in the wind farm area with the use of deterrent resulted in lower probabilities for seals on land (Fig. 7). This decline was not consistent for all months. The probability of seals on land in August declined from an average 87%–69% of the days with seals (21% reduction), in September from 56% to 30% (57% reduction), in October from 19% to 7% (63% reduction), and in November from 26% to 11% (58% reduction). The difference between pile driving activities around Gedser without deploying deterrents and no pile driving activity was also significant ($\chi^2_1 = 4.22$, $P = 0.04$). The probability of

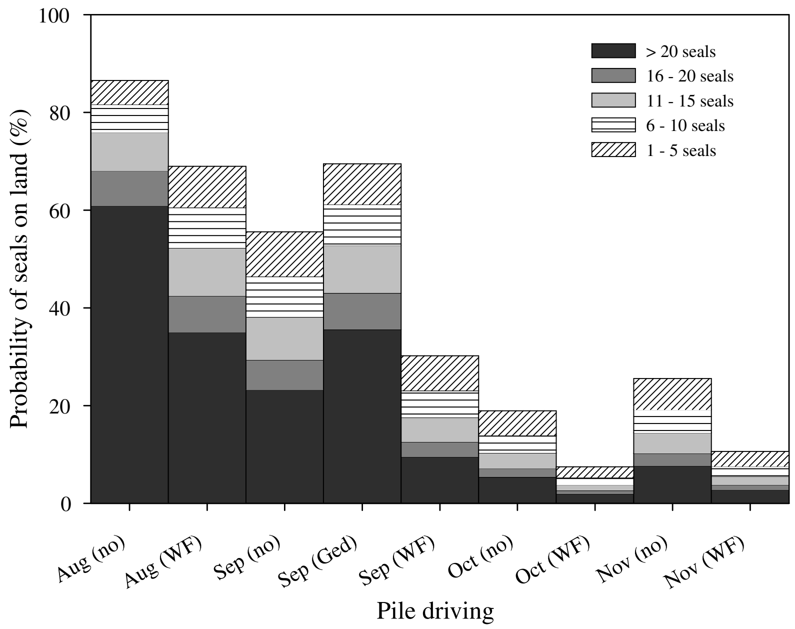

Figure 7. Time-lapse photography. Estimated mean probability of observing each of the six seal group size classes on land during pile driving activities in the wind farm area (WF) and at Gedser harbor and lighthouse (Ged) and no pile driving (no). The probabilities of the various categories were calculated as marginal means from a multinomial model and showed a significant effect of pile driving on seal haul-out probability (see text). Note the decrease in seals on land during each pile-driving episode in the wind farm area with the use of deterrents, and the increase in seals on land during pile driving at Gedser without deterrents. Distinction between species was not possible from the images.

seals on land increased from an average of 56%–70% of the day, corresponding to an increase of 25%.

Discussion

Natural Variation in Seal Haul-out

We observed a maximum number of both harbor and gray seals at Rødsand Seal Sanctuary during their respective molts in August and April–June (Heide-Jørgensen and Härkönen 1988, Reeves *et al.* 1992). Our study showed that from 1990 to 2000, prior to the construction of the wind farm, the seal population in general increased both in the sanctuary and at haul-outs in the vicinity, which was the general trend in the rest of southern Scandinavia (Olsen *et al.* in press). During the summer of 2002, 16% of the harbor seal population in the southwestern Baltic died due to an epidemic of phocine distemper virus (PDV) in northern Europe (Härkönen *et al.* 2006). The number of seals in the sanctuary increased more rapidly during the first years following the epidemic, as also seen at other sites in the vicinity. This showed that the Rødsand Seal Sanctuary was not abandoned by the seals during construction or operation of the wind farm.

The seal sanctuary is not affected by the tide, but by the Atlantic Decadal Oscillation that influences the speed and orientation of the westerly winds toward northern Europe. Periods with strong westerly winds forces the North Atlantic waters into the inner Danish waters, leading to a rise in water level. This study showed that westerly winds lead to an increase in the probability of seals on land in the sanctuary. The sanctuary was never completely flooded during these winds, but some of the scattered stones at the nearby haul-out site (Vitten) could have been flooded, resulting in more seals moving into the sanctuary. Another reason for the increase of seals on land during westerly winds could be that the seals preferred to haul-out on the northeastern side of the western tip of the sand bank, and therefore achieved more shelter from the waves when the wind was coming from the open sea to the south, southwest, and west. The sound in the air from the wind farm (if detectable at the sand bank, not measured) would be strongest at the sand bank during southwesterly winds. It is however, unlikely to have a negative effect on the seals' haul-out behavior because this wind direction was found to have the highest number of seals on land.

Effects of Construction and Operation

The analysis of the time-lapse images showed a 20%–60% reduction in the number of seals hauling out on the sand bank during the pile driving periods (with deterrents) compared to periods with no pile driving (and no deterrent). In contrast, we observed an increase in probability of seals hauling out in the sanctuary during pile driving in Gedser without the prior use of deterrents. These seals might have moved to the seal sanctuary where the sand bank blocked all sounds from east and southeast. Noise from the wind farm area would not be blocked and would therefore be much stronger around the sanctuary, and could probably be heard by the seals under water in a large part of their foraging area (Dietz *et al.* 2003), causing the seals to move further away instead of towards the sanctuary. It is unknown whether the seals in the water reacted to underwater noise by leaving the area resulting in fewer seals at the haul-out site, but the reaction on land however, was short term. The smallest reduction in the number of seals on land was found during the molting period in August, when harbor seals are strongly dependent on land. The largest reduction was observed in November, when seals show less affinity to being on land.

Another large offshore wind farm, Horns Reef Offshore Wind Farm, was constructed in 2002 in the Danish North Sea. Seals here were seen inside the park during construction, although not during pile driving (Teilmann *et al.* 2006*b*). Pile driving noise was not measured at Nysted, however, at Horns Reef noise with pulses up to 235 dB re 1 μPa at 1 m was measured (Tougaard *et al.* 2009). This is significantly higher than the deterrent devices (up to 189 dB re 1 μPa at 1 m) and the pile driving is therefore considered to be the cause of behavioral effects rather than the deterrent devices. We suggest that the increasing number of seals on land when deterrents were not used and the opposite when deterrents were used was due to the location of the pile driving rather than due to the deterrents.

During parturition of harbor seals in June, the number of seals on land in the sanctuary as well as the proportion of seals compared to the nearby locations decreased during the construction period. The reason for this may be due to a higher number of pups being born on rock localities (Vitten) 16 km west of Rødsand compared to the Rødsand Seal Sanctuary[1]. This is in agreement with observations from other harbor seal populations that disperse to other haul-out sites during the breeding season (Heide-Jørgensen and Härkönen 1988, Kovacs *et al.* 1990).

The birth of gray seal pups in Rødsand Seal Sanctuary during the early phase of the construction and again during the operation of the wind farm is the first registered successful breeding of gray seals in Denmark in more than 100 yr. This observation suggests that the gray seals found the sanctuary to be a safe place for breeding and the effect from the wind farm to be negligible within the first year of operation.

Offshore wind farms are still a fairly new technology and no long-term study of the effects of such installations are known.

Conclusions and Recommendations

This study has shown an effect of pile driving on the haul-out behavior of harbor and gray seals. We observed a reduction in the probability of seals hauling out during pile driving in or near the wind farm. During pile driving (further away from the wind farm), we observed a less pronounced increase in probability of seals on land. Though the effect from the pile driving was short-termed, we recommend that deterrents always be used prior to pile driving in areas with marine mammals to insure that seals and porpoises are outside the range of physical damage. The number of harbor seals in Rødsand Seal Sanctuary has shown the same growth rate from first preconstruction to operation as the neighboring seal localities also used by the population, suggesting that seals did not abandon the area and no impact on general population growth in the region was observed. A decrease was observed, however, in the number of seals on land in June, suggesting that seals used haul-out sites further away from the wind farm for parturition during the construction period.

We recommend that disturbances from offshore wind farms should be assessed separately during construction activities, such as pile driving, which may give strong behavioral effects. This study focuses only on seals on land and not in the water. Thus, we highly recommend studies using data loggers that are able to measure the exact

[1]Personal communication from A. Rugaard, sanctuary ranger at Nysted, The Danish Forest and Nature Agency, June 2004.

position and behavior of seals in water since visual monitoring of animals at the surface give very little information on the presence and behavior of seals at sea. The operational phase could give less obvious behavioral responses and the long-term effect remains to be investigated.

The effect on seals from wind farm operation may be specific to the type of wind farm (for example, the type of construction and turbine size), the physical environment, the general ecological characteristics of the area, and the behavioral patterns of the seals in the area. These issues need to be taken into consideration in the planning phase of offshore wind farms. The response by marine mammals to an offshore installation is different for different species, but most importantly it may be different for the same species in different habitats. This implies that the experiences from one offshore installation may not directly be applied to a different locality.

Acknowledgments

Jens Larsen from Ikaros did the skillful and safe flying of the aircraft. Daniel Zats from SeeMore Wildlife helped set up the camera system and has been extremely helpful in keeping the video camera operational during the years. Employees at SEAS are acknowledged for constructing the video tower and helping to rise and move it. We would like to thank National Environmental Research Institute (NERI) at Kalø for letting us use their bird tower for seal monitoring. We also thank Bernhard Fabricius for making the transfer and back-up of all images feasible. Allan Rugaard, ranger at Rødsand seal sanctuary, is greatly acknowledged for his tireless help during all parts of this project. Frank Riget, NERI, Roskilde, provided statistical support on some of the calculations. Several volunteers have helped in the field during the years and deserve our sincere thanks. We would also like to thank Charlotte Boesen, Hans Ohrt, and Pernille Holm Skyt from the energy company E2 A/S for comments on an earlier draft. The present investigation was funded through E2 A/S as part of the government provided grants for studying the effect of wind farms on fauna.

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Received: 26 November 2008
Accepted: 26 October 2009

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Time schedule of the construction of Nysted Offshore Wind Farm. The construction of Nysted Offshore Wind Farm was separated into two major phases. The first phase included preparations for the actual construction work, such as excavation for the foundations, digging of cable furrows and a single case of seabed securing with steel sheet piles. The second phase included cabling and the wind turbine construction. Each of the two phases was divided into several activities scheduled as shown in the figure. The construction work began 20 June with excavation for foundations. The last wind turbine was mounted 27 July 2003 and the park was in full operation 1 December 2003.

Figure S1. Time schedule of the construction of Nysted Offshore Wind Farm

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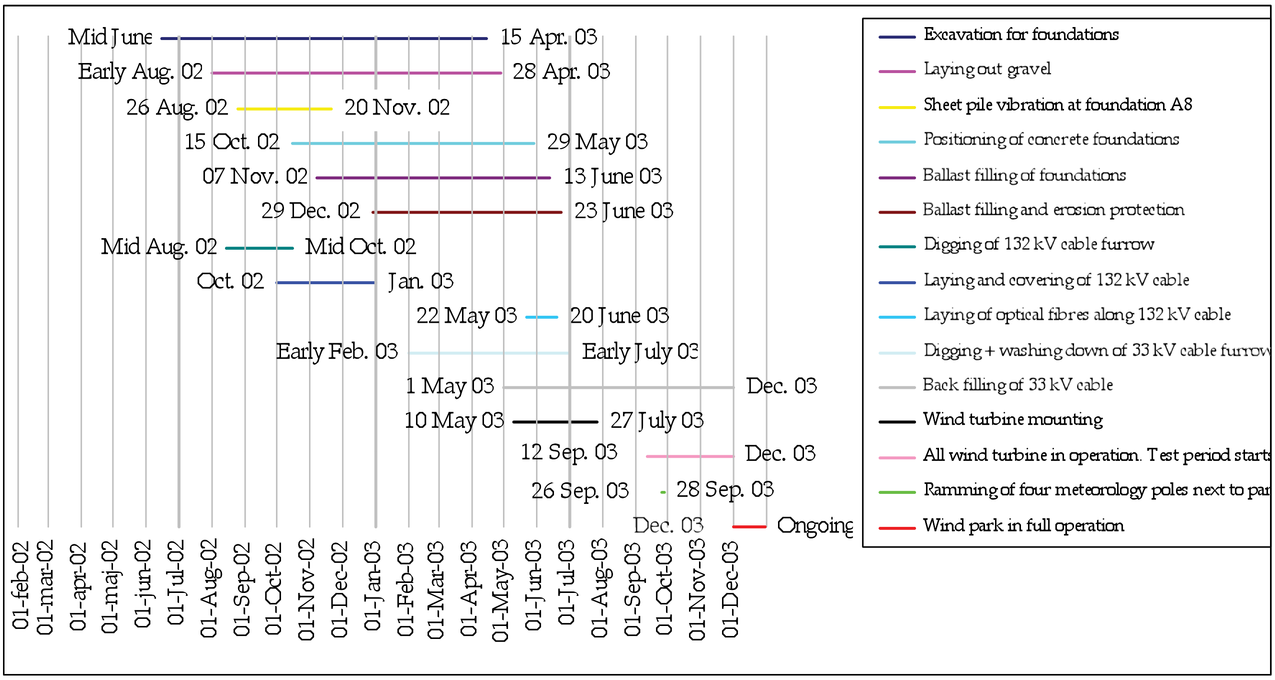

PAPER IV

BEHAVIOURAL RESPONSES OF HARBOUR SEALS TO HUMAN-INDUCED DISTURBANCES

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Resubmitted to Aquatic Conservation: Marine and Freshwater Ecosystems

Photo: Signe May Andersen.

BEHAVIOURAL RESPONSES OF HARBOUR SEALS TO HUMAN-INDUCED DISTURBANCES

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ABSTRACT

1. In Denmark, harbour seals, *Phoca vitulina*, were first protected in 1977, and since then a number of seal reserves have been established in Danish waters. The effectiveness of these reserves to prevent human-induced disturbances to the seal population have, however, not yet been evaluated.
2. To evaluate this, we therefore conducted experimental disturbances in one of the most important seal reserves in Denmark (Anholt seal reserve). Specifically, we studied the behavioural responses (alert distance, flight initiation distance, flee distances and flight duration) of harbour seals to approaching pedestrians and boats.
3. The project was conducted during three periods related to the breeding cycle of harbour seals. In all periods, harbour seals were alerted by boats at significantly greater distances compared to pedestrian disturbances (range 560-850 m and 200-425 m, respectively). Similar differences between the flight initiation distances were observed (range 510-830 and 165-260 m, for boats and pedestrians respectively). In most cases seals were alerted and initiated flight when the approaching boat was outside the reserve, whereas seals did not respond to approaching pedestrians until after these had entered the reserve.
4. Harbour seal responses to disturbances also varied with period, and seals seemingly exhibited weaker and shorter-lasting responses during the breeding season, by being more reluctant to flee and returning to the haul-out site immediately after being disturbed, and in some cases even during the disturbance. This seasonal tolerance is most likely attributable to a trade-off between fleeing and nursing during the breeding season, and hence not an indication of habituation.
5. Based on the maximum response distances observed in this study we suggest that in order to secure adequate year-round protection from disturbances reserve boundaries should on land be positioned at least 425 m from the haul-out area and the sea-territory must extent at least 850 m from the haul-out area.

KEY WORDS: anthropogenic disturbance; boat; conservation; pedestrian; *Phoca vitulina*; pinnipeds; wildlife management; wildlife tourism.

INTRODUCTION

Knowing and evaluating the impacts of human activities on wildlife is a central issue in today's management and conservation strategies for many wildlife species (Gill *et al.*, 1996; Arroyo and Razin, 2006; Bejder *et al.*, 2006b; Bejder *et al.*, 2009; Bennett *et al.*, 2009). Long-term consequences of human disturbance are often complicated to assess, yet previous studies have shown that human activities can cause declines in populations of dolphins (Bejder *et al.*, 2006a), and Hawaiian monk seals (Kenyon, 1972; Gerrodette and Gilmartin, 1990; Ragen, 1999). Short-term effects, on the other hand, are more easily studied by observing the animals' behaviour in response to human activities. To quantify the effect of human disturbance, many studies often measure the flight-initiation distance, the distance at which the animal flee an approaching disturber (Blumstein *et al.*, 2003; Taylor and Knight, 2003; Stankowich and Coss, 2007; Whitfield *et al.*, 2008). The interpretation of such a behavioural response is, however, not straightforward, and one need to take into consideration the context, such as breeding stage, in which they appear. Additionally, the behavioural response of an animal may be determined by multiple, interacting factors, such as visitor group size (Cassini, 2001; Cassini *et al.*, 2004; Baird *et al.*, 2005), type of disturbance (Rodgers and Smith, 1997; Boren *et al.*, 2002; Rees *et al.*, 2005), stage in the breeding cycle (Boren *et al.*, 2002; Rees *et al.*, 2005; Petel *et al.*, 2007), hunting pressure on the population (Arroyo and Razin, 2006; Casas *et al.*, 2009), as well as the cumulative effect of repeated disturbances leading to either sensitisation or habituation (Bejder *et al.*, 2009).

