Population biology and activity patterns of harbour seals (Phoca vitulina) in the Wadden Sea

Ries, Edith

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Summarising discussion

Introduction

The Wadden Sea harbour seal population has been drastically depleted in the course of this century as a result of habitat deterioration, overhunting and pollution. Parts of the Wadden Sea were lost due to embankments and an increasing number of tourists causing disturbances use the Wadden Sea for recreational purposes. After hunting was stopped throughout the Wadden Sea in 1972, the population started to recover gradually (Reijnders 1992). However, during the 1988 phocine distemper epizootic this development was abruptly interrupted and the seal population was reduced by almost 60% (Dietz *et al.* 1989).

To provide favourable conditions for a recovery of the Wadden Sea harbour seal population, a long-term conservation and management plan was designed (CWSS 1992). The development and implementation of that plan required close co-operation between the countries involved. Also a comprehensive research plan was drafted. The main objectives of this Joint Seal Study were to provide estimates of the population size, to investigate trends in abundance and distribution and to assess the vital population parameters. The development and application of VHF telemetry techniques were essential to investigate the activity patterns, diving behaviour and habitat use of a sample of free-ranging seals in different parts of the Wadden Sea.

The present thesis reports on work performed in the frame of the Joint Seal Study between 1989 and 1996 at the DLO Institute of Forestry and Nature Research, Department of Aquatic Ecology at Texel, The Netherlands.

Estimation of population size

The harbour seal population in the Wadden Sea has been closely monitored using aerial surveys of the haul-out sites providing minimum population estimates. The exact population size cannot be assessed in this way as always some animals remain in the water and do not show up.

We decided to investigate the potential of mark-recapture techniques using light-weight radio transmitters in combination with repeated aerial surveys to produce estimates of the absolute number of seals in the Dutch part of the Wadden Sea. The primary aim was to develop a general technique for correcting counts from aerial surveys of harbour seals.

In spring 1994, we instrumented 15 seals with purpose-built VHF tags at a haul-out site located in the centre of the study area. The number of harbour seals hauled out and the presence of any radio-tagged seals was tracked throughout the breeding season during aerial surveys covering all known haul out sites in the Dutch Wadden Sea. Since during the breeding season the animals also moult, radio tags were gradually shed. A maximum likelihood estimator (ML) was developed to infer the rate of tag loss and the size of the local population. The highest survey result of 1994 was 1038 seals and the maximum proportion of tagged animals on the haul-out sites was 68%. The ML estimate on the number of seals in the Dutch Wadden Sea was 1536; 95% confidence limits were 1225 and 2200 (Ries *et al.* 1998).

Generally, the haul-out behaviour of seals is influenced by biotic factors (sex, age, reproductive stage) as well as abiotic factors (tide, season, weather condition, time of day) (Pitcher & McAllister 1981; Pauli & Terhune 1987a; Yochem *et al.* 1987; Thompson 1989; Kovacs *et al.* 1990; Watts 1992; Vogel 1994). In estuarine habitats such as the Wadden Sea where the seals use intertidal haul-out sites, the pattern and duration of the haul-out bouts are largely determined by the tidal cycle and the exposure period of the sandbank (Pauli & Terhune 1987b; Thompson *et al.* 1994b; Nørgaard 1996).

The technique described in this paper can be used directly to estimate abundance by radio-tagging a sample of seals within each surveyed area, or indirectly as a way of deriving general correction factors for surveys. Which of these approaches is more appropriate depends on the relative importance of biotic and abiotic factors in influencing the haul-out behaviour of harbour seals. If abiotic factors dominate, a correction factor derived in one area may not be valid for another, suggesting that telemetry data should be collected for each area to be surveyed. If biotic factors are more important, a correction factor derived in one area may be appropriate for other areas, too. But in that case it is vital that the sex ratio and age structure of seals selected to carry radio tags is representative of the population. In the current study the tagged sample was clearly not representative and so the validity of the results depended on the assumption that - in the Dutch Wadden Sea - the biotic factors are negligible. Yet the sample size was too small to test this assumption. Two possibilities are available for future studies. One is to obtain more representative samples in terms of sex and age to ensure that the haul-out behaviour of the tagged sample matches that of the population as a whole, even if biotic factors do have a large influence on behaviour. The other is to deliberately pick samples biased to given sex or age groups and check the sensitivity of the estimate to the type of sample used. For example, this strategy should be followed if for management purposes information is needed on a specific section of the population, e.g. only from adult females.

