Introduction

The harbour seal population in the entire Wadden Sea (Denmark, Schleswig-Holstein, Lower Saxony, and the Netherlands) has been monitored for more than half a century now (Reijnders 1976, 1992; Drescher 1979; Tougaard 1989; Traut 1997; Reijnders et al. 1997; Abt 2002). The primary objectives are to assess the status of the population and to evaluate the efficacy of the chosen management measures, and secondary to that to use the changes in status as a parameter for the environmental condition of the ecosystem. This unique data set will permit furthermore an in-depth analysis of the development of the population including the estimation of several population parameters and the changes thereof. Monitoring is done by carrying out annually several aerial surveys during different seasons. Since the end of the 1980s, the surveys in the Wadden Sea have been synchronized and standardized in the framework of the Seal Agreement concluded under the Bonn Convention. This agreement is implemented through the Seal Management Plan (SMP) and the Trilateral Monitoring and Assessment Program in the frame of the trilateral Wadden Sea Cooperation.

Standardization and synchronization is necessary because only seals hauled-out on land can be counted, and haul-out is influenced by a number of environmental and intrinsic factors such as tidal cycles, time of the day, season, weather, disturbances, food availability, timing of breeding and moult, and exposure time of sandbanks during low tide (Reijnders 1978; Drescher 1979; Thompson et al. 1989, 1997; Thompson & Miller 1990; CWSS 1995; Nørgaard 1996; Ries 1996; Traut 1997; Härkönen et al. 1999; Abt 2002).

It has been common practice that the authorities in each sub-area (Denmark, Schleswig-Holstein, Lower Saxony, and the Netherlands) publish the maximum count obtained in each region irrespective of the period it was obtained. The figure for the entire Wadden Sea was obtained by summing up the annual maximum counts from the respective four sub-areas, rather than synchronous counts of a particular season. From a scientific point of view, this procedure is questionable because the different factors influencing haul-out behavior are not necessarily occurring to the same extent and/or simultaneously in each region of the Wadden Sea. For that reason, the maximum counts in each region are not recorded at the same time in the year. For instance, in the last decade, the maximum count in Schleswig-Holstein and Lower Saxony was usually obtained in June,
whereas this was in the Netherlands and Denmark in August. The sum of each of the four maxima obtained this way differed usually from the maximum for the population obtained by adding counts acquired at similar time-points in the season. Because of the likelihood that migration between areas happens between June and August, and furthermore that different segments of the population are counted in both months (Thompson 1989; Thompson et al. 1997; Härkönen et al. 1999), using the maximum number or the relative maximum in either June or August, may give different abundance indices and could lead to false conclusions about the real population trend. The Trilateral Seal Expert Group (TSEG), which is according to the SMP supervising the implementation of monitoring activities and the assessment of results, has evaluated this matter.

It is the intention of this paper to discuss possible differences in estimating abundance trends for the entire Wadden Sea seal population when using different methods to incorporate regional counts.

Seasonal timing of surveys

Particularly the research by Thompson & Rothery (1987), Thompson et al. (1989), Thompson & Miller (1990), Nørgaard (1996), and Härkönen et al. (1999) has elucidated seasonal changes in haul-out behavior of various age-classes of both sexes of harbour seals. There are marked changes between June-September, connected to the breeding and moult of the seals. In general terms: the females as a whole, but particularly the ones four years and older (mature animals), were more numerous in June and early July. Males, and particularly the adults, were more numerous around mid till end of August. Because of the differences in haul-out behavior performed by the different population segments, and the fact that considerable migration can occur over short periods of time (e.g. Thompson 1989; Nørgaard 1996), it is trilaterally agreed and included in the SMP to carry out time-wise synchronized surveys in the Wadden Sea during the whelping period as well as the mouling period.

In addition to this general behavioral pattern, it has also been observed that the phenology of pupping and moult has been shifted towards earlier in the season, by about 2-3 weeks (Ries & Reijnders 1996; Abt 2002). This observation underlines the importance of having repeated surveys in both periods to detect these changes and reschedule the surveys accordingly.

Which of the counts is the closest reflection of the true development?

It is evident that from a point of view of population ecology, the synchronized counts are the correct figures to be used for estimating abundance indices and population trends. However, because there is also a third series of non-synchronized counts - the summed maximum counts - in existence, three series of counts are compared here. The respective counts for each period: maximum (minus pups) in the whelping period, maximum during moult, and the summed maximum count of either period between 1989 and 2001 are given in Figure 1. The whelping minus pups counts are used here instead of the total peak whelping counts, because sometimes the trend of the 1+ population segment differs from the pup trend (Abt 2002). Such information will be lost unless both age groups are treated separately.

The important question now is, retrospectively, whether choosing the whelping, mouling (max or average) or “maximum” data, would have lead to differences in abundance estimates and hence population trends.

This has been investigated through a regression analysis of the exponential relation between years and counts, and statistical testing the parameters provided by the different indices. All graphs in Figure 1 show a
clear increase in numbers counted over the years. The moult counts show more fluctuations, compared to the other two series. This could be a true phenomenon, however, could also be due to the fact that fewer surveys have been carried out during the moult than in the whelping period and/or due to uncertainties about the ideal timing of the moult counts caused by a gradual shift of the cycle. The results of the regression analyses are shown in Table 1. It can be concluded that the correlation coefficients differ only marginally. The relative annual increase for the entire period for all series varies between 0.119 and 0.122, the corresponding rates of annual population increase range from 12.6 till 13.0 %. There is no statistical difference between the three ($a < 0.32$).