Human-induced disturbances of pinnipeds often take place at their haul-out sites (Renouf *et al.*, 1981; Henry and Hammill, 2001; Boren *et al.*, 2002; Petel *et al.*, 2006; Edrén *et al.*, 2010), and the short-term effects on these animals are hence relatively simple to measure. In Danish and adjacent waters, harbour seals (*Phoca vitulina*) may be affected both directly by human activities (Reijnders, 1981; Edrén *et al.*, 2010) and indirectly through competition with fishing (Andersen *et al.*, 2007). Since hunting was banned and the protection of harbour seals enforced in 1977, the population has since then increased steadily from around 2200 to 14500 harbour seals in Danish waters in 2009 (Teilmann *et al.*, 2010), albeit with two marked declines in 1988 and 2002 as a result of outbreaks of Phocine Distember Virus (PDV) (Härkönen *et al.*, 2006; Kreutzer *et al.*, 2008). During the last 30 years a number of seal reserves have been established in Denmark. In the same period human use of marine areas (including fisheries and recreation, transport and construction activities) has also increased considerably, and the seal reserves may therefore be some of the few undisturbed places for the seals. However, the effectiveness of these reserves to protect seals has never been evaluated, though protected and undisturbed haul-out sites are important in today's harbour seal management (Jepsen, 2005; Olsen *et al.*, 2010).

In the present study we therefore examine the effectiveness of one of the most important seal reserves in Denmark, the Anholt seal reserve, to protect seals from human disturbance. We evaluate the current regulations for human activity around the seal reserve at Anholt by examining the behavioural responses of harbour seals to experimental human disturbance. The most common forms of human disturbance are from approaching pedestrians and boats. Therefore, we quantified harbour seal responses to standardized and controlled disturbances from pedestrians and boats in and around the reserve throughout the year.

METHODS

Field site and study population

The study was conducted during 2006-2009 in the seal reserve on the eastern tip of Anholt (56°44N, 11°39E), an island in the middle of Kattegat, Denmark (Figure 1). The reserve extents between 300 to 500 m from the seals preferred haul-out area. The reserve covers 19 hectares on land and the sea-territory covers 82 hectares. Access is prohibited on land and in the surrounding sea-territory year round (Danish Nature Agency, 2009). These restrictions, however, are frequently violated, in particular during holidays where the island Anholt, and hence the reserve, is visited by large numbers of tourists.

The Anholt seal reserve is one of the most important haul-out sites for harbour seals in Danish waters, both in terms of breeding and moulting site. As many as 1000 harbour seals make use of the Anholt seal reserve (Department of Bioscience, unpublished data), in addition to a smaller group of around 25 grey seals (*Halichoerus grypus*), mainly in spring (pers.obs.).

Experimental design

A number of experimentally controlled disturbances were conducted while recording the seals' responses and the distances at which the seals responded. The experiments were designed to resemble the two types of disturbance most frequently occurring in the Anholt seal reserve (i.e. pedestrian and boat disturbances). Experimental disturbances were conducted in three different periods between October 2006 and November 2009. The pre-breeding period were restricted to the period 21 April to 21 May, the breeding period to 24 June to 27 July, and the post-breeding period to 30 September to 19 October. Table 1 summarises the disturbances included in this study, as well as the abiotic conditions during these. Due to logistically constraints, not all periods were evaluated every year. To minimize the disturbance of the seals during the main breeding season, no experimental disturbances were conducted during the period of 22 May to 16 July. To supplement for the controlled disturbances during the main breeding season we therefore included a number of unplanned disturbances occurring in the reserve in the analyses (Table 1). In April 2007 two remotely controlled cameras (SeeMore Wildlife System Inc., Alaska, USA (www.seemorewildlife.com), and see Edrén *et al.* (2010) for more details) were mounted inside the top of Anholt lighthouse on the border of the seal reserve (600 m away from the seals preferred haul-out area and at a

Figure 1. Map of the study site: the seal reserve on the eastern tip of the Danish island, Anholt, in Kattegat, marked with a cross.

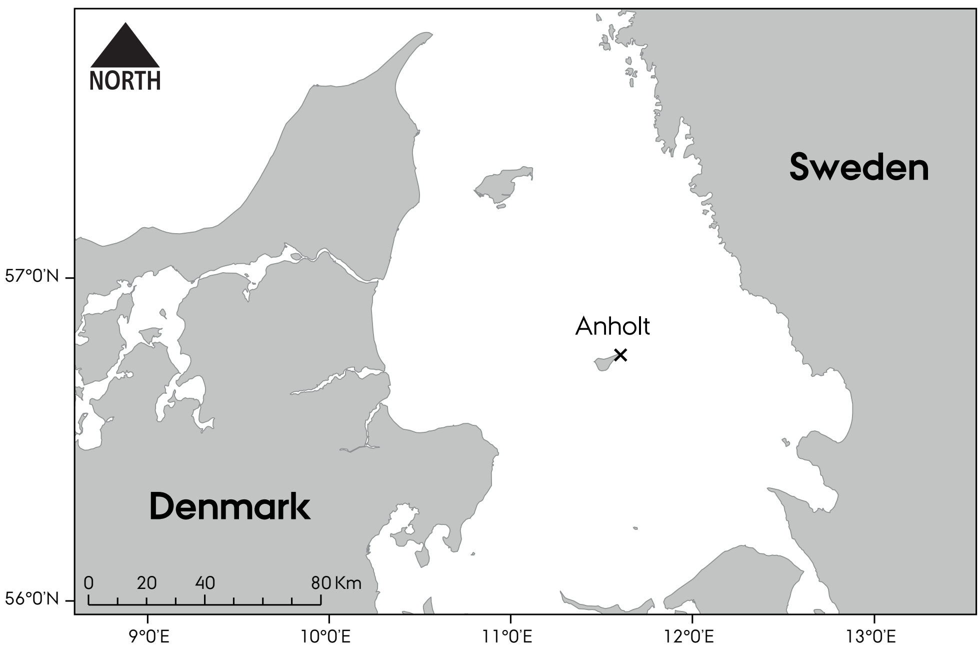


Table 1. Number of disturbances conducted in the study. Disturbances were conducted under comparable weather conditions, and never on days with precipitation.

Period	Type	Number of harbour seals on land before disturbance	Number of disturbances		Weather conditions during disturbances	
			Boat	Pedestrian	Temperature (°C)	Wind speed m/s
Pre-breeding	Experimental	111-521	3	6	19-21	2-5
Breeding	Experimental	250-531	2	4	22-28	1-3
	Un-planned	68-220	1	2		
Post-breeding	Experimental	78-346	3	5	11-20	0-5

height of 32 m). Images either viewed in real time or stored as time-lapse pictures allowed for the registration of un-planned disturbances caused by pedestrians and boats not participating in the project. The response positions of the un-planned disturbances were estimated from the surveillance pictures and landmarks with known positions.

Each controlled disturbance involved two persons, a "disturber" and an "observer". The observer was positioned in a dune as far from the seals as possible while still able to have a clear view of both the disturber and the seals. The disturber and the observer communicated through walkie-talkies during the disturbance approach. If wind direction or the location of the seals made it impossible to find a suitable dune for observing, the nearby lighthouse just outside the reserve was used as an alternative place for observing. Before each controlled disturbance, the observer counted the number of hauled out seals in the reserve. To standardize the experimental disturbances the disturber walked the same route along the beach to the seals. Also all disturbances were conducted between 8 AM and 2 PM, and when at least 75 seals were hauled out in the reserve, and under comparable weather conditions (Table 1). The few un-planned disturbances included in this study took place between 2 PM and 5 PM, and with between 68 and 220 harbour seals present (Table 1). Tides are almost absent in the Kattegat region (Danish Maritime Safety Administration, 2011). A minimum of 24 hours separated consecutive disturbances to reduce the risk of cumulative effects from disturbances closely related in time.

We are aware that our use of experimental disturbances may raise ethical concerns. Hence, to mitigate research impact we restricted the experimental disturbances conducted to the periods outside the main breeding season, and we never approached seals closer than approximately 10 m. Also, during the periods where we worked in the reserve, our presence hindered several un-planned disturbances from taking place.

Boat approaches

Boat approaches were conducted with the assistance of Danish Maritime Safety Administration. A 10 m motorboat was used for all boat disturbances. Boat approaches were initiated approximately 1 nautical mile outside the reserve, and the boat moved into the reserve with an approximate speed of 5 knots. Seals were approached more or less directly, depending on wind direction and wave height. A person on the approaching boat took a GPS position each time the observer noted one of the four responses (see Table 2).

Pedestrian approaches

Out of sight of the seals, the disturber started walking from the border of the reserve directly towards the seals at a slow pace along the beach. While walking, the

Table 2. Definitions of response categories for which the distance between the approaching disturber and the closest seal was measured and used to analyse the response of harbour seals to human disturbance.

Response	Definition
First alert	When at least one seal had registered the disturber shown by lifting its head in the direction of the disturber
First flee	Flight initiation distance = when the first seal fled the haul-out site
50% flee	When 50% of the seals fled into the water
100% flee	When 98% to all seals at the haul-out site fled into the water

observer informed the disturber to mark the positions with a small flag when each of four pre-defined responses (see below and Table 2) occurred. On the way back the disturber noted the GPS coordinates of the position of each flag. Also, the GPS coordinates of the position of the seals lying closest to the approaching disturber at the start of the experiment were registered. A disturbance was considered finished when the disturber left the reserve.

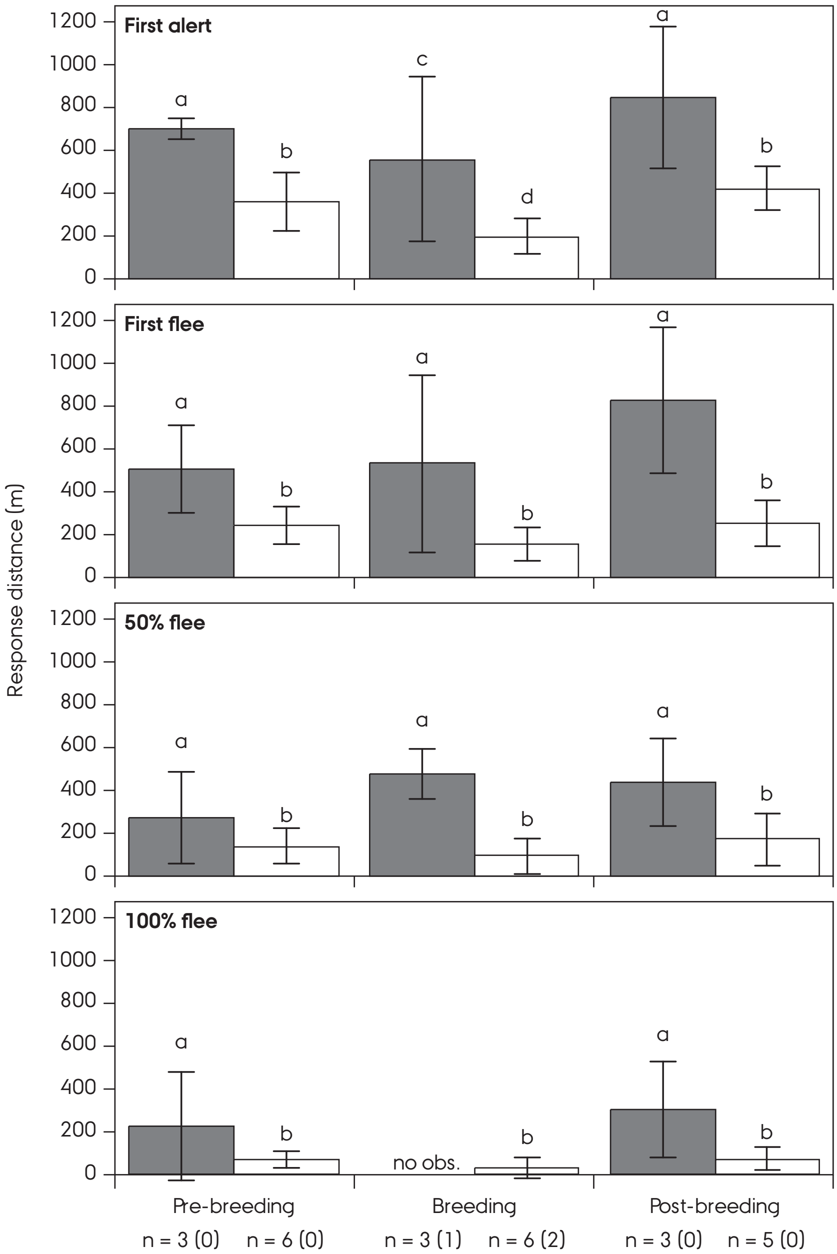


Figure 2. Behavioural responses to boat (grey) and pedestrian (white) approaches during pre-breeding, breeding and post-breeding. Error bars show the standard deviation of the mean. Different letters (a-d) denote significant differences within each behavioural response category ($p < 0.05$). The number (n) of disturbances analysed in this study is shown below the figure, with the number of un-planned disturbances in parentheses. Note that during the breeding season, 100% flee in response to boat disturbances was never observed.

Behavioural responses

Response distances

We measured the distance between the approaching disturber and the closest seal when the following pre-defined responses occurred using GPS coordinates: "first alert", "first flee", "50% flee" and "100% flee" (Table 2 and Figure 2). On a few occasions, 1-2 presumable sick or weakened seals stayed on land during the disturbance, and hence 98-100% flee was accepted as "100% flee".

Flight duration

Following a disturbance, the number of harbour seals returning to the reserve was counted every hour from the end of the disturbance until sundown. The times of the returning seals were noted and allocated to the following return categories: 1-9 seals, 10-19 seals, 20-49 seals, 50-99, seals and 100-199 seals on land. Since the animals were not individually marked in this study, we do not know if the individuals returning were the same as those that were disturbed, and full recovery (a number matching the pre-disturbed level) was therefore not aimed for. If the return of the seals following our experimental disturbances were deterred by other disturbing activities, we discharged these registrations.

Statistical analyses

Response distance

For each of the four response categories (first alert, first flee, 50% flee and 100% flee) we tested the effect of disturber type (boat or pedestrian), the period (pre-breeding, breeding and post-breeding), along with their interactions, using the $\log_e$-transformed distances in General Linear Models (GLM). We also included the number of seals hauled out before the disturbance as covariate to examine the potential effect of group size on the responsiveness of the seals. Model reduction was conducted by successive removal of non-significant parameters, starting with the interaction term. As post hoc test we used Tukey-Kramer. All statistical tests were performed in SAS 9.2 (SAS Institute Inc.) and were considered significant when $p<0.05$.

Flight duration

Similarly, for each of the six return categories (time of return for 1-9 seals, 10-19 seals, 20-49 seals, 50-99, seals and 100-199 seals) we tested the effect of disturber type and period, as well as their interaction on the $\log_e$-transformed distances using GLMs. Model reduction and post hoc tests were conducted as outlined above. The maps were generated using ArcMap (version 9.3).

RESULTS

The disturbing activities conducted had a marked influence on seal behaviour in the reserve, and in most cases seals ultimately responded to the approaching disturber by fleeing. Also, we observed the harbour seal decision-making to be highly influenced by the fleeing of neighbouring seals, and the group generally reacted collectively and more or less simultaneously.

Response distance

Harbour seals responded to boat disturbances at significantly greater distances compared to those provoked by pedestrian disturbances. This pattern was consistent across all response categories and periods ($P<0.026$). Generally harbour seals were alerted by boats when these were still outside the sea-territory (range 560-850 m), whereas pedestrians in most cases did not alert the seals until they had entered the reserve (range 200-425 m). Harbour seal flight responses were initiated at significantly greater distances by boats (range 510-830 m) compared to pedestrians (range 165-260 m) (see Figure 2).

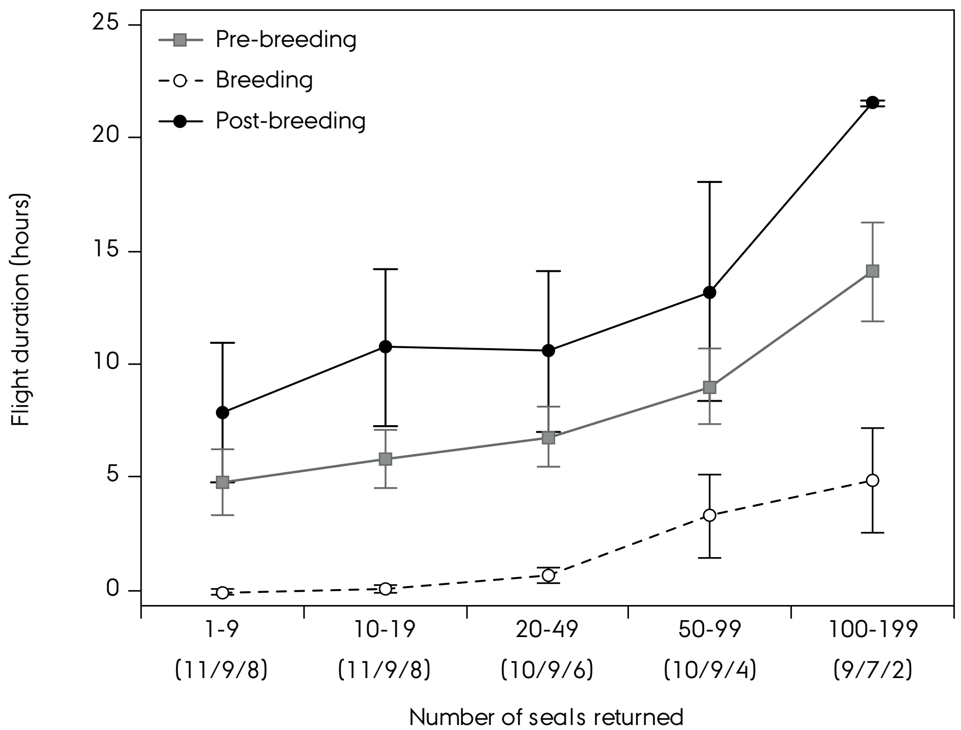
The distances at which harbour seals showed alertness to approaching disturbers were significantly shorter during breeding season than during pre-breeding ($P=0.0382$) and post-breeding season ($P=0.0013$; Figure 2), irrespective of disturber type. No significant difference in alert distance between pre-breeding and post-breeding season was observed ($P=0.2478$; Figure 2). None of the remaining response categories varied significantly with period ($P>0.1154$; Figure 2). The distances observed for the behavioural response "First alert" was significantly correlated with the number of seals on shore before a disturbance ($P=0.0228$), and seals became alert at greater distances with increasing group size. For the remaining responses, no significant correlation was found with group size ($p>0.3203$).

