Sex and age related summer migration and site fidelity in the Skagerrak harbour seal population

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Abstract. Information about animals distribution and migration is vital since these parameters strongly affect such issues as population structure and gene differentiation for sub-populations. In this study, data collected by Härkönen and co-workers were used to investigate the migration behaviour and site fidelity of harbour seals (Phoca vitulina) at the Swedish west coast. Male biased migration were observed and male subadults were found to be most mobile. Contradictory to most previous studies, juveniles showed the most stationary behaviour. Seals that hauled out at more isolated localities showed a greater site fidelity than animals in an area where alternative localities are closer together. A new method that was used to estimate the migration behavior of the harbour seal proved to be useful.

Introduction

Animal distribution and migration patterns are crucial as these factors influence the structure of populations. Sex and age related differences in site preferences and migration behaviour are likely to result in deviations in the structure of sub-populations even within a relatively small area. The same discrepancy could occur if animals at separate locations exhibit varying degree of site fidelity. Furthermore, migration is vital for the gene flow between sub-populations, thereby decreasing genetic differentiation of the populations and also the risk of inbreeding. However, dissimilarity in the migration behaviour of males and females will lead to bias in the gene flow.

For endangered populations, our knowledge about the animal behaviour is important in a more straightforward way. In order to make any protection effective it is necessary that we understand the different stages in an animal’s life and know were important events take place.

Studies on marine animals are often difficult to execute because surveys and methods of data gathering have to be adapted to the conditions that prevail at sea. In this paper, data collected by Härkönen and co-workers have been used to investigate the behaviour of the harbour seal population on the Swedish west coast.

The harbour seal is distributed widely over the world, occurring in a large variety of habitats (Härkönen & Heide-Jørgensen 1990, Bjørge et al. 1995, Thompson et al. 1997).


At the beginning of the breeding season the females come ashore to give birth and to lactate (Thompson et al 1994). After 23-31 days of lactation (Boulva & McLaren 1979, Godsell 1988, Härkönen & Heide-Jørgensen 1990, Bjørge et al. 1995) the pup is weaned. During this period opportunities for foraging are very limited and Härkönen & Heide-Jørgensen (1990) observed that an average female loose 37% of their body weight in these few weeks. Because of hunger, the females are forced to give up their fast and start to forage again near the end of lactation (Boness et al. 1994, Thompson et al. 1994). Although foraging has been resumed the female returns to the haul out site to feed her pup every day (Thompson 1989, Boness et al 1994). The length of the fast correlates positively with the size of the female (Thompson et al. 1994). A small female does not have as much energy stored as fat, and will have to start making feeding trips earlier than a large female. This will probably result in a lower rate of survival for pups born by small females.
When the females ovulate, shortly after the pups are weaned, the male harbour seals decrease their range size (Thompson et al. 1989, Van Parijs et al. 1997) and start showing a display behaviour in the vicinity of females (Sullivan 1979, Bjørge et al. 1995). By staying close to oestrous females the males increase their chances of mating (Thompson et al. 1989, Coltman et al. 1997, Van Parijs et al. 1997). However, the mating behaviour involves a reduction in the time males spend foraging (Thompson et al. 1989) and is therefore energetically very costly (Thompson 1989, Walker & Bowen 1993). Consequently, Coltman et al. found that large males appeared to change their behaviour earlier than small males, presumably resulting in a greater amount of copulations acquired.

As has also been found for the ringed seal (*Phoca hispida*) in the Baltic Sea (Härkönen & Lunneryd 1992), the largest number of seals hauled-out are observed during the annual moult (Thompson et al. 1989, Helander & Bignert 1992, Härkönen et al. 1999), occurring after the mating season. The seals probably haul out in order to increase the temperature in the skin, facilitating the shedding of the old fur (Ling & Bryden 1981). At this time the females are in a poor condition after the period of lactation (Härkönen & Heide-Jørgensen 1990) and have to forage intensively in order to recover from the fast (Thompson et al. 1994). Accordingly, during the moult the females do not haul out as frequently as the males (Godsell 1988, Thompson 1989).

Furthermore, number of animals hauled out vary with time of day (Yochem et al. 1987, Thompson et al. 1989, Roen & Bjørge 1995). Harbour seals commonly haul out according to a diurnal pattern with peak numbers occurring when low tide takes place in the early afternoon (Roen & Bjørge 1995, Watts 1996). Watts (1996) argues that if the following four conditions are met, a diurnal hauling-out cycle with a midday peak should arise:

1) Seals have time to haul out if they wish;
2) Immersion carries some cost which motivates seals to leave the water when not foraging;
3) Foraging payoffs are greater during darkness than daylight;
4) The costs of commuting are lower than those of remaining at sea between foraging boots.

In accordance with Watts (1996) third condition harbour seals have been found to mainly forage at night, probably owing to a greater availability of prey (Thompson 1989, Thompson et al. 1989, Bjørge et al. 1995). On the other hand, during longer feeding trips the seals have been observed to rest in the water (Thompson & Miller 1990), which contradict the fourth condition Watts (1996) stated. Bjørge et al. (1995) reported that seals on the coast of Norway used a variety of habitats, foraging on or near the bottom, at depths ranging from 50 to 200 m. Individual seals showed a strong tendency to return to the same, individually preferred, foraging grounds on several occasions. This behaviour could result in a low intra-specific competition (Bjørge et al. 1995).

The influence of tidal height on the diurnal hauling-out pattern is often less important than the photoperiodic cycle, but is more pronounced at localities where it influence the availability of haul-out sites (Thompson et al. 1989, Thompson & Miller 1990).

Composition of haul-out groups have been investigated in a few studies, but the results are very inconclusive. Some authors have reported that haul-out groups consist of animals of both sex and all ages (Biggs 1981, Sullivan 1982, Godsell 1988). On the other hand, in Orkney, Scotland, Thompson (1989) found a significant difference in the sex-ratio of groups at two sites: at one site males predominated and on another, nearby, mothers and pups were regularly seen.
Although the seals often have several possible haul-out sites, a number of authors have reported that individual seals show a strong site fidelity, often using only one or two different sites (Pitcher & McAllister 1981). There are, however, indications that harbour seals undertake short seasonal movements between different haul-out areas (Yochem et al. 1987, Thompson 1989, Thompson et al. 1996). Yochem et al. (1987) and Godsell (1988) identified more extensive movements which Yochem interpreted as inter-seasonal migrations. These longer trips might also have been dispersal movements by young seals, as reported by Bonner & Witthames (1974) and Thompson (1989).

Most previous studies assessing site fidelity and migration base their conclusions on observations made in one or a few years (e.g. Yochem et al. 1987, Godsell 1988, Thompson & Miller 1990). However, Härkönen & Hårding (in press) used the same set of long term data that was used for the present study, to examine the migration behaviour of harbour seals. In short, they found that young females migrate extensively, but as they become sexually mature the females show a much greater fidelity towards the site where they were born. Males, on the other hand, were found to migrate increasingly as they grew older. These results will be discussed, in relation to the results from the present study, later in this report.

The objectives of this study were to examine how the migration behaviour and site fidelity of harbour seals differ between females and males, and how the age of the seal influences the animals behaviour. For future research, such differences makes it possible to evaluate which areas are more important to the harbour seal population and how these areas should be protected. The results are also vital when the dispersal of female and male genes are to be examined. Beside more conventional