The seasonal change in haul-out behavior brings about that at no point in the annual cycle all animals in a population are ashore. Therefore surveys do not provide an absolute abundance estimate, but rather an abundance index. The fact that different fractions of the population are counted in different seasons will not pose any problems for population analysis as long as counts from different seasons are not mixed. Problems can arise, however, when the normal demographic structure of the population is disturbed. This happened in certain areas during the epidemic mass die-off of harbour seals in 1988. Severe changes in the demographic structure of the seal population will influence the per capita birth rate, per capita death rate, and also the fraction of seals on land in particular seasons (Härkönen et al. 1999). For limited periods, all this can produce count data which are misleading about population development and growth potential (Härkönen et al. 1999; Abt 2002; Reijnders & Brasseur 2003).

When comparing the relative annual increase of the seal population in the Wadden Sea over the years 1989–2001, it appears that it was high early in the period but leveled off from 1994 onwards. This may reflect a demographic effect with subsequent stabilization of the age-structure, as was suggested by Abt (2002) and Reijnders & Brasseur (2003). By calculating the asymptotic rate of increase over a longer time series of counts, the current estimate of around 0.12 is considered realistic.

**Conclusion**

The overall conclusion is that a steadily increasing seal population has been observed between 1989–2001. There is no difference in assessing the population trend over the entire period whether the whelp counts, moult counts or summed maximum counts are used. However, given the fact that between the whelping and moultng period migration occurs, that different segments of the population are counted in the whelping period vs. the moultng period, it is strongly recommended to use the synchronized whelping counts and moult counts and not the non-synchronized maximum counts. Indeed, adding (non‐synchronized) regional maximum counts to arrive at a total number for the entire Wadden Sea is basically summing up “pears and apples”.

The choice between either the whelping or moult (maximum or averaged) count is complicated. Some authors argue for moult counts because of the higher and more consistent counts which could be made later in the summer (Tougaard 1989; Thompson 1989; Thompson et al. 1989; Heide-Jørgensen 1990). In another study though, Thompson et al. (1997) concluded that counts during the pupping season would provide the best estimates of abundance in their specific study area. Their conclusion holds for that specific situation and was largely based on the fact that no telemetry data for the moult were available. It is therefore in our view not generally applicable.

For the Wadden Sea, the difference in the quality of data from either period is not clear, as was discussed earlier in this paper. Both periods provide valuable data on specific segments of the population: whelping counts provide figures on pup production and are biased towards females, and moult counts are more biased towards males. We therefore recommend to continue conducting annual counts in both the whelping and the moultng period as was already agreed in the SMP.

The answer to which data should be used as the annual survey result for the entire Wadden Sea seal population is less straightforward. The hitherto used practice since the start of aerial sur-

---

**Table 1:**

Parameters of exponential regression curves on times series ($x$) of harbour seal counts ($y$) in the Wadden Sea (the regression equation is: $y = a.e^{bx}$). Three different series were explored:

- **MOULT** = counts from the moulting period,
- **WHHELPING-PUPS** = counts from the whelping period (minus pups), and
- **MAXIMUM** = summed regional maxima of either period.

$R^2$ = multiple correlation coefficient, $b= $ relative annual increase, $SE.b =$ standard error of $b$.

<table>
<thead>
<tr>
<th>MOULT</th>
<th>MAXIMUM</th>
<th>WHHELPING-PUPS</th>
</tr>
</thead>
<tbody>
<tr>
<td>$R^2$</td>
<td>0.9821</td>
<td>0.9903</td>
</tr>
<tr>
<td>$b$</td>
<td>0.1221</td>
<td>0.1218</td>
</tr>
<tr>
<td>$SE.b$</td>
<td>0.0050</td>
<td>0.0036</td>
</tr>
</tbody>
</table>
vey in Europe, including in the Wadden Sea area, has been to use the moult counts (Reijnders & Brasseur 2003). Counts in the whelping season are more sensitive to short-term changes in reproductive success, whereas this is less likely during the moult. From the data produced by Härkönen et al. (1999), it can be concluded that in non-stable age-structured populations the influence of the differential haul-out behavior on estimating abundance is likely to have more effect during the whelping period compared to the moult. Based on the differences in phenology of the harbour seal population within the Wadden Sea, Abt (2002) concludes that the peak moult data are the most comparable among different areas.

Based on the above, we conclude that by using the moult count data, a suitable and consistent index of population abundance is obtained and recommend this to be applied from the season 2003 onwards. Future survey data and subsequent population modeling, including power analyses, will reveal whether this procedure needs to be revised.

References


Peter Reijnders & Sophie Brasseur
Alterra, Marine & Coastal Zone Research
P.O. Box 167
NL - 1790 AD Den Burg
Peter.Reijnders@wur.nl

Kai Abt & Ursula Siebert
FTZ-Büsum, Germany

Svend Tougaard
Fiskeri- og Søfartsmuseum, Esbjerg, Denmark

Ekkehard Vareschi
Universität Oldenburg, Germany

Peter Reijnders & Sophie Brasseur
Alterra, Marine & Coastal Zone Research
P.O. Box 167
NL - 1790 AD Den Burg
Peter.Reijnders@wur.nl

Kai Abt & Ursula Siebert
FTZ-Büsum, Germany

Svend Tougaard
Fiskeri- og Søfartsmuseum, Esbjerg, Denmark

Ekkehard Vareschi
Universität Oldenburg, Germany