In relation to other areas of the Wadden Sea it does not seem appropriate to adopt the estimates of proportion of seals hauled out from the current study for use throughout the area. Given the variation in availability of sandbanks in the Wadden Sea, we recommend instead that the combined aerial survey/radio-tagging technique be repeated in the other areas when estimating the total population size.

Population development after the 1988 virus epizootic

Based on simultaneous aerial surveys performed in the Wadden Sea we investigated the post-epizootic population development. In the years after the epidemic, the population recovered prosperously and in 1994 the maximum count for the entire Wadden Sea was 8800 animals, which is more than double the survey result of 1989, the year following the epidemic. The annual rate of increase was on average 16%, with the highest rate observed in The Netherlands (21%) and the lowest in Denmark (10%). The post-epizootic population increase was substantially higher than the recovery after a similar low level in The Netherlands during the late 1970's when the population increased by only 9% per year (Reijnders *et al.* 1997).

Before the epidemic substantial differences in reproductive rates existed among the various regions of the Wadden Sea, ranging from 13% in The Netherlands to 23% in Schleswig-Holstein. Since 1989 these rates vary around 20%. Especially in The Netherlands, the reproductive rate is significantly higher than before. This might be due to a selective mortality during the epidemic, in that a higher mortality may have affected more severely the non-reproducing animals. In the present population seals seem to have lower pollutant levels increasing their chances of survival and reproduction.

The initial juvenile mortality was 66% during the 1970's. Compared to other harbour seal populations it was quite high. The post-epizootic first-year mortality in the Wadden Sea harbour seal population was estimated to be 42.7%, a significantly lower level than before but still higher than in other harbour seal populations. Although the Wadden Sea population is recovering well, its present size is only a quarter of an estimated reference number of 37000 seals at the beginning of this century (Reijnders *et al.* 1997).

Net dispersal of seals within the Wadden Sea

Based on geomorphological features of the Wadden Sea we investigated the spatial distribution of harbour seals over 38 designated subareas during the pre-epizootic and the post-epizootic period. The average proportion of seals observed during the annual maximum surveys in each subarea differed partly due to substantial differences in the size of the areas. The corresponding proportion of pups in the different colonies did not follow the spatial distribution of the total population. In some subareas the number of seals increased throughout the study period although the local pup production remained at a very low level. This could only be explained by the immigration of animals from other areas where the pup production was high (Reijnders *et al.* 1981).

As the Wadden Sea population can be regarded as a virtually closed unit, between-year numerical changes in the total population could be used to estimate the overall mortality. Based on between-year population changes and the number of pups reported, net dispersal fluxes among the four regions of the Wadden Sea were estimated for two time intervals. During the pre-epizootic period, only in Schleswig-Holstein, Germany, a surplus of animals was produced which counterbalanced the low recruitment in the other regions. During the post-epizootic period, the net dispersal fluxes were much lower. Nevertheless, in The Netherlands a continuous influx of seals was needed because the recruitment was insufficient to explain the observed numerical increase.

At the level of the 38 separate subareas, the pattern of dispersal revealed that the majority of the areas were not self-supporting with respect to local pup production and thus depended on an influx of animals. More than 65% of all immigrants originated from only seven subareas which are considered key breeding areas of vital importance for the Wadden Sea harbour seal population. The two most important areas were in the eastern part of Niedersachsen, a third area was in the central Danish Wadden Sea followed by three areas in the centre of Schleswig-Holstein. The Dollard embayment was the only key area in the Dutch Wadden Sea.

It is assumed that differences in habitat quality such as low disturbance pressure, are responsible for the observed differences in abundance and distribution among harbour seals in the Wadden Sea. The seasonal distribution and habitat requirements of harbour seals suggest that during the breeding season adult females concentrate at pupping sites in sheltered inshore waters (Thompson *et al.* 1989, 1994a; Kovacs *et al.* 1990) Thompson *et al.* 1994a). During the past decades a high intensity of human use of the Wadden Sea was observed, ranging from professional fisheries and military training to recreational activities. Data on the number and distribution of leisure boats counted during aerial surveys have shown that the identified key breeding areas coincide with areas where human presence and disturbance levels were comparatively low (Thiel *et al.* 1992; Klug & Klug 1994; Vogel 1994).

Characteristics of a core breeding area: the Eems-Dollard estuary

The Eems-Dollard estuary, situated at the border between Germany and The Netherlands, holds about 12% of the total Wadden Sea harbour seal population. We selected this area as an example of a high-quality breeding area and investigated the importance of this seal colony during the pre- and post-epizootic period.