For all response categories, there was no significant interaction between disturber type and period ($P>0.2658$), thus the response was consistent across the periods. However, during the breeding season no estimates could be obtained of 100% fleeing in response to boat disturbances as harbour seals were very reluctant to flee completely from the haul-out site during the breeding season (see Figure 2).

Figure 3. Flight durations of the seals following boat and pedestrian disturbances during pre-breeding, breeding and post-breeding season. Error bars indicate one standard error of the mean. Sample size of each return category is shown below the figure for pre-breeding/breeding/post-breeding.

Flight duration

During the breeding season, harbour seals generally returned to the reserve shortly after the end of the disturbances, and sometimes even before the disturbance had ended and within less than 20 m from the disturber. Seals returned significantly sooner in the breeding season compared to post-breeding season in all return categories ($P<0.0392$). During the breeding season seals returned significantly sooner in the "*20-49 seals returned*" ($P=0.0371$) and "*100-199 seals returned*" categories ($P=0.0235$) when compared to the pre-breeding season, whereas remaining categories did not differ significantly (Figure 3). No significant differences were found between the returning of seals in pre-breeding and post-breeding seasons. The interaction between disturber type and period was not significant ($P>0.5232$).



DISCUSSION

Harbour seals in the Anholt seal reserve were highly responsive towards human-induced disturbances in and around the reserve, and in most cases ultimately reacted by fleeing the haul-out site. However, the distance at which the seals responded to an approaching disturber varied with disturber type and period.

Disturber type

Seals began to flee approaching boats when these were still outside the sea-territory (range 510-830 m). In comparison, Johnson & Acevedo-Gutierrez (2007) observed harbour seals to flee approaching powerboats at distances of approximately 400 m, whereas seals were unaffected by powerboats and kayaks passing by (Allen *et al.*, 1984; Suryan and Harvey, 1999; Johnson and Acevedo-Gutierrez, 2007). Hence, the approach pattern of the disturber is important. The great variety of boat types in the waters around Anholt (kayaks, motorboats, sailboats, zodiacs, fishing boats and cruise ships) and, hence, the low predictability of these may lower the possibility of habituation (see below). The very large response distances to boats during the post-breeding season were often brought about by a chain reaction of events initiated by boats disturbing huge flocks of eiders (*Somateria molissima*) resting on the water around the reserve. The birds subsequently flew over the reserve, causing the seals to flee into the water. Pedestrian disturbances also caused the seals to flee the site, though first after the pedestrian disturber had entered the reserve (range 165-260 m). The greater response towards boats compared to pedestrians was consistent in all periods examined, indicating that boats per se inflict a strong response. The noise made by the boats may to some extent have caused this difference, but also the fact that boats, unlike pedestrians, approach the seals from the direction of their escape route may attribute to the greater sensitivity towards boats compared to pedestrians.

Seasonal response

The state of an animal, such as reproductive state or general condition, may influence its response to disturbances. Harbour seals on Anholt were generally less responsive during the breeding season by not showing signs of alertness until at relative close range and by being more reluctant to flee from an approaching disturber. This weaker response is most likely attributable to the presence of the pups. In previous studies Renouf *et al.* (1981) and Kovacs and Innes (1990) found that harbour seals and harp seals exhibited a very high tolerance to approaching disturbers during the breeding season. Henry and Hammill (2001) also observed harbour seals to be reluctant to flee during moult, another period with strong association to land. As harbour seal haul-out behaviour may vary with the current state of the animal, e.g. reproducing or moulting (Cunningham *et al.*, 2009), the responsiveness to disturbances may inevitably also vary with these events in life. Additionally, we observed seals to return very promptly after, and even before, the departure of the disturber during the breeding season. This was also observed for harp seals and harbour seals by Kovacs and Innes (1990) and Johnson and Acevedo-Gutierrez (2007), respectively, emphasizing the seals' strong association with land during the breeding season. Thus, the reason for the unexpected low level of alertness during the breeding season is probably related to the focus on breeding-related activities such as pupping, nursing and mating (Venables *et al.*, 1955). Though not all seals in the group were reproducing, the instant return of nursing females in particular, most likely caused the non-breeders to follow, i.e. a collective return pattern as also observed for the fleeing response.

Seals seemingly also benefitted from being in groups, as we, similarly to Da Silva and Terhune (1988), observed harbour seal alertness to increase with group size.

Seals did not return until sunset irrespective of disturber type when disturbances occurred outside the breeding season, which most likely reflects a lesser association with land during these periods. Thus the negative effects of reoccurring human disturbances are probably limited outside breeding season. On the other hand, reoccurring disturbances during breeding season, when the seals are more dependent on land, may result in a further energetic burden on the seals and may have a considerable negative impact on breeding success (see Suryan and Harvey, 1999).

It is important to keep in mind that the observed behaviour alone, here the avoidance behaviour, may not reflect the actual impact on the animals. Animals being reluctant to flee despite an approaching threat were previously regarded as being least affected or even habituated (Foster and Rahs, 1983; Fowler, 1999; Holcomb *et al.*, 2009). However, when taking into account the context in which the behavioural response appears (Gill *et al.*, 2001; Stillman and Goss-Custard, 2002; Bejder *et al.*, 2006b; Lusseau and Bejder, 2007; Beale, 2007; Bejder *et al.*, 2009), it is most likely the breeding-related activities such as breeding, nursing and mating that caused the apparently increased tolerance observed in this study. Conclusions based on results from the breeding season alone would erroneously depict that human disturbance has only limited effect on harbour seals during breeding season, and we might have risked misinterpreting their responses as habituation. However, since the seal responses were stronger both before and after the breeding season, the strength of the seal responses were not persistently waning, and therefore do not imply habituation (Bejder *et al.*, 2006b). Hence, due to the potential discrepancy between observable behaviour and actual impact on

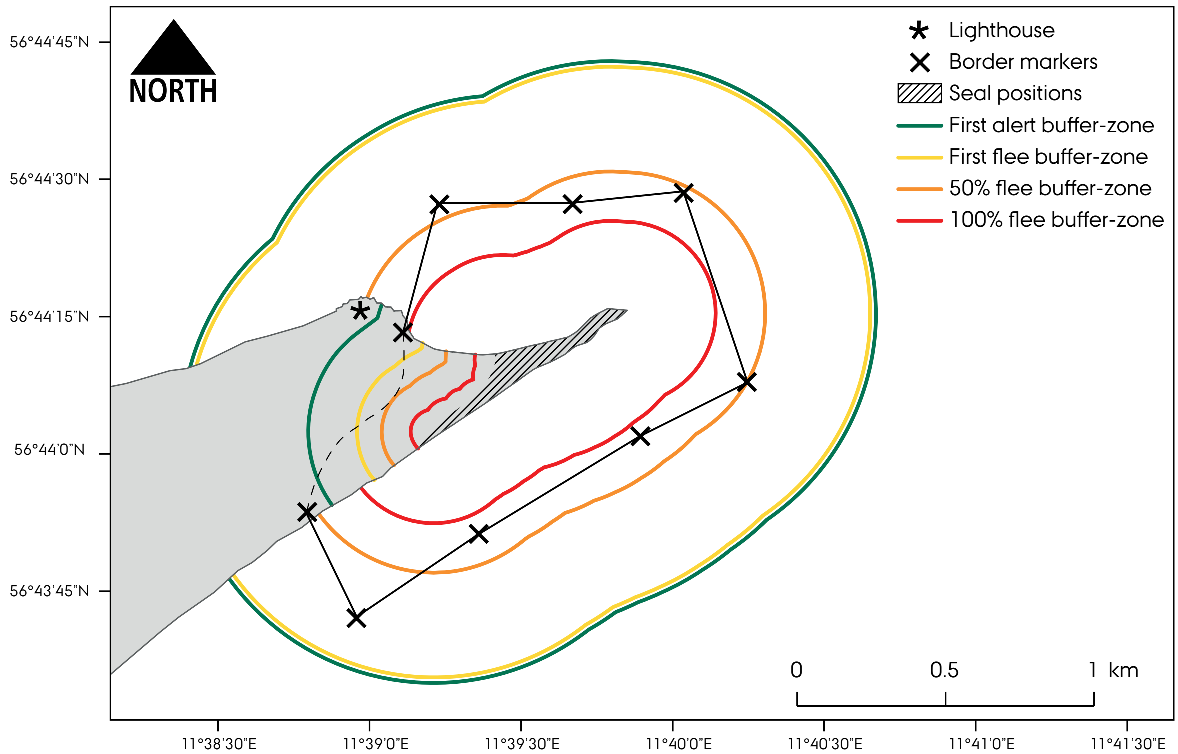


Figure 4. Buffer-zones indicating harbour seal response distances to pedestrian disturbances on land (broad lines) and boat disturbances at sea (narrow lines) in the Anholt seal reserve, Denmark. Shaded area indicates harbour seal haul-out locations in the reserve. Current reserve borders are shown by the black line. The dashed part of this line indicates the area where local topography prevents pedestrians from disturbing the seals. Maximum response distances (cf. Figure 2) for each of the four response types observed in the study were used to draw buffer zones for year-round harbour seal protection (see Legend and Table 2).

the animal, assessments of human disturbance activities have to cover the various seasons corresponding to the various states of the animal, thereby overcoming the possibility that a seasonal tolerance to human activities (sensu Higham and Shelton, 2011) would be interpreted as a general lack of impact.

Management implications

Based on the maximum response distances observed in our studies, boundaries of harbour seal reserves must on land be positioned at least 425 m from the haul-out area and the sea-territory must extent at least 850 m from the haul-out area to prevent human-induced disturbances from pedestrians and boats on a year-round basis (Figure 4). As the Anholt seal reserve extent between 300 to 500 m from the preferred haul-out area, the current sea-territory in the Anholt reserve is thus clearly insufficient to prevent human activities from alerting, and more importantly from causing seals to flee (Figure 4). Generally, the on-land boundaries at the Anholt reserve thus offers adequate protection, also because local topography, here in terms of sand dunes, often prevents the seals from actually seeing the pedestrians, unless these are approaching along the beach (Figure 4). Hence, local conditions may allow for smaller protected zones. It is, however, very important that restrictions in reserves are evaluated periodically in order to keep up with changes in the patterns of human-induced disturbances, as well as changes in the physical parameters, such as shape and size of sandbanks and beaches on which the harbour seals haul-out, to ensure a proper level of protection of the seals.

Finally, in many seal reserves, including the Anholt reserve, current restrictions are violated repeatedly, particularly during the breeding season, which coincides with the prime months of tourism on Anholt. To reduce the number of people trespassing, information stands and reserve border markers must be of high standard.

ACKNOWLEDGEMENTS

First of all we are indebted to Morten Abildstrøm, without whom the field work of this project would have been impossible. We are thankful to Annette Bombosch, Magda Chudzinska, Theis Taarnby Nygaard and the personnel from the Danish Maritime Safety Administration for their assistance in the field. We are grateful to Bendt Nielsen, Jan Nielsen and Kjeld Moser who helped us with the camera system. This study was generously supported by Aage V. Jensen Charity Foundation, the Danish Outdoor Council and the Danish Nature Agency.

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PAPER V

DISTURBANCE-INDUCED RESPONSES OF INDIVIDUAL HARBOUR SEALS

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Manuscript

Photo: Signe May Andersen.

DISTURBANCE-INDUCED RESPONSES OF INDIVIDUAL HARBOUR SEALS

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ABSTRACT

We studied the responses of harbour seals (*Phoca vitulina*) to disturbing activities at their haul-out site (the Anholt seal reserve, Denmark) during the pre-breeding period. For this purpose we equipped eight harbour seals with VHF and satellite transmitters to determine haul-out patterns and post-disturbance movements in and around the haul-out site and compare these measures to those from un-disturbed trips. Disturbances from pedestrians, boats, low-flying aeroplanes and grey seals (*Halichoerus grypus*) were observed in or near the reserve.

Both disturbed and un-disturbed seals returned to the haul-out site from around sundown and during the dark hours. Only trips following pedestrian disturbances lasted significantly longer than un-disturbed trips, while remaining disturbance types did not affect trip duration. Maximum extent and area-use of disturbed and un-disturbed trips were comparable. Harbour seals generally stayed within few kilometres and most locations were within 40 km from the haul-out site. The maximum extent of post-disturbance trips, however, varied among individuals and disturbance type as well as being strongly correlated with the duration of trips. The areas to which the individual seals fled following a disturbance were the same as those used during un-disturbed trips, suggesting that these areas included the foraging areas of the individual seals, and thus indicated that disturbed seals went foraging. Hence, during the pre-breeding period the Anholt harbour seals exhibited a flexible behaviour following disturbances. Still they showed a very high site-fidelity by consistently returning to the same haul-out site, and were thus subject to the repeated disturbances there.

KEY WORDS: conservation; *Phoca vitulina*; pinnipeds; area-use; site-fidelity; telemetry; wildlife management.

INTRODUCTION

Harbour seals spend a significant amount of time hauled out on land. They gather at haul-outs for varies reasons, such as to rest (Da Silva and Terhune, 1988), to escape aquatic predators (Terhune, 1985; Da Silva and Terhune, 1988), to moult (Reder *et al.*, 2003) and to give birth and rear their pups (Bigg, 1981; Thompson, 1989). Their haul-out patterns vary with the annual cycle of reproduction and moulting (Brown and Mate, 1983; Thompson *et al.*, 1989). Their haul-out behaviour is influenced by many factors operating together, such as several environmental factors including wind chill, wind speed, wave intensity, tide, temperature, precipitation, cloud cover, and time of day (e.g. Sullivan, 1980; Schneider and Payne, 1983; Stewart, 1984; Yochem *et al.*, 1987; Bjørge *et al.*, 2002; Reder *et al.*, 2003; Edrén *et al.*, 2010). The quality and location of feeding areas may also influence the haul-out pattern of harbour seals (Härkönen, 1987; Thompson *et al.*, 1991). When on land, pinnipeds may be subjected to disturbances, which might decrease the duration of their haul-out periods. During times when access to haul-out sites is most important, like during pup rearing and moulting, disturbances may increase energy expenditure (Suryan and Harvey, 1999).

Information on the potential impacts of disturbance on haul-out site usage is important for conservation and management purposes. Short-term effects of disturbances are often easy to assess and typically quantified by measuring flight distances and the return to pre-disturbed numbers (Allen *et al.*, 1984; Henry and Hammill, 2001; Boren *et al.*, 2002; Andersen *et al.*, in review), whereas long-term effects, such as collapsing of populations or long-term abandonment of haul-out sites, are more difficult to assess (Kenyon, 1972; Reijnders, 1985; Gerrodette and Gilmartin, 1990; Ragen, 1999).

In Denmark, harbour seals were totally protected from hunting in 1977 (Jepsen, 2005), where the population had declined to about 2200 seals after several hundred years of intense hunting (Søndergaard *et al.*, 1976). Today (2009) aerial surveys suggested that approximately 14500 harbour seals are found in Danish waters (Department of Bioscience, unpublished data). Approximately 30% of these utilize ten haul-out sites in the Kattegat including the Anholt seal reserve, which is one of the most important haul-out sites in Denmark (Olsen *et al.*, 2010; Teilmann *et al.*, 2010; Dietz *et al.*, in prep) (Figure 1). Despite being a seal reserve, disturbing activities, including human activities, often occur in the Anholt reserve (Andersen *et al.*, in review).

In a previous study (Andersen *et al.*, in review) we observed the harbour seal group in the Anholt seal reserve to flee disturbances collectively and simultaneously during the pre-breeding and post-breeding periods. The seals on the other hand were reluctant to flee during the breeding period. Also the returning of the seals to the haul-out site following a disturbance was dependent on the time of year in which the disturbance took place, and during pre-breeding and post-breeding periods seals returned from around sundown and throughout the night, whereas during the breeding period seals returned immediately after a disturbance (Andersen *et al.*, in review). In the present study we elaborate on the group response reported by Andersen *et al.* (in review) by examining the response of individually marked harbour seals to various disturbances. Using VHF and satellite transmitters we investigate the duration, maximum extent and area-use of individual harbour seal post-disturbance trips, and compare these measures to those of un-disturbed trips.

METHODS

Study site

The study was conducted in the pre-breeding period (29/4-21/5) in 2008 in the seal reserve on the eastern tip of the island Anholt (56°74'N; 11°66'E), in the Kattegat, Denmark (Figure 1). The seal reserve covers 19 ha on land and 82 ha at sea, and is closed to the public year-round. Anholt is mainly surrounded by shallow water with sandy bottom (down to 10 m), except southeast of the island where water depth goes down to 25 m. The amplitude of the tides is small in the Kattegat area (Danish Maritime Safety Administration, 2011), but strong currents and heavy storms can change the size and shape of the seal reserve by relocation of sand (Härkönen, 1987). During spring up to 500 harbour seals make use of the Anholt seal reserve, in the company of a small group of around 25 grey seals (pers.obs.).

Capture and tagging

In late April 2008 eight harbour seals were caught in monofilament surface gillnets (Table 1). Up to ten 100 m nets were deployed 25-300 m from the haul-out site. Nets were inspected regularly for entangled seals. Due to a float line on the nets the seals were able to rest at the surface until they were removed. They were dragged into an inflatable Zodiac and placed in individual nets and transported to shore. Two types of transmitters were glued to the pelage of the seals using quick-setting two-component epoxy (Araldite 2012) after drying with denaturised alcohol and degreasing with acetone. The satellite transmitter (SPOT 4 or 5, Wildlife Computers, Redmond, WA, USA) was head-mounted to ensure satellite transmission whenever the seal surfaced. The satellite transmitters were programmed to transmit 500 uplinks per day. The VHF transmitter (Sirtrack, New Zealand) was mounted on the seals' back, which assured contact with the receiver only when the seals were on land. Both transmitters are shed when the seals undergo their annual moult.

Figure 1. Map showing the locations of the most important haul-out sites in Kattegat (Modified from Olsen *et al.*, 2010). The size of the circles indicates the number of harbour seals counted on land at each haul-out site in late august 2009. The boundaries of the Anholt seal reserve is shown in the insert.

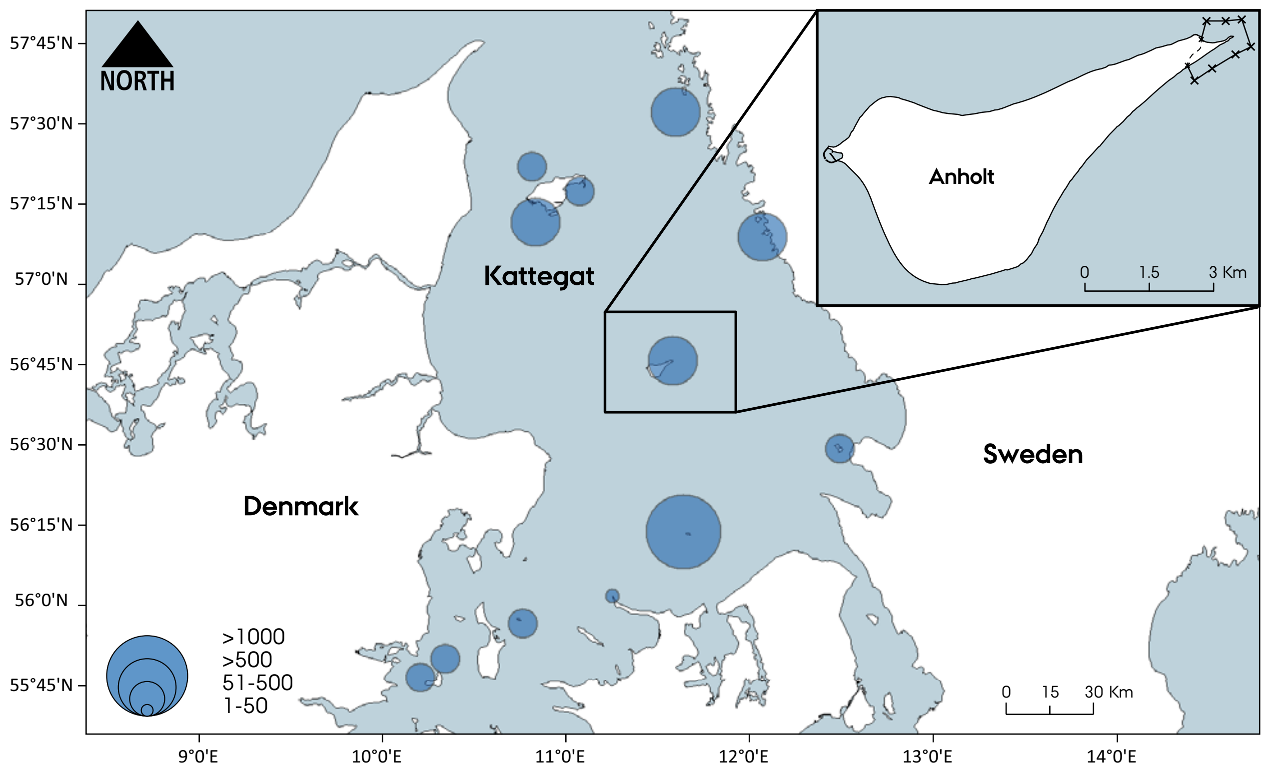


Table 1. Summary data on the eight harbour seals monitored in this study, each equipped with a VHF radio and a satellite transmitter. When an individual seal is mentioned in the text, the last three numbers of its VHF frequency are used as an identification (ID) number. Results from blood analyses revealed that the adult female caught was not pregnant.

Sex	Age	Weight (kg)	Std. length (cm)	Deployment date	VHF frequency + seal ID	Last transmission date	
						VHF transmitter	Satellite transmitters
M	Yearling	26	nd	25-Apr-08	142 040	14-Jul-08	17-Jul-08
M	Subadult	48	102	28-Apr-08	142 060	16-Jul-08	27-Jun-08
F	Yearling	24	102	26-Apr-08	142 080	18-Jun-08	25-Jun-08
M	Subadult	46	118	28-Apr-08	142 100	5-Jun-08	12-Jun-08
F	Yearling	28	101	26-Apr-08	142 120	19-Jun-08	01-Aug-08
M	Subadult	38	118	26-Apr-08	142 160	14-Jun-08	18-Jun-08
F	Adult	46	120	26-Apr-08	142 180	4-Aug-08	22-Jun-08
M	Adult	62	140	25-Apr-08	142 220	27-Jul-08	11-Jul-08

All individuals were examined for sex, age class, standard length, girth, and mass, and in addition a blood sample was taken to determine health and reproductive status.

VHF telemetry

An automatic VHF receiver station (Advanced Telemetry Systems (ATS), R4500S, USA) was set up inside the top of the 32 m high lighthouse, placed just outside the reserve, approximately 600 m from the hauled out seals. The radio station was equipped with two 3-element Yagi antennas and continuously recorded the presence of VHF-tagged seals in the reserve. We tested that VHF transmissions were fully detectable from all parts of the seal reserve. The receiver station ran 24 h/day and scanned each frequency for five seconds. Transmitter detections were stored every five min. The haul-out patterns of the individual seals were determined from these recordings.

Satellite telemetry

From the satellite transmitters we obtained location data via the Argos system (Harris *et al*., 1990). Locations were processed using the Kalman filter (Lopez and Malardé, 2011), and classified by the Argos system into six location classes according to level of accuracy (3, 2, 1, 0, A, and B). All location classes were used in the present study after filtering out unlikely locations with swim speeds in excess of 10 km/h. However, distances less than 5 km between two consecutive locations, allowed for the retaining of both locations, since swim speed calculations may be unrealistic as a result of the inaccuracies associated with the positions. Data from a wet/dry sensor on the satellite transmitters also yielded information on haul-out patterns of the individual seals. When the sensor indicated dry for minimum 80% of an hour, the seal was defined as hauled out during that particular hour.

Types of disturbance

In order to examine the individual responses to different disturbance types a number of experimentally controlled pedestrian (n=5) and boat (n=3) disturbances were conducted. Additionally, we continuously observed the reserve from the lighthouse and nearby dunes during all the light hours to detect for sporadically occurring disturbances. We included 18 sporadic occurring disturbances, which

Table 2. An overview of the planned and sporadic occurring disturbances. The number of tagged seals present and, hence, involved in the various disturbances are also listed. Not all eight tagged harbour seals were present in the reserve at the time of all the 26 disturbances. The total number of individual responses was 85.

Disturbance type	Number of disturbances		Number of tagged individuals involved in the disturbances	
	Planned	Sporadic	Planned	Sporadic
Pedestrian	5	3	20	3
Boat	3	2	12	3
Grey seal	0	4	0	16
Aeroplane	0	2	0	4
Unknown	0	7	0	27
Total	**8**	**18**	**32**	**53**

were categorised according to their cause. In addition to pedestrian and boat disturbances these were disturbances from grey seals and aeroplanes. The cause of some disturbances could not be determined and were categorised as unknown, but no pedestrians, boats or aeroplanes were observed in the reserve during those disturbances (Table 2). The numbers of tagged seals present during the 26 disturbances varied, and the total number of individual responses was hence 85. All disturbances occurred between 5 AM and 2 PM. More than 82% of the disturbances occurred before noon.

To compare post-disturbance trip measures to those of un-disturbed trips, we included data on 116 un-disturbed trips taken by the VHF tagged seals during the study period (hereafter referred to as the un-disturbed control). Un-disturbed trips for the individual seals were defined as trips where no disturbances were registered and where the VHF receiver indicated that individual tagged seals left the haul-out site independently of other tagged seals.

Some transmitters were still transmitting into the breeding season (Table 1), but since most disturbances registered in that period could not be categorized we restricted our analyses to the pre-breeding period.

Post-disturbance movements

Duration of post-disturbance trips

The returning of the individual seals, and hence the duration of post-disturbance trips and timing of haul-out bouts, were recorded by the VHF receiver station. Occasionally, haul-out bouts were interrupted by smaller periods with no received signals. Consequently, we first regarded a seal to have resumed hauling out on Anholt when three continuous signals were stored by the VHF receiver station, indicating a minimum haul-out bout of 15 min. This criterion was used to reduce the risk of swimming seals with the VHF transmitter above the water for just a short period to be registered as having returned. Data on haul-out pattern from the wet/dry sensor in the satellite transmitters was only used to support and verify the haul-out pattern revealed by the VHF data. The time an individual seal had spent hauled out prior to a disturbance was also recorded.

The duration of post-disturbance trips was compared to the duration of un-disturbed trips conducted by the seals.

Extent of post-disturbance trips and post-disturbance area-use

Individual post-disturbance locations were obtained from satellite positions during the period from the time the seal fled the haul-out site due to a disturbance until the seal again started hauling out. We calculated the linear distances between each satellite position and the haul-out site on Anholt during each individual post-disturbance trip to estimate the maximum extent of individual trips. We compared satellite locations obtained during the post-disturbance trips to locations obtained during un-disturbed trips to examine differences in trip extent and areas used.

Statistical analyses

Duration of post-disturbance trips

We tested the effect of disturbance type (including the un-disturbed control) and individual along with their interactions on trip duration, using the $\log_e$-transformed durations in General Linear Models (GLMs). The amount of time hauled out before leaving the haul-out site was included as covariate as this might influence seals motivation to resume haul-out, and, thus, the duration of trips. Model reduction was conducted by successive removal of non-significant parameters, starting with the interaction term. As post hoc test we used Tukey-Kramer. All statistical tests were performed in SAS 9.2 (SAS Institute Inc.) and were considered significant when $p<0.05$.

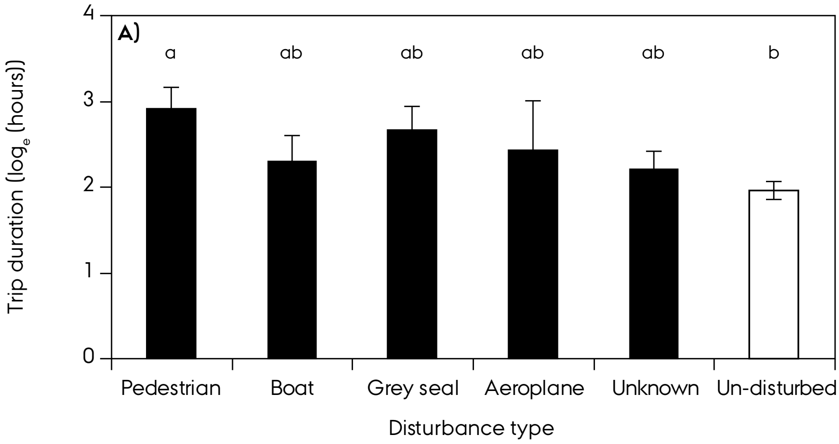
Extent of post-disturbance trips and post-disturbance area-use

We tested the effect of disturbance type (including the un-disturbed control), individual, as well as their interaction on the $\log_e$-transformed maximum extent of trips using GLMs. Model reduction and post hoc tests were conducted as described above. To compare un-disturbed and post-disturbed area-use, we also calculated the 95% fixed kernel density estimates for the un-disturbed area-use (Hawth's Analysis Tool V3.27 in ArcMap version 9.3; with smoothing factor 15.000 and output cell size to 1 km^2), and compared these to locations visited during post-disturbance trips by each individual seal.

RESULTS

Haul-out and location data

During the study period the automatic VHF receiver station recorded 11812 recordings revealing a total of 219 haul-out bouts performed by the eight tagged harbour seals. Haul-out bouts revealed by the wet/dry sensor in the satellite transmitters confirmed the VHF findings, and we are therefore confident that we did not miss any haul-out bouts during the study period. Also, due to the remoteness of Anholt, with approximately 50 km to the nearest haul-out site (Figure 1), we were convinced that all VHF signals indicated the presence of the seal on Anholt. After filtering of the satellite data, 3065 locations were extracted (overall mean = 12.2 locations/post-disturbance trip/animal, and 13.7 locations/un-disturbed trip/animal). During one post-disturbance trip and 27 un-disturbed trips no locations were obtained.



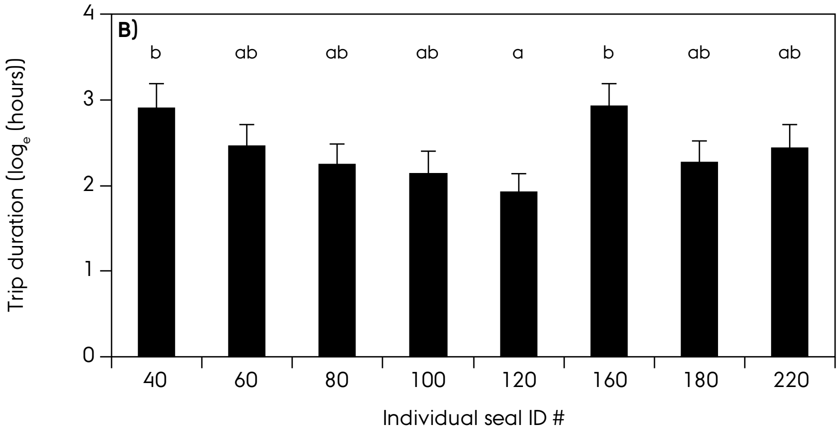


Figure 2. Least square means of post-disturbance trip duration. A) shows the trip duration caused by the different disturbance types (black) and un-disturbed trip duration (white). B) shows the trip durations of individual seals (disturbed and un-disturbed trips combined). Error bars indicate one standard error of the mean. Different letters denote significant differences (P<0.05).

Trip duration

The average duration of post-disturbance trips was 16.1 hours (range: 0.5-53.7) and the un-disturbed trips on average lasted for 15.1 hours (range: 1.0-94.9). However, trip duration varied among disturbance types with trips following pedestrian disturbances lasting significantly longer than un-disturbed trips (P=0.005) (Figure 2a). The duration of trips for the remaining disturbance types did not vary significantly (P>0.209). Also, the duration of trips varied between individuals (P=0.0165), and the trip duration was significantly shorter for #120 compared to #40 (P=0.036) and #160 (P=0.019) (Figure 2b). There was no significant interaction between any of the variables (P>0.416). The duration of the time hauled out before the seals left the haul-out site was not related to trip duration (P=0.983), irrespective the seals left the haul-out site due to a disturbance or not. Regardless the cause of departure (disturbed or un-disturbed) most seals resumed hauling out during darkness. Hence, 65% of the disturbed seals returned to the reserve within 1 hour before sundown to 1 hour after sunrise (referred to as the dark period), and 67% of the seals returned during the dark period after un-disturbed trips (Figure 3). Consequently, the earlier a disturbance occurred during the day, the longer the time span until the dark period and the likely returning of the seals. However, as seals returned to the haul-out site throughout the dark period, and in 12 cases not even in the first coming dark period following a disturbance, no correlation was found between the time the disturbance occurred and the return time of the seals. One seal in particular differed markedly from the general pattern by having more than 90% of its post-disturbance returns outside the dark period, whereas 88% of the un-disturbed returns were in the dark period (seal #100; Figure 3).