The number of seals observed within the Eems-Dollard estuary increased parallel to the remainder of the Wadden Sea during the pre-epizootic period with an annual rate of 10%. During the post-epizootic period the rate of population increase in the estuary colony was substantially higher, and by 1996 the number of seals was 3.4 times the initial number at the start of study period in 1979, while this figure was only 2.7 in the remainder population. The detrimental effects of the 1988 epizootic, which reduced the total Wadden Sea population by 60%, were less drastic in the estuary, where the mortality was on average only 43%. In the inner part of the Dollard embayment, the survey results of 1989 showed even no decline at all of the number of seals using haul-out sites

The seals of the Eems-Dollard estuary use eight major haul-out sites during the breeding season where overall between 40 and 300 seals were hauled out. The proportion of pups found on the different sites varied between 2 and over 30%. Breeding banks were located in the inner Dollard embayment and at the western edge of the study area. These haul-out sites have in common that they are sheltered, have a long period of emergence and a comparatively low disturbance pressure. At the seaside of the barrier islands and along the river Eems, other large haul-out sites were observed but here the proportions of pups were low. These sites are either close to a very busy shipping lane or can be reached by pedestrians.

During the pre-epizootic period, the mean date of the annual maximum count was 19 July. After the epidemic, the pupping season in the Eems-Dollard estuary as well as in the entire Wadden Sea shifted abruptly and remained consistently two weeks earlier. Such sudden and dramatic shifts in the pupping season have to our knowledge not yet been reported for any pinniped species. One possible explanation could be a relation between the age structure and the timing of parturition in the population. There are strong indications that age structure has changed markedly due to selective mortality during the epidemic. The proportion of young age classes has increased as a result of higher juvenile survival and an increase in the reproductive rate (Reijnders *et al.* 1997). Additionally, as lower pollutant levels occur in the present seal population, the fitness of most individuals may have increased. We hypothesise that the timing of the pupping season during the post-epizootic period is normal, while the delay during the pre-epizootic period was unnatural.

Time budgets and haul-out patterns

Between 1989 and 1994, a total of 44 seals were captured and radio-tagged at seven different haul-out sites in three study areas in the Dutch Wadden Sea. The animals were tracked for periods up to seven months by permanent and mobile receiving stations. The time budgets and haul-out patterns of 15 seals including a total of 1375 tidal cycles respectively 1364 seal days were analysed. Except for August, when tags were shed during moult, data covered all months of the year.

The overall time budgets of the individual seals varied considerably and animals spent between 10 and 40% of the tracking time hauled out. The highest proportion of haul-out bouts lasted between 3 and 6 hours and did not exceed 10 hours. In intertidal habitats, the maximum duration of haul-out bouts is limited by the exposure time of the sites during the tidal cycle. In the western Wadden Sea, most haul-out sites are exposed for periods of 6 to 7 hours, while in Denmark and Schleswig-Holstein some high sands exist which are available as haul-out sites throughout most of the tides. In these areas the maximum duration of the haul-out bouts was not limited and lasted up to 50 hours (Nørgaard 1996; Schwarz 1997; Traut 1997).

The average proportion of the low-tide periods seals used to haul out varied between 20 and 90% in the different months. During the months May to September the average haul-out frequency was significantly higher (69%) than during the remainder of the year (41%). The seasonal changes in the haul-out pattern found in the present study are in line with the results from the other parts of the Wadden Sea (Nørgaard 1996; Schwarz 1997; Traut 1997) and this is similar in all other European harbour seal populations. In winter seals alternate between periods of several days foraging in the adjacent North Sea and periods of regular haul-outs. In summer, including the pupping and suckling season and the moulting period, seals have the highest motivation to haul out (Drescher 1979; Thompson & Rothery 1987; Thompson *et al.* 1989). A radio-tagged female with pup increased her haul-out rate significantly during the lactation period. Especially for mother-pup pairs the availability of undisturbed haul-out sites with long exposure times is crucial as the survival of the pup depends on sufficient intake of milk.