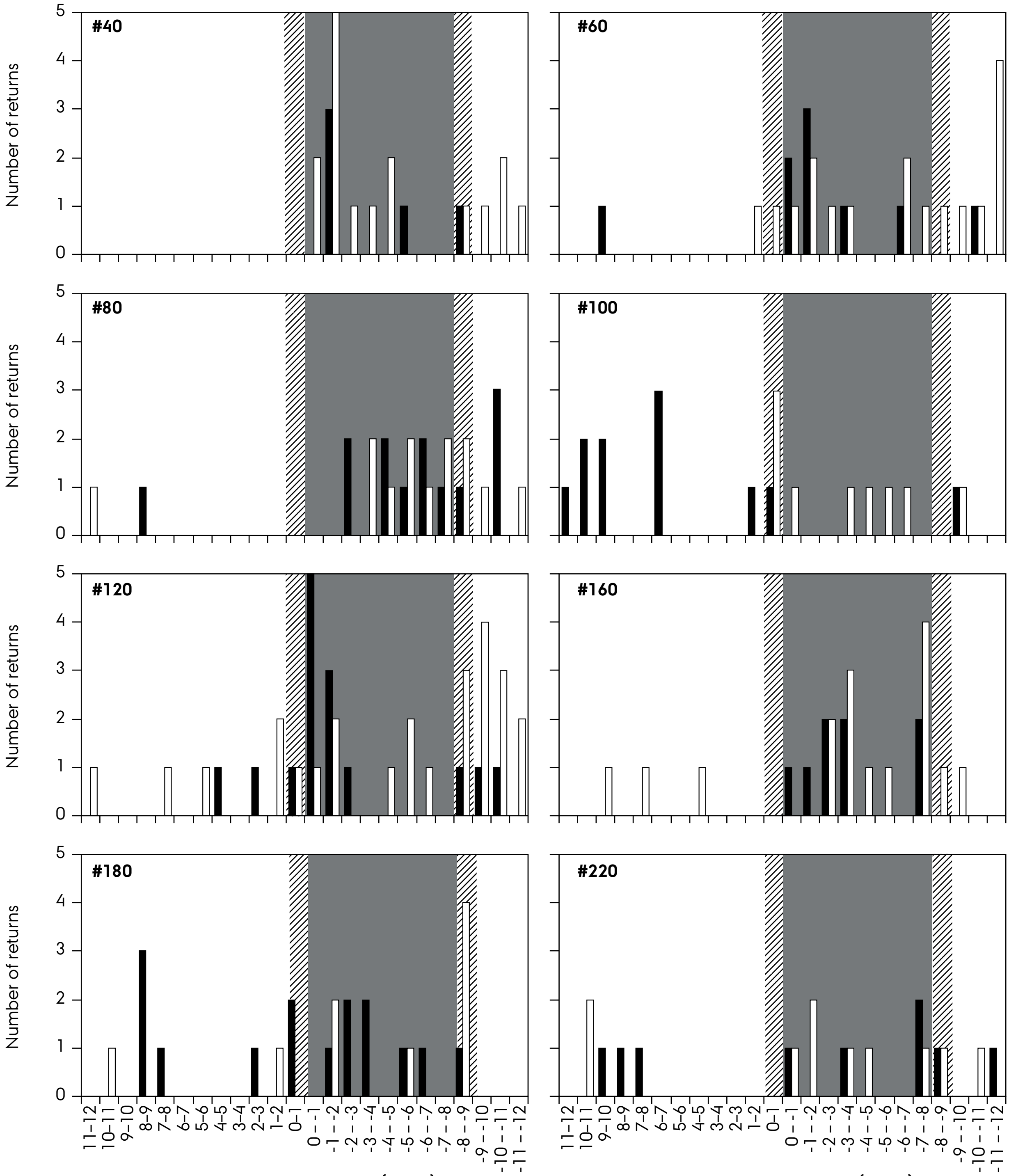
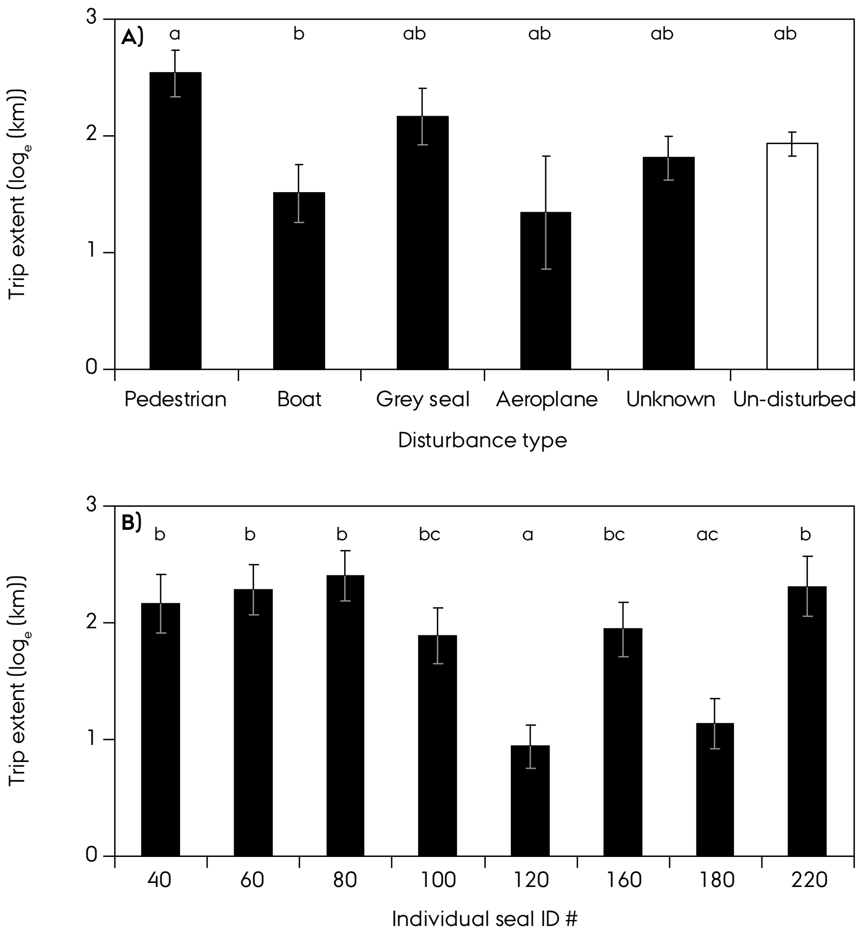


Figure 3. Distribution and number of returns to the haul-out site after un-disturbed trips (white) and after disturbances (dark) (hours in relation to sundown) for each of the eight individually tagged harbour seals. Shaded areas indicate the hours between sundown and sunrise, and hatched areas illustrate 1 hour before sundown and 1 hour after sunrise, respectively.

Trip extent and area-use

Fifty-eight percent of all satellite locations were within 5 km from the haul-out site. Almost all (99%) the trips were within 40 km from the Anholt seal reserve, and the overall mean maximum extent of the post-disturbance trips was 10.7 km (range: 0.5-51.9 km), and 11.7 km for un-disturbed trips (range 0.5-84.5 km). The maximum extent moved by the tagged seals varied with disturbance type, and pedestrians caused the seals to move further away than boats (P=0.019). Remaining disturbance types, including the un-disturbed control, did not differ

Figure 4. Least square means of maximum extent of A) post-disturbance trips for the different disturbance types (black) and un-disturbed trips (white), and B) the eight individual harbour seals (disturbed and un-disturbed trips combined). Error bars indicate one standard error of the mean. Different letters denote significant differences (P<0.05)



significantly (P>0.094) (Figure 4a). Also, the mean maximum extent of trips differed among individual seals (P<0.001), and seal #120 conducted significantly shorter trips than all others except #180 (P<0.023). Seal #180 had significantly shorter trips than seal #40, #60, #80 and #220 (P<0.021) (Figure 4b). The interaction was not statistically significant (P=0.291).

Also, we found large overlaps between areas visited by individual seals during post-disturbance trips and those visited during un-disturbed trips (Figure 5). The post-disturbed locations for four of the seals fell completely within the areas used during un-disturbed trips, while for remaining seals the area-use during disturbed and un-disturbed trips overlapped with >96% (Figure 5). Furthermore, there was a positive relationship between the maximum extent and duration of trips (R^2=0.40, P<0.001, with no significant effect of disturbance type or the interaction) (Figure 6). Hence, seals moved further away with increasing trip duration.

DISCUSSION

In the present study, harbour seals responded to different disturbance types in the pre-breeding period by fleeing the haul-out site, and generally by resuming hauling out from sundown and throughout the dark period. Generally, the duration of post-disturbance trips was not related to disturbance type, though pedestrians caused seals to undertake longer lasting trips than when leaving the haul-out site voluntarily. Thus, the results reported here, at the individual harbour seal level,

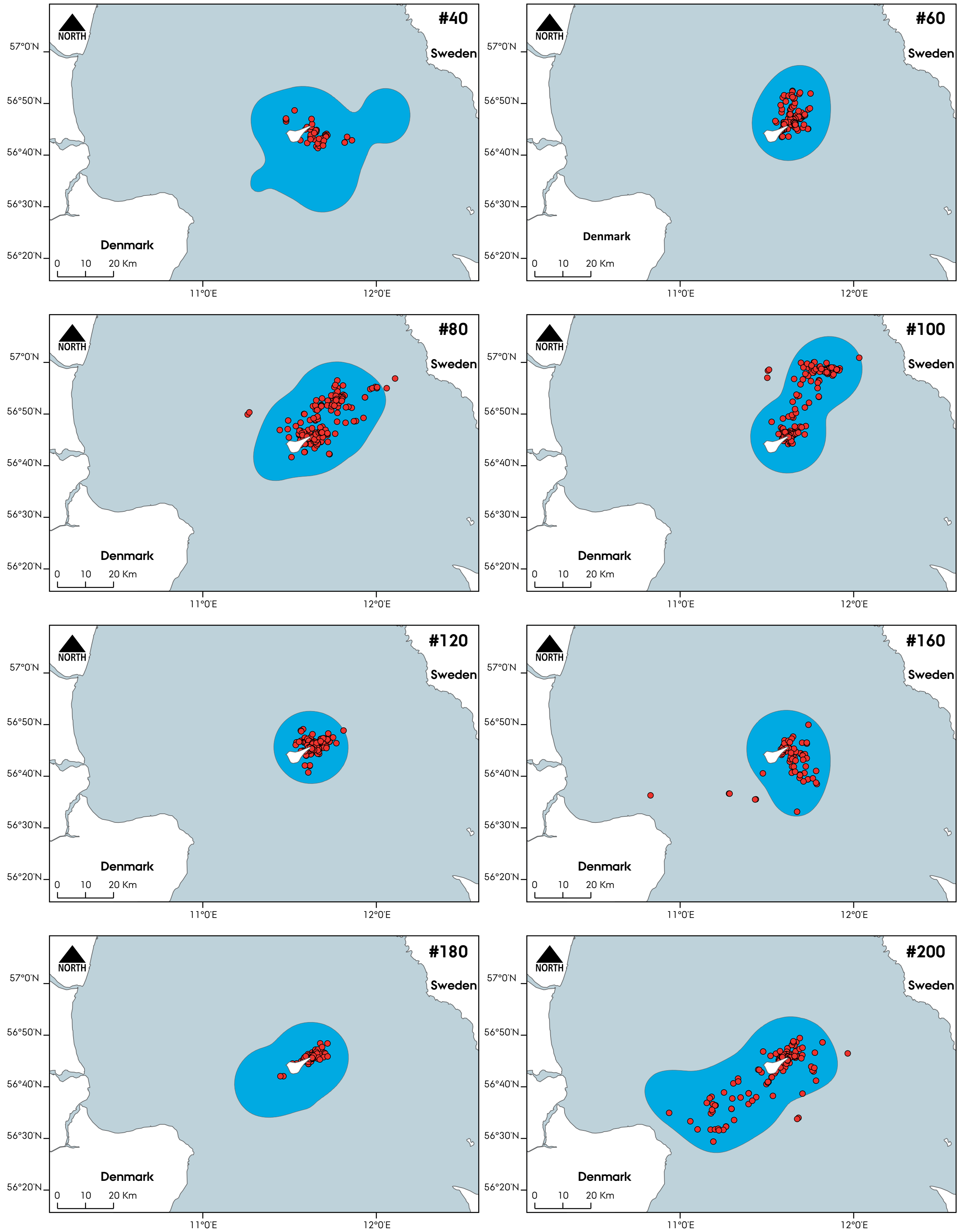
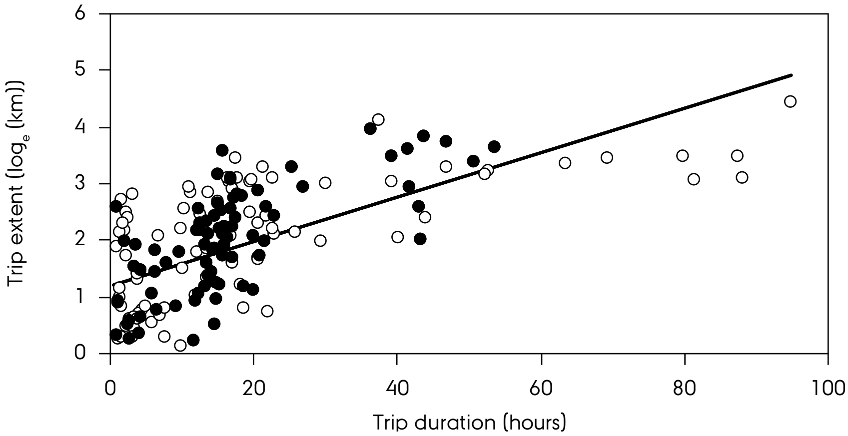


Figure 5. Areas visited during post-disturbance trips (red dots) and un-disturbed trips (blue areas), inferred from satellite locations of eight individually tagged harbour seals from Anholt (see Table 1). Blue areas are 95% fixed kernel density estimates.

Figure 6. The correlation between the maximum extent of post-disturbance trips (black) and un-disturbed trips (white) versus trip duration (R^2=0.40, P<0.001).



support the group-level response observed in the Anholt reserve, where Andersen *et al.* (in review) found that whilst harbour seal fleeing behaviour differed between disturbance types, seals resumed hauling out by the end of the day, irrespective of disturbance type and cause of departure.

Once disturbed, the individually tagged seals rushed to sea together with those with which they hauled out. Post-disturbance trip extent, however, varied between disturbance types, and seals travelled longer distances after being disturbed by pedestrians compared to boats. Andersen *et al.* (in review) found boats to inflict far greater flight responses of harbour seals than did pedestrians. Seemingly, seals on the haul-out site are highly responsive to boats, but are less reactive once in the water, while the reverse is true for disturbances caused by pedestrians.

Generally, the eight tagged harbour seals in this study remained within 40 km from the Anholt seal reserve during their post-disturbance movements, with only few longer trips. The same was true for at-sea movements during un-disturbed trips. Hence, this study is consistent with the previously reported distances of locally moving and foraging harbour seals (Thompson *et al.*, 1998; Tollit *et al.*, 1998; Suryan and Harvey, 1998). However, though staying relatively close to the haul-out site when at sea, we found a positive association between the individual trip duration and maximum trip extent, with seals moving farther away having increased trip duration. Moreover, harbour seal sex and age may affect the duration and range of foraging trips (Thompson *et al.*, 1998) and seasonal movements in general (Dietz *et al.*, in prep), but unfortunately, the potential effect of sex and age in our study could not be rigorously tested due to our limited sample size.

Our prediction that seals would be more eager to return if the haul-out bout before disturbance was short was not supported, as we found no relationship between the amount of time hauled out before leaving the haul-out site and trip duration. In areas with distinct tidal cycles, the arrivals and departures of harbour seals may not be distributed randomly in time (Da Silva and Terhune, 1988), whereas in Kattegat with small tidal amplitudes, the opposite would have been expected, had it not been for the disturbance pressure. However, as seals generally were observed to return during the dark period, it is likely the diel rhythm, and perhaps the declining level of disturbance in and around the reserve towards the end of the day, which governs the return of the seals.

We found all examined characteristics of un-disturbed and post-disturbed trips to be largely comparable except for trips induced by pedestrian disturbances compared with un-disturbed trips. This strongly suggests that disturbed harbour seals do not simply reside close to the haul-out site until the dark period begins, but rather behave like un-disturbed seals at sea. First, both trip duration and the time of return were generally similar for un-disturbed and post-disturbance trips. In this respect it is, however, important to note that the duration of the un-disturbed trips was generally shorter than that of disturbed trips, but not significantly so. Secondly, and more importantly, the area-use of disturbed and un-disturbed harbour seals overlapped almost completely. Half of the tagged harbour seals always stayed close to the haul-out site, while the other half visited specific areas far from the haul-out site, irrespective having left the haul-out site voluntarily or because of disturbances. Hence, these areas most likely include the prime foraging grounds for the same individuals. Indeed, these same areas have been categorised as foraging areas using dive profiles (Chudzinska, 2009). Hence, once disturbed, harbour seals seemingly use the opportunity to forage.

The stable area-use of the individual harbour seals may also point to different foraging strategies, but also that by travelling to specific areas far from the haul-out site, harbour seals may help reduce the intra-specific competition, which otherwise could arise from high site-fidelity (Bjørge *et al.*, 1995). In this study, harbour seals did exhibit a high degree of site-fidelity, and the Anholt reserve was the only haul-out site visited during the pre-breeding period, even for the group of non-breeding individuals examined here. Previous studies have described harbour seals to display seasonal variation in site-fidelity, with more uniformly usage of sites during periods with specific habitat requirements, such as breeding and moulting (Thompson, 1989; Härkönen and Harding, 2001; Small *et al.*, 2005). Whilst the isolated location of Anholt in Kattegat with approximately 50 km to the nearest haul-out site in itself might increase the tendency of site-fidelity, Dietz *et al.* (in prep) showed that when examined on a year-round basis, the Anholt harbour seals indeed roam all over the Kattegat, visiting several haul-out sites. However, high site-fidelity, especially during sensitive periods such as around breeding (Dietz *et al.* in prep; this study), may be of importance for the impact of disturbances.

Management implications

The strong degree of site-fidelity during pre-breeding is an important component when assessing the effect of disturbance on individual seals. Like Murphy and Hoover (1981, cf. Suryan and Harvey, 1999) observed, harbour seals may tend to search for a new haul-out site after a disturbance. In our study, where harbour seals exhibit a strong degree of site-fidelity, seals are more exposed to disturbances reoccurring at the haul-out site, and cumulative disturbance effects are expected. Such repetition of disturbances on the same individuals are likely to change their tolerance towards disturbances (Bejder *et al.*, 2009). In a previous study we concluded that the Anholt harbour seals were not habituated to the disturbance level in the Anholt seal reserve (Andersen *et al.*, in review). However, in the present study, conducted in a period where seals are less associated to land, we find signs of other behavioural adaptations in response to disturbances, in that seals seemingly initiated foraging trips following a disturbance. Thus, in this period, they may to some extent be able to reduce the costs of such disturbances, if later allowed to hauling out sufficiently.

It is, however, important to keep in mind that the un-disturbed trips included as "control" in the present study, do not necessarily reflect true un-disturbed harbour seal behaviour. Not only has the Anholt seals in general been subject to repeated disturbances over many years, the individual seal has also experienced multiple disturbing activities during its lifetime. The Anholt seals may therefore not be regarded as naïve, as their behaviour may be influenced by this "ghost of disturbance".

ACKNOWLEDGEMENTS

We are especially thankful to Morten Abildstrøm for his invaluable help during this project. We would also like to thank our colleagues at the Department of Bioscience: Susi Edrén, Jakob Tougaard, Signe Sveegaard, Magda Chudzinska, Jesper Møller, Rikke Danøe and Nikolaj Bech, and Henrike Seibel, Eydfinn Stefansson, Bjarni Mikkelsen, Aqqalu R. Asvid, Annette Bombosch, Theis Nygaard, Bendt Nielsen, and the personnel from the Danish Maritime Safety Administration for assistance in the field. This study was financially supported by Aage V. Jensen Charity Foundation, the Danish Outdoor Council, the Danish Nature Agency, Gorenje and Knud Højgaards Fond, and carried out with permission from the Danish Nature Agency (SNS-3446-00054 and SNS-3446-00058) and the Animal Welfare Division (Ministry of Justice, 2005/561-976).

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PAPER VI

MOVEMENT PATTERNS OF HARBOUR SEALS (*PHOCA VITULINA*) IN KATTEGAT, DENMARK

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Manuscript

Photo: Aqqalu Rosing Asvid.

MOVEMENT PATTERNS OF HARBOUR SEALS (*PHOCA VITULINA*) IN KATTEGAT, DENMARK

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ABSTRACT

Twenty-seven harbour seals were caught and tagged at Anholt in the middle of Kattegat, Denmark. The satellite tagging shows that harbour seals from Anholt move all over Kattegat with a maximum distance of 249 km from the tagging haul-out site. Sex and age groups move differently within seasons. Distances moved and home range sizes increased across autumn, peaked in February-March and decreased through spring. During the breeding season in spring all seals were very stationary around Anholt. The strong site fidelity during the breeding period indicates limited gene flow between the haul-out sites in Kattegat and between the different management areas of the Danish harbour seal populations. Young seals were less stationary than older seals. Yearlings (n=14) had large home ranges over winter and visited many sites in Kattegat, including Hesselø (40%), Læsø (40%), Gilleleje (29%), Sjællands Rev (14%), Hirsholmene (7%) and Skagen (7%). Along the Swedish coast Varberg (36%), Hallands Väderö (21%) and Tislarna (7%) were visited. Subadults (n=5) showed a more restricted dispersal, of which 40% visited Hesselø and 20% visited Læsø. The calculated home ranges provide a tool for designating marine protected areas for seals at sea.

KEY WORDS: Distribution, dispersal, age related seasonal behaviour, harbour seal, *Phoca vitulina*, satellite telemetry, Kernel Home Range, area use, haul-out.

INTRODUCTION

The management and conservation of marine species requires a detailed understanding of species movement behaviour and how this may vary temporally, spatially and individually. For marine species such assessments are often difficult because direct observations are hard to get and because generally little is known about the physical and environmental features that promote or halt movements. Satellite telemetry provides a powerful technique for tracking the movements of marine species and has been used widely on pinnipeds, whales, turtles, fish, sharks, and seabirds (Block *et al.* 2011). Telemetry allows for a detailed contemporary assessment of individual movement and space use patterns which unlike most genetic approaches provides the temporal and spatial resolution necessary for designation of local marine protected areas.

The harbour seal (*Phoca vitulina* L.) is the most common seal species present in the cold temperate waters of the North Atlantic. They come ashore to give birth, rest, and moult (e.g. Bonner 1972; Bigg 1981). Populations of harbour seals are considered non-migratory but, as a species, use a wide range of habitats across their geographical distribution (Bigg 1981). Usually they are found as concentrated colonies on sandy beaches or as more dispersed groups along rocky shores (Bigg 1981). The harbour seal forage on a wide range of cephalic and fish species. In Kattegat, it is one of only a few apex predators in the marine ecosystem and may thus play a key role in maintaining local ecosystem stability and productivity.

The harbour seals in Kattegat have experienced substantial population declines at regular intervals over the past century. From 1889 and 40 years forward, the Danish and Swedish harbour seals were targets for massive hunting campaigns to eradicate the species due to its competition with fisheries (see e.g. Andersen *et al.* 2007). The declines experienced during this period were so severe that increases in abundance first were accomplished with the initiation of total protection and closed seal reserves in the late 1970s (Olsen *et al.* 2010). Within the past decades, the harbour seal populations of northern Europe have experienced repeated disease outbreaks caused by the Phocine Distemper Virus (PDV) in 1988 and 2002 (Härkönen *et al.* 2006) and other unknown pathogens in 2007 with high mortalities as a consequence (Härkönen *et al.* 2008).

The unstable population trajectory of Kattegat harbour seals, the fact that most severe disease outbreaks observed in northern Europe initiated on Anholt, and the potential key role of harbour seals in the local marine ecosystem indicates that a detailed examination of temporal and spatial movement patterns of harbour seals in Kattegat is timely. The Kattegat region is characterised by intense shipping activities and other anthropogenic activities (Edrén *et al.* 2010), but holds several areas where harbour seals are protected (Olsen *et al.* 2010). These areas, however, does not always offer adequate protection from disturbance activities (Andersen *et al.* in prep; Andersen *et al.* in review).

In this study, we use information on the at-sea distribution of satellite-tagged seals to identify the areas used by harbour seals from the haul-out site at Anholt. We analyse the sex and age specific seasonal movement pattern. This study covers the entire annual cycle from one of the most important haul-out sites in the Kattegat region.

METHODS

The study area

The island of Anholt is located in the central part of the Kattegat in southern Scandinavia (Figure 1). The average water depth in Kattegat is around 20 m with a maximum depth of around 100 m. The deeper waters are located along the Swedish west coast in the eastern part of Kattegat. The waters around Anholt are mainly shallow (down to 10 m) except for the area southeast of Anholt where water depth extends to 25 m. Sandy bottom occurs mainly in the shallow areas and mud dominates in deeper areas of the Kattegat (Härkönen 1987). Tides are barely detectable in the Kattegat but strong wind driven currents may occur.

During summer harbour seals mainly haul-out on the eastern tip of Anholt in the Totten seal sanctuary (56.73°N; 11.66°E, Figure 1). The seal sanctuary was established in 1990 and access is prohibited year-round (Jepsen 2005). The seals mainly prefer the eastern tip of Anholt during summer, when tourists visit the island. During winter the seals often haul-out near at the northern shores of Anholt. The seal site at Anholt has been surveyed during moult (late August) for the past 25 years and the 2010 estimate of seals around Anholt (corrected for seals in the water) is 1,800 harbour seals. Together with Hesselø this haul-out location holds the highest number of harbour seals in Denmark (Olsen *et al.* 2010; Teilmann *et al.* 2010).

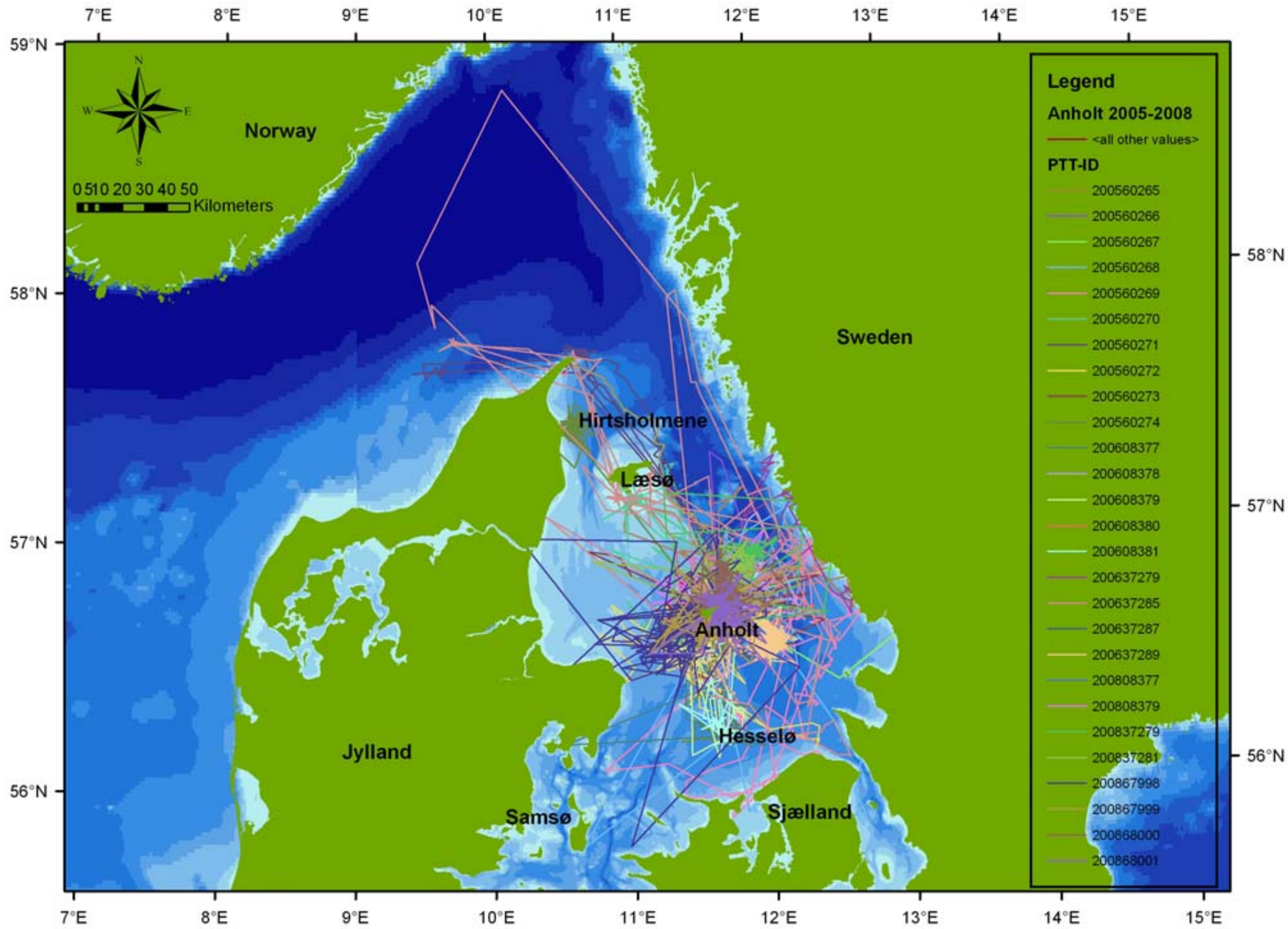


Figure 1. Map showing the satellite tracks of the 27 harbour seals tagged in September 2005 and 2006 and April 2008.

Satellite telemetry

Netting of the seals

Chains of two to five 100 m nets were set 25-300 m from the shore at 3 to 8 m depth. Green, blue and black coloured monofilament and twisted nylon nets with mesh sizes of 180×180 mm were used. Twine size 0.60 mm and net depth and length of 2.5×100 m, a float line with an uplift of 38 g/m and lead line with 23 g/m weight were used.

The nets were "fishing" continuously for up to 5 days and tended regularly for seals entangled. Due to the float line and the thin lead line the seals were able to rest at the surface until they were disentangled, tagged and released.

In total twenty-seven harbour seals were captured during three field periods. Ten seals were captured and tagged during 14-17 September 2005, 9 seals during 21-22 September 2006, and 8 seals during 25-28 April 2008.

Handling of the seals

Upon capture, seals were lifted into the boat using a pole net, transported to shore and placed in a hoop net and fixed on a specially designed board with mounting straps. The fur was cleaned with acetone and the transmitter was attached to the fur using fast-hardening two-component epoxy glue (Araldite 2012). During the handling of the seals, the species, sex, length, circumference and weight were recorded (Table 1). In addition seals were tagged with conventional flipper tags and freeze branded on each side, while hair and tissue biopsy samples were taken for later contaminant and genetic analyses.

Transmitter type

Seals were instrumented with Argos position only tags (n=25, SPOT4 and 5, Wildlife Computers, Seattle, USA) or Argos/Fastloc GPS tags (n=2, Wildlife Computers) all powered by 2 AA batteries. The tags were capable of providing 70,000 transmissions and programmed to transmit 250-500 uplinks every or every second day depending on the period of tagging proving a battery longevity of 140-280 days.

Data collection and analysis

Data on movements and transmitter status were collected via the Argos Location Service Plus system (Harris *et al.* 1990). Locations are classified by the Argos system into one of six location classes (LC) according to level of accuracy (3, 2, 1, 0, A, B). Studies have shown that there can be significant error in all location classes (up to several kilometres), but that even the low accuracy locations may provide useful and valid information if they are appropriately filtered (e.g. Sveegaard *et al.* 2010). Thus, all location classes were used in the present study after filtering by a SAS-routine, Argos Filter V7.02 (Douglas 2006). The filter is comparable to the R-based SDA-filter (Speed, Distance, Angle) tested by Freitas *et al.* (2008). The filter settings for this study were: Maximum swim speed: 10 km/h (minrate = 10), i.e. excluding swim speed between two locations > 10 km/h. If, however, the distance between locations were less than 5 km (maxredun = 5), they were both retained, because the swim speed calculations may be unrealistic due to even smaller inaccuracies of closely spaced positions. Finally positions were excluded if the angle between consecutive vector lines between previous and following location were less than 10 degrees (ratecoef = 10). All other settings were set as default. Excel 97 (SR2), SAS Enterprice Guide V4.1 and StatView V5.0.1 were used for statistical analysis and graph presentations. The maps were generated using ArcMap (version 9.3).

Table 1. Basic biological and tagging information from the 27 harbour seals tagged in September 2005 and 2006 and April 2008 at Anholt. Information on visits to neighbouring haul-out sites is also shown.