Diving patterns

The diving patterns of 25 free-ranging harbour seals of varying body length were monitored by means of VHF telemetry at different locations in the Dutch and German Wadden Sea. The recorded dive and surface times were highly variable, both within and across individuals. Median dive durations for individual seals ranged from 46 s to 2.9 min. The longest dive recorded was 31 min, performed by an adult male. Dive endurance increased significantly in relation to body length, and the frequency distribution of dive times was different among the sexes. Female harbour seals tended to perform fewer short dives and had a narrower distribution of dive times. We detected no diurnal differences in dive behaviour, and only the ambient air temperature was found to be correlated with the duration of surface periods. Surface intervals tended to be shorter when temperatures were below 9 °C. The overall mean percentage of diving time during complete dive cycles was 85%, with individuals varying from 76 to 93%. It was generally higher in females (Ries *et al.* 1997).

The dive durations in our study tended to be shorter than the average dive durations of 2.5 min for harbour seals observed around Orkney and in Norway (Fedak *et al.* 1988; Bjørge *et al.* 1995). This could be related to the substantial difference in water depth in these areas. While foraging in the Wadden Sea, harbour seals were observed to dive along the edge of tidal channels, usually no deeper than 5-10 m, whereas in the Norwegian study some of the animals were foraging and diving down to 200 m. In terms of foraging efficiency, shallow dives take up less travel time, permitting the animal to spend a higher proportion of time hunting. However, with the high prey density encountered in the Wadden Sea continuously searching for food and hence performing longer dives is not necessary (Dankers & De Veen 1978; Thompson *et al.* 1991). The comparatively high proportion of short dives and the occasionally recorded long surface intervals observed in older seals could be related to activities other than foraging. Dive durations in our study were found to be highly variable, especially in older seals, sometimes exceeding the aerobic dive limit. During such long dives, recorded also in other seal species, animals were occasionally observed to rest, apparently asleep, in shallow water (Fedak *et al.* 1988; Thompson *et al.* 1991; McConnell *et al.* 1992; Hyvärinen *et al.* 1995).

Conclusions

The development and application of telemetry techniques to study habitat use and activity patterns as well as revealing important aspects of the population dynamics of harbour seals in the Wadden Sea were the objectives underlying the present thesis. Main results and conclusions from this work are:

- Aerial census results provide minimum population estimates. Based on a mark-recapture experiment a correction factor for the Dutch population was determined. The maximum aerial survey result represented 68% of the population.
- The seal population recovered exceptionally well after the 1988 virus epizootic which was due to a higher reproductive rate and a lower juvenile mortality.
- Within the Wadden Sea only seven out of 38 subareas produced a surplus of animals which sustained the entire population. These key breeding areas correspond with regions of low disturbance.
- The Eems-Dollard estuary is such a key breeding area with a significantly higher reproductive rate than in the remainder of the Wadden Sea. Spatial distribution is obviously influenced by the availability of high-quality haul-out sites and low disturbance pressure.
- Seals spent on average between 10 and 40% of time hauled out. The highest proportion of haul-out bouts lasted between 3 and 6 hours. The haul-out rate

was significantly higher during summer.
- Diving patterns were highly variable among individual seals. Dive durations in general were shorter and the proportion of dive time higher than in harbour seals in other areas.

The combination of telemetry techniques with aerial surveys has proven to be a valuable research methodology for investigating various aspects of population dynamics, migration, habitat use and activity patterns of harbour seals. Nevertheless, knowledge of important subjects such as foraging ecology and the physiological effects of disturbance are still lacking. The recent developments in satellite telemetry provide the tools needed to investigate these aspects.

It is highly likely that conflicting interests between the various professional and recreational users of the Wadden Sea severely threaten the seal population in the near future. Instead of only reacting after problems have occurred it would be an effective strategy to anticipate the foreseeable conflicts.

Therefore, the general conclusions on the management of the Wadden Sea seal population are:
- Monitoring and research programmes should be continued as it is essential to keep track with the development of the population.
- Studies on foraging ecology are urgently needed as the interactions between seals and fisheries are considered to become a major issue.
- Highest attention should be paid to the core breeding areas such as the Eems-Dollard estuary. One obvious habitat prerequisite is the availability of sheltered haul-out sites with a long period of emergence and low disturbance pressure. They offer the favourable circumstances characterising core breeding areas. The core breeding areas should be designated as high priority protection zones.
- The physiological effects of disturbance on seals as well as the impacts on the population level should be studied to ensure appropriate management strategies.
- The positive demographic development of the Wadden Sea harbour seal population during the post-epizootic period should not lead to the 'all clear' signal. The occurrence of catastrophic events cannot be predicted. Managers and scientists must be well prepared to respond adequately and quickly.

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