					Tracking				Length	Weight		Denmark							Sweden		
	Number	PTT no.	Tagging date	Last position date	Longevity (days)	Distance (km)	Sex	Age class	(cm)	(kg)	Transmitter type	Skagen	Hirsholmene	Læsø	Anholt	Hesselø	Gilleleje	Sjællands Rev	Tislarna	Varberg	Hallands Väderö
2005	1	200560265	9/14/2005	6/9/2006	268	2391	F	Yearling	104	24	SPOT5			x	x					x	
	2	200560266	9/14/2005	11/22/2005	69	878	M	Yearling	107	27	SPOT5				x						
	3	200560267	9/14/2005	2/4/2006	143	973	F	Yearling	93	19	SPOT5				x						
	4	200560268	9/14/2005	5/23/2006	251	1547	M	Yearling	96	22	SPOT5			x	x	x	x	x		x	x
	5	200560269	9/17/2005	12/4/2005	78	1471	F	Yearling	93	21	SPOT5				x	x	x	x		x	x
	6	200560270	9/17/2005	5/11/2006	236	2278	M	Yearling	102	24	SPOT5			x	x						
	7	200560271	9/17/2005	10/29/2005	42	1018	F	Yearling	95	20	SPOT5	x		x	x						
	8	200560272	9/17/2005	5/17/2006	242	2746	F	Yearling	97	22	SPOT5				x	x	x				
	9	200560273	9/17/2005	6/10/2006	266	2613	F	Subadult	114	41	SPOT5				x						
	10	200560274	9/17/2005	2/16/2006	152	2395	F	Yearling	104	25	SPOT5		x	x	x	x					
2006	11	200608377	9/21/2006	3/13/2007	173	1509	F	Subadult	116	35	SPOT5				x	x					
	12	200608378	9/21/2006	2/5/2007	137	1760	F	Yearling	95	21	SPOT5				x	x					
	13	200608379	9/21/2006	1/23/2007	124	1735	F	Yearling	96	21	SPOT5				x	x					
	14	200608380	9/22/2006	1/16/2007	116	709	M	Subadult	116	33	Fastloc GPS			x	x						
	15	200608381	9/22/2006	3/2/2007	161	1431	F	Subadult	114	33	Fastloc GPS				x	x					
	16	200637279	9/22/2006	12/4/2006	73	584	M	Yearling	102	22	SPOT4				x					x	
	17	200637285	9/22/2006	1/28/2007	128	3434	F	Yearling	95	26	SPOT5			x	x		x		x	x	x
	18	200637287	9/22/2006	12/6/2006	75	973	F	Yearling	99	21	SPOT5				x						
	19	200637289	9/22/2006	4/16/2007	206	3536	M	Subadult	108	27	SPOT5				x						
2008	20	200867999	4/25/2008	7/17/2008	83	2649	M	Yearling	?	26	SPOT5			x	x						
	21	200837281	4/28/2008	6/28/2008	61	2882	M	Subadult	102	48	SPOT4				x						
	22	200808379	4/26/2008	6/25/2008	60	2533	F	Yearling	102	24	SPOT5				x						
	23	200837279	4/28/2008	6/13/2008	46	2481	M	Subadult	118	46	SPOT4				x						
	24	200868000	4/26/2008	9/2/2008	129	4168	F	Yearling	101	28	SPOT5				x						
	25	200868001	4/26/2008	6/19/2008	54	1523	M	Subadult	118	38	SPOT5				x						
	26	200808377	4/26/2008	6/23/2008	58	1025	F	Adult	120	46	SPOT4				x						
	27	200867998	4/25/2008	7/30/2008	96	4058	M	Adult	140	62	SPOT5				x						
Tagged September 2005 and 2006 (%)								**All**				**5**	**5**	**37**	**100**	**42**	**21**	**11**	**5**	**26**	**16**
								Yearling				**7**	**7**	**43**	**100**	**43**	**29**	**14**	**7**	**36**	**21**
								Subadult						**20**	**100**	**40**					
Tagged April 2008 (%)								**All**						**13**	**100**						

The bathymetrical depth contours are based on 1-degree resolution GEBCO data (version 1.00). Hawth's Analysis Tools V3.27 was used as an extension to ArcMap to generate track-lines, Kernel Home Range and area calculations.

Data handling

The seasonal categories and the exact date for these were defined by shifts in movement patterns (summer: 6 June-15 September; autumn: 16 September-13 December; winter: 14 December-21 February and spring: 22 Februar-5 June extrapolated from Figure 4 These categories were used in the consecutive statistical examination.

Distance data from the haul-out site was log-transformed as the distribution was highly right skewed. The distance data was analysed by a linear mixed effect model with age group, season and sex as fixed factors and seal individual as random grouping factor. The interaction factors between season and sex and between age group and sex were included, as a removal of the interaction between age group and sex did not result in a significantly better model (log-likelihood, P=0.051), though very close. However, data did not allow including the interaction factor between season and age group.

RESULTS

Basic information about the captured seals

Of the 27 harbour seals tagged in the present study the majority were yearlings (17) and subadults (8), whereas only two were adults (Table 1). Age determination was based on weight and length information from the literature (e.g. Pitcher and Calkins 1979; Härkönen and Heide-Jørgensen 1990). A similar age and sex distribution and number of seals were tagged each year. The 27 seals were tracked for a total of 3,527 days (mean/seal = 131 days; range = 42-268 days) providing 55,300 km of travelling routes (mean = 2,048 km; range = 584-4,168 km) based on 8,826 positions (after filtering).

Contact to other haul-out sites and regions

Harbour seals from Anholt move all over Kattegat with a maximum distance of 249 km for one individual and average weekly distances of up to ca. 85 km for yearling, 35 km for subadults and 20 km for adults from the tagging haul-out site (Figure 4). The seals tagged during autumn (14 September-9 June) showed a wider dispersal than the seals tagged during spring (25 April-9 September, Figure 4 and 5). Hence the seals had larger home ranges over winter and visited many sites in Kattegat (Figure 5; Table 1 and 3). In addition to Anholt the preferred Danish localities for juveniles in declining importance were: Hesselø (43%), Læsø (43%), Gilleleje (29%, Sjællands Rev (14%), Hirsholmene (7%) and Skagen (7%) (Table 1). Along the Swedish coast yearlings visited three haul-out sites: Varberg (36%), Hallands Väderö (21%) and Tislarna (7%). There was a strong and significant correlation between the percent of yearling (2005 and 2006) that visited a locality and the locality's geographical distance from Anholt (R^2=0.595, F=10.27, P=0.015) (Figure 6). Subadults (n=5) showed a more restricted dispersal, of which only two (40%) visited Hesselø and one (20%) visited Læsø (Table 1). No information was obtained from adult seals from the autumn tagging. The seals tagged during spring were all very stationary and only one individual (13%) out of the eight tagged visited Læsø (see details below).

Distance from the tagging site relative to age, season and sex

All class variables: age group, season and sex had significant effect on distance moved from the tagging site, and imply that sex and age groups move differently within seasons (Table 2). Yearlings showed the least site fidelity during winter and spring (Range means: 43.9 and 48.1 km) and females travelled further than males during autumn (30.4 vs. 9.5 km), winter (47.1 vs. 27.6 km) and spring (49.1 vs. 45.4 km) (Table 3). All sex and age groups showed strong site fidelity during the

Table 2. Results of the linear mixed effect model conducted on the distance (km) from the tagging site of the 8,826 positions from the 27 harbour seals.

Source	DF	F Value	P Value
Intercept	1	97.8	<0.0001
Age group	2	185.2	<0.0001
Season	3	112.3	<0.0001
Sex	1	5.61	0.018
Season*Sex	4	41.7	<0.0001

Table 3. Seasonal, sex and age related average distribution distance from tagging site (km) for the 27 harbour seals tagged at Anholt.

Sex group	Age group	Spring	Summer	Autumn	Winter	Year round
Males	Yearling	45.4	13.8	9.5	27.6	19.0
	Subadult	6.6	8.5	15.8	12.5	9.8
	Adult	8.4	13.7			12.6
	All age groups	19.0	10.7	12.3	17.7	13.1
Females	Yearling	49.1	9.7	30.4	47.1	27.1
	Subadult	29.9	5.3	10.0	39.2	16.9
	Adult	4.3	3.1			3.3
	All age groups	42.9	8.7	25.7	45.4	24.3
Both sexes	Yearling	48.1	10.5	26.7	43.9	25.5
	Subadult	11.9	8.4	12.1	24.1	12.0
	Adult	7.0	9.4			8.9
	All age groups	31.2	9.7	22.6	36.9	20.0

summer breeding and moulting period (average: 9.7 km). Hence, during summer more or less all seals stayed at Anholt and the surrounding waters, except for one subadult female (#2008-67999), which visited Læsø in mid July 2008). During summer, none of the adults frequented other localities than Anholt, indicating very strong site fidelity at this time of the year.

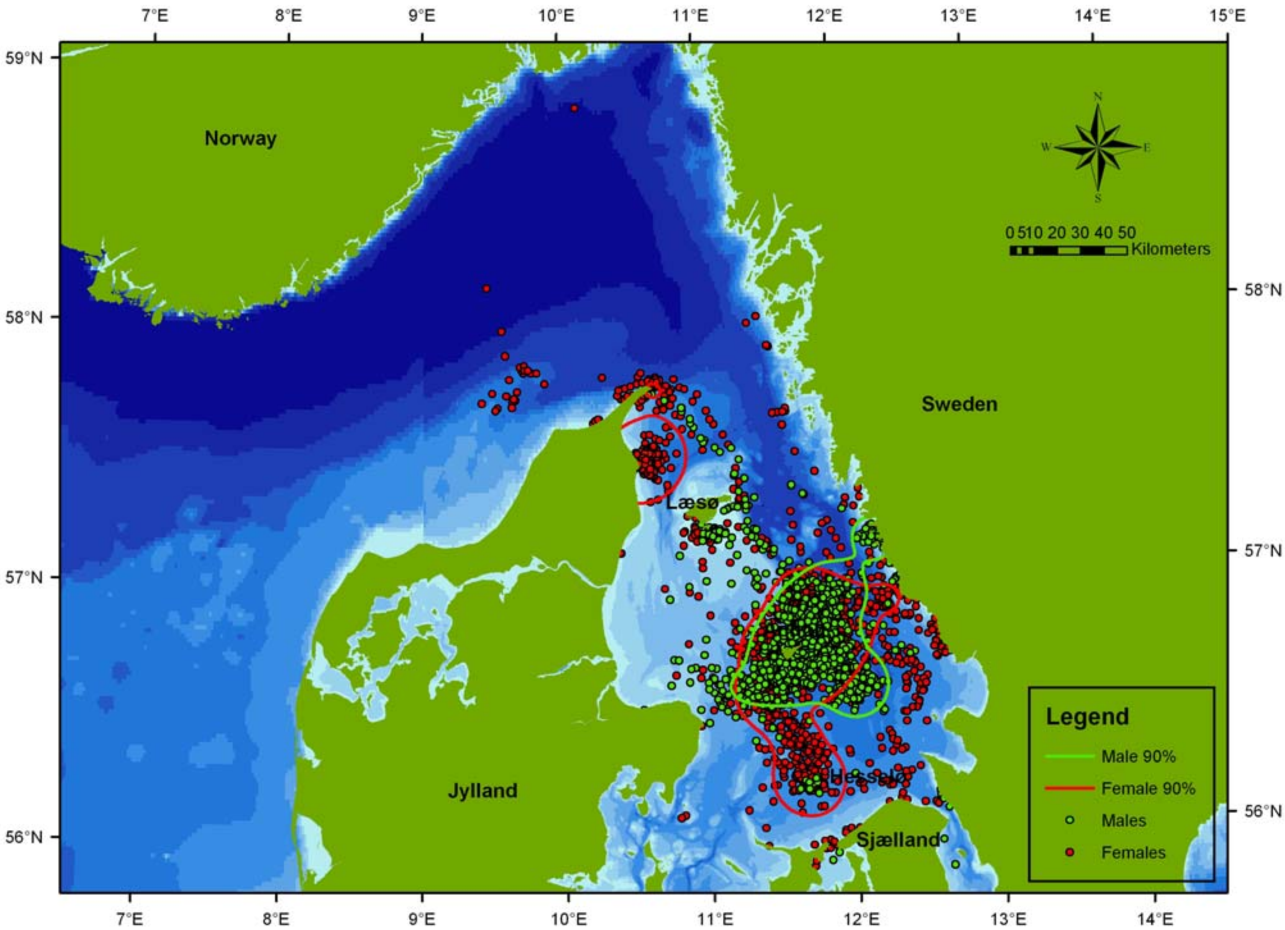


Figure 2. Map showing the positions of 27 harbour seals tagged in September 2005 and 2006 and April 2008 at Anholt divided by sex. Males; green dots and green outline showing 90% Kernel Home Range (3,293 km²) and females; red dots and red outline (5,189 km²).

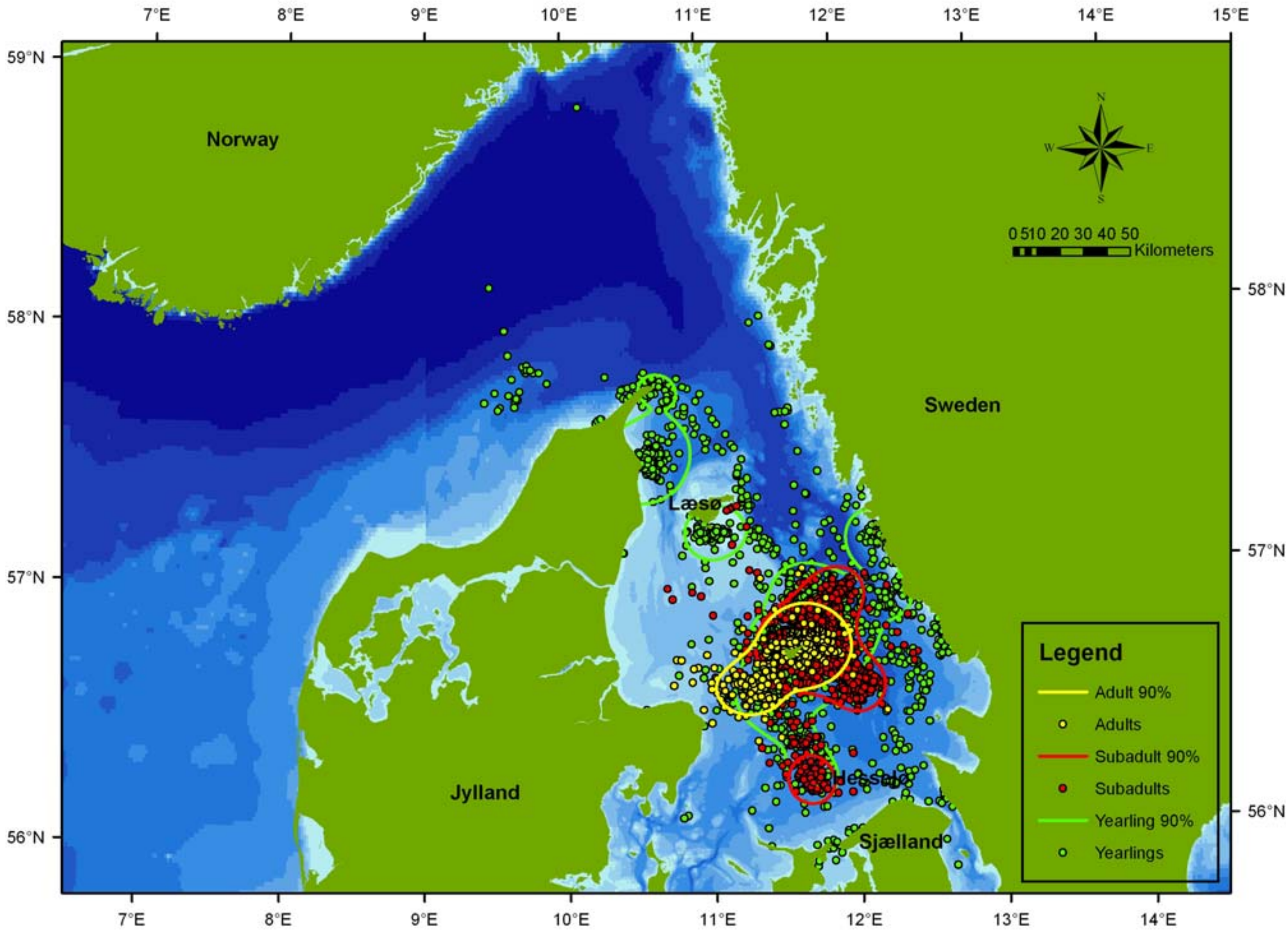


Figure 3. Map showing the age related distribution of the 27 tagged harbour seals. Dots indicate satellite locations and circles the 90% Kernel Home Ranges for the adults (1,713 km²), subadults (2,534 km²) and yearlings (6,414 km²).

Sex differences in the Kernel Home Range distribution

Overall, females travelled over a wider area compared to males (males: 3,293 km²; females: 5,189 km²) (Figure 2). However, this movement pattern was mainly driven by yearlings in autumn and winter and the subadult in winter and spring (Table 3).

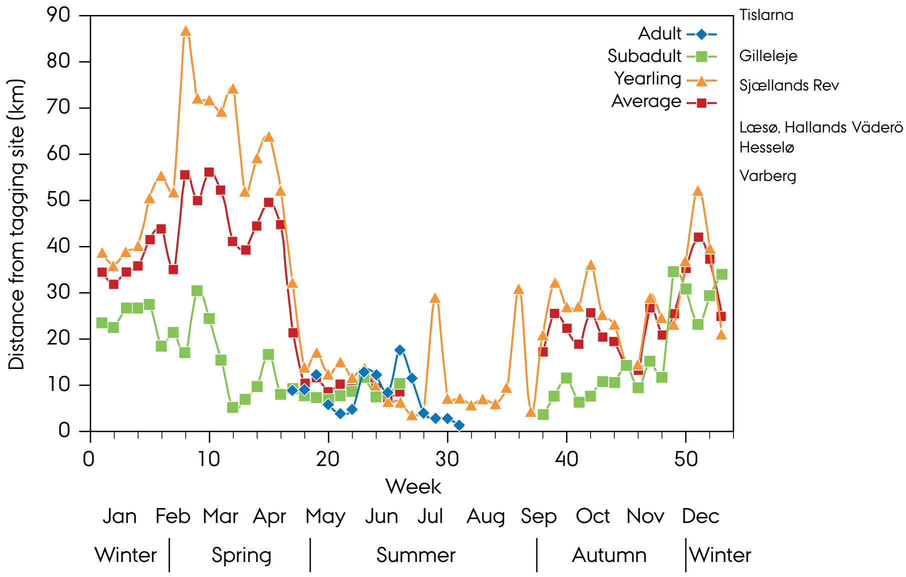
Age related differences in distribution

The strength of site fidelity increases with age (especially from yearlings to subadults), as seen on the age separated plots on both a geographic and a distance related scale (Figure 3 and 4). Summarized over sex and season, the 90% Kernel Home Ranges calculated for the yearlings (6,414 km²) is larger than for subadults (2,534 km²), which again is larger than for adult seals (1,713 km²). Likewise, yearlings move further away from the haul-out site (25.5 km) than subadults (12.0 km), which again exceeds adult movements (8.9 km). However, the pattern of adults should be interpreted with caution since only two seals were tagged and only in spring and summer.

Overall seasonal distribution

As evident from the seasonal plots all tagged harbour seals show the strongest site fidelity to the haul-out site on Anholt during summer (week 19 until week 37-38) with a 90% Kernel Home Range of 1,722 km² and an average travelling distance of 9.7 km from the tagging haul-out site (Figure 4 and 5; Table 3). Hereafter the seals move further away (average distance: 22.6 km; 90% Kernel Home Ranges: 6,885 km²) during autumn until week 49 after which they range even further away

Figure 4. Age specific seasonal site fidelity for harbour seals tagged at Anholt. Week number, month and season is shown in relation to the weekly average distance from the tagging site at Anholt. The approximate distances to the closest haul-out sites are included on the second y-axis.



from the haul-out site during winter (average distance: 36.9 km; 90% Kernel Home Ranges: 10,608 km²) (Figure 5; Table 3). Finally during spring from week 7 to week 19 the seals gradually approach the haul-out site on average going from 55 km down to 10 km (average distance: 31.2 km; 90% Kernel Home Ranges: 5,730 km²). All visits to the Swedish coast took place during autumn and winter, as well as the trips into the Skagerrak and along the northern coast of Sjælland (Figure 5).

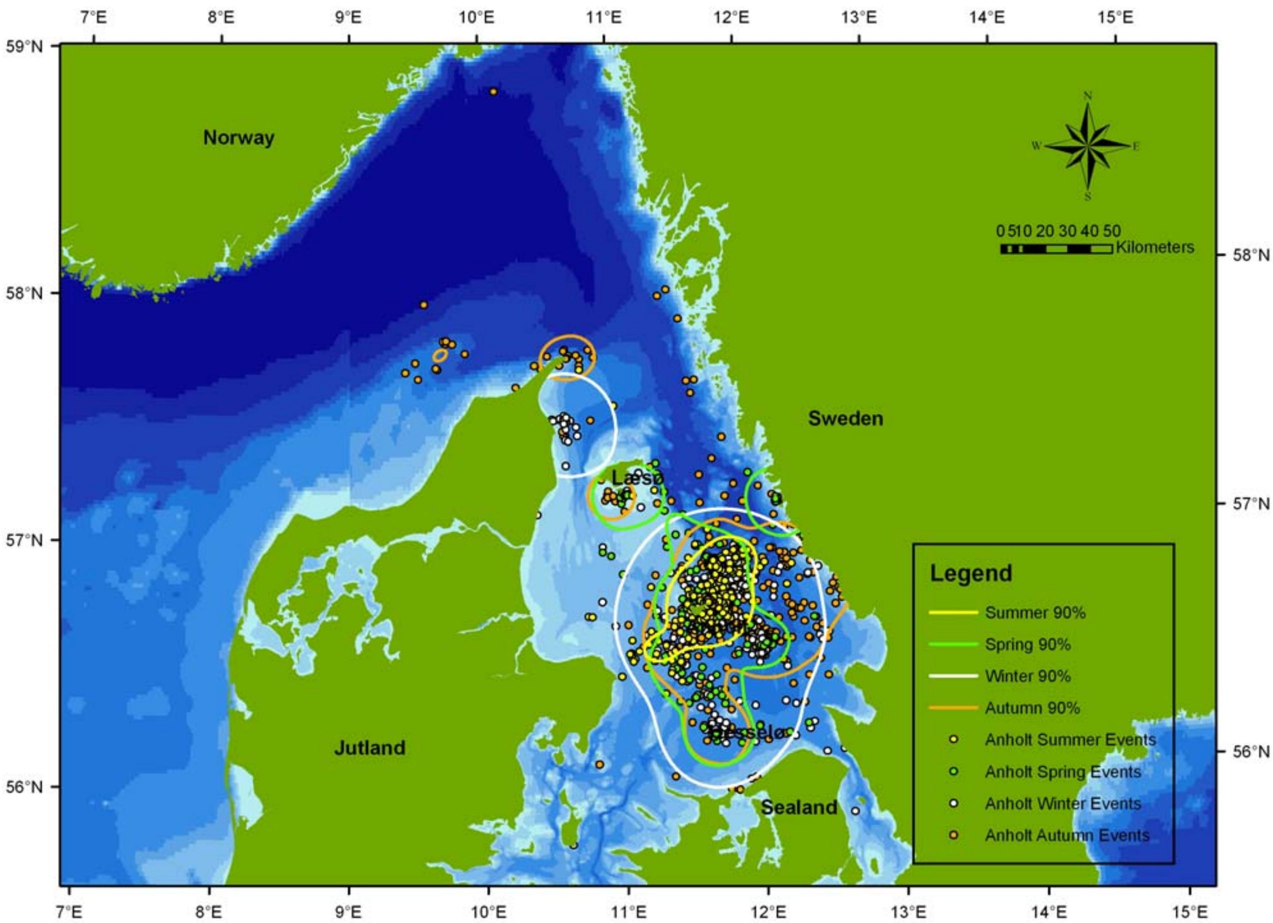
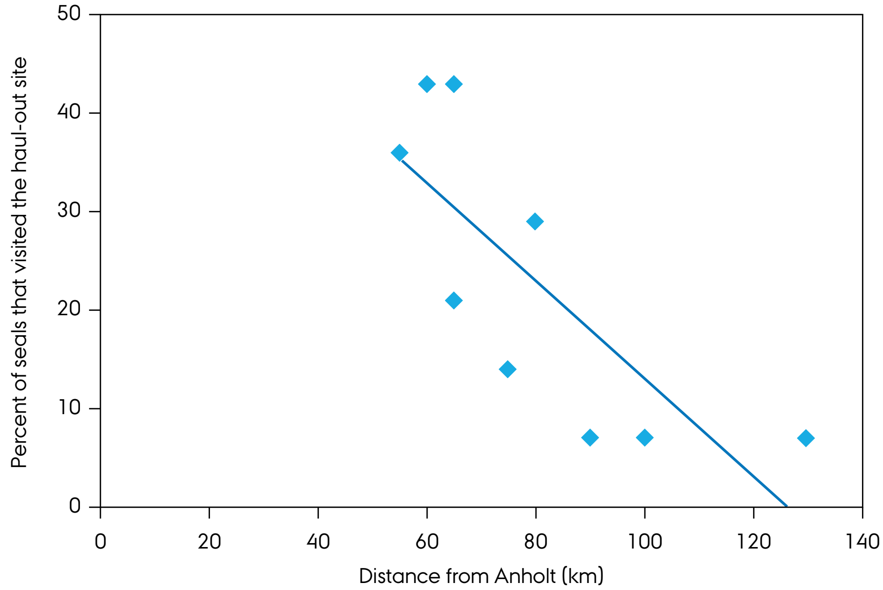


Figure 5. Map showing the seasonal distribution of the 27 harbour seals tagged at Anholt separated into four seasons with locations (dots) and 90% Kernel Home Ranges (outlines) (summer: 1,722 km²; autumn: 6,885 km²; winter: 10,608 km²; spring: 5,730 km²).

Figure 6. Correlation between each haul-out sites' geographical distance from Anholt and the percent of yearlings that visited the site in 2005 and 2006. The trend line had a $R^2=0.595$ and was described by the formula $y=-0.496x+62.64$



DISCUSSION

Sex, age and seasonal related differences in distribution

Our findings that harbour seal sex and age groups move differently within seasons have been observed for other populations of harbour seals. Lowry *et al.* (2001) found that the dispersal of harbour seals tagged in Prince Williams Sound, Alaska, was significantly affected by sex and season. Mean monthly home ranges varied from less than 100 km^2 to more than 1,500 km^2, and were smallest during June-July. Females had larger mean home ranges than males during most of fall and winter, and in some months up to four times larger in the Alaskan study. Females also tended to move relatively more than males during fall-winter in California (Allen 1988 cf. Lowry *et al.* 2001) and in Moray Firth, Scotland (Thompson 1993).

Movement patterns during the summer months have previously been recorded by Härkönen and Harding (2001), who found that female harbour seals in Skagerrak generally show stronger site fidelity during summer than males. Van Parijs *et al.* (1997) found that male harbour seals in Moray Firth, Scotland, travelled widely in June, and after this restricted their ranges in early July when females began foraging in late lactation. In that study, mean 7-d home ranges decreased from 65-480 km^2 in June to 4-70 km^2 in July. Home ranges of females in Moray Firth decreased in size about two weeks earlier than males, with the onset of pupping (Thompson *et al.* 1994). Similar decrease in dispersal was seen at Anholt prior to the pupping season, although the data did not contain enough information to assess sex-related differences specifically during summer. In another study from Moray Firth, Thompson *et al.* (1996) estimated that 21 tagged harbour seals moved only to haul-out sites within a range of 75 km. The summer foraging areas were estimated for 31 harbour seals by Tollit *et al.* (1998), where the majority of the seals foraged within 30 km of their haul-out site. In another study from southeast Scotland from the Tay and Eden estuaries the seasonal haul-out pattern of harbour seals was monitored (Sharples *et al.* 2009). Here the calculated probability of hauling out was highest during June and July which reflect a more stationary behaviour, whereas the lowest probability of hauling out was observed during November, December and January, which was the months where the Anholt seals moved furthest around. Similar results were reported from ten harbour seals tagged in the Kenmare River in southwest Ireland (Cronin and McConnell 2008). In this study the haul-out frequency declined from October to January, where the lowest frequency was observed. Hereafter the frequencies increased again until April, from where a relatively stable haul-pattern was observed until July, where the tags were lost due to the moulting. Another study from western Scotland conducted on Isles of Skye and of Islay and Jura conducted on adult harbour seals revealed a quite stationary pattern (Cunningham *et al.* 2009). This study showed that harbour seals generally remained within a 25 km radius of haul-out sites, and only occasionally travelled over 100 km away from the haul-out sites. The localised movements and the lack of variation with sex, age, and season in the study by Cunningham *et al.* (2009) contrasts the finding of our study and other studies (Thompson *et al.* 1998; Lowry *et al.* 2001). This discrepancy may be due to the fact that Cunningham (2009) only tagged adult seals, but may also suggest that food availability in the vicinity of the western Scotland haul-out sites was adequate throughout the year.

As suggested by e.g. Lowry *et al.* (2001) and Small *et al.* (2005), the age or sex-related differences in movements and home range sizes during late spring and summer are most likely attributed to behaviour associated with reproduction and moulting. At present, however, an explanation for the gender specific difference in winter movements is still unclear.

The successively stronger site fidelity to the haul-out site found for older seals is consistent with information from other regions and species. Lowry *et al.* (2001) found that juvenile harbour seals from Prince Williams Sound moved more than adults and had larger home ranges. Movements were significantly affected by age and month interactions. In all months, mean distances between successively used haul-outs in Prince Williams Sound were <10 km for adult and <20 km for juvenile seals. Mean distance from haul-out to at-sea locations was 5-10 km for adults and generally 10-25 km for juveniles (Lowry *et al.* 2001), which is comparable to our findings from Anholt with 12 and 26 km for yearlings and subadults, respectively, and 8.9 km for adult seals. Similar patterns have been observed in Skagerrak, where yearlings generally exhibited larger home ranges than adults (Härkönen and Harding 2001). These age-related differences in movements likely reflect that the inexperienced yearlings and subadults are going through a learning process in which they devote substantial amounts of time (and resources) towards locating foraging and haul-out sites.

Regional differences in dispersal

Both tagging and genetic studies have documented regional differences in the movement range of harbour seals. The present study revealed that seals at Anholt had much larger average home ranges (range: 1,722 to 10,608 km^2) than seals from Rødsand in the western Baltic with average home ranges (95% fixed kernel) of 215 km^2 (range: 114 to 316 km^2), but much smaller than harbour seals in the Wadden Sea, which frequently make long-range foraging trips into the North Sea (Dietz *et al.* 2003; Tougaard *et al.* 2008). These trends have also been supported by genetic studies where harbour seals in both western Baltic and the Skagerrak were much more restricted in their dispersal as measured by levels of genetic differentiation, than harbour seals in the Kattegat. Still, although not as strong as between the two other regions, Kattegat seals did exhibit some degree of genetic differentiation among haul-out sites, which is consistent with the strong site fidelity during the breeding period recorded in the present study. The factors accounting for the site fidelity of seal may relate to spatial differences in availability of haul-out, feeding sites, hunting history and disturbances. Although literature information seldom provide dispersal information in a uniform and comparable way, examples from e.g. Scotland and Alaska show that movement patterns is variable in different regions and appear to correlate with local and regional distributions of food resources.

Management implications

Although the strong site fidelity around the breeding period observed at Anholt could be a local phenomenon, several reports on restricted movement patterns in other harbour seal populations, suggest that site fidelity is a general characteristic of the harbour seal. This finding has several management implications: first, it strongly indicates that harbour seals in southern Scandinavia comprise several distinct population units both ecologically and genetically with specific requirements in terms of management and conservation. Second, although harbour seals exhibit strong site fidelity during the breeding period, contact with other localities does occur at other times of year. We found that the percent of seals that visited a locality other than Anholt correlated strongly with the locality's distance from Anholt, suggesting that geographical distance rather than preference for certain haul-out sites is the main factor governing movement between haul-out sites in Kattegat. Similar patterns have been observed in a genetic study (Olsen *et al.* in prep) and during the PDV epidemics in 1988 and 2002, where the virus spread outward in concentric circles from the epicentre on Anholt to other harbour seal localities in the Kattegat-Skagerrak-Baltic area (Härkönen *et al.* 2006). Third, the strong site fidelity observed during summer suggest that seals are not likely to travel between the haul-out sites during late August where the yearly aerial surveys is conducted in Denmark and Sweden (e.g. Olsen *et al.* 2010; Teilmann *et al.* 2010). Thus the estimates of population abundance and trends obtained from these surveys can be regarded as reliable with no or only little bias introduced by movements of seals during the survey period. Finally, because the observed fidelity to certain sites and marine areas appears relatively stable across seasons and years, the Kernel Home Ranges calculated in the present study are likely to reflect marine and coastal regions of special importance to harbour seal foraging and breeding in Kattegat. As such they provide a good starting point for designating marine protected areas, and may serve as a guideline for the minimal area of existing harbour seal reserves.

ACKNOWLEDGEMENTS

The study was financed by Aage V. Jensens Fondations, the Danish Nature Agency (Danish Ministry of Environment), Gorenje and the Danish Outdoor Council. Our colleagues Susi M.C. Edrén, Jesper Møller, Rikke Danøe, Jakob Tougaard, Nikolaj I. Bech, Signe Sveegaard (all from Department of Bioscience, Aarhus University), Minna B. Sørensen, Maja F. Rasmussen (Kattegatcentret), Morten Abildstrøm (Forest and Nature Agency), Lee Miller (Odense University), Henrike Seibel (FTZ), Bjarni Mikkelsen and Eyðfinnur Stefansson (Museum of Natural History Torshavn) and Aqqalu Rosing-Asvid (Greenland Institute of Natural Resources) are likewise acknowledged for their help during the tagging operations. The study was carried out with permission from the Danish Nature Agency (SNS-3446-00054 and SN 2001-34461/SN-0005) and the Animal Welfare Division (Ministry of Justice, 2005/561-976).

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HARBOUR SEALS AND HUMAN INTERACTIONS IN DANISH WATERS

Since the protection of the Danish harbour seals in 1977 several seal reserves have been established, and the Danish harbour seal population has increased from around 2000 to approximately 16000 individuals. At the same time human activity in the marine environment has increased, both in terms of commercial and recreational use, and calls for a thorough evaluation of current management and its data basis is needed. Specifically, in order to manage the Danish harbour seals properly more detailed information on the current abundance and reproduction, as well as detailed information on harbour seal movements, and the importance of the interactions between harbour seals and human activities, such as fisheries and disturbance activities is needed.

The six papers included in the present PhD thesis starts out by providing an overview of the status of the Danish harbour seal populations (**Paper I**), where after examinations of management-related issues are addressed: the harbour seal – cormorant – fishery interactions in Limfjord (**Paper II**), the effects of constructional activity from an offshore wind farm on harbour seal haul-out numbers in the Rødsand seal reserve (**Paper III**), the effectiveness of current regulations in the Anholt seal reserve to protect harbour seals from disturbances (**Paper IV** and **V**), and the seasonal movements of harbour seal in Kattegat (**Paper VI**).

Based on the findings in the PhD, several suggestions to improve the current management of the Danish harbour seals are given.

ISBN: 978-87-92825-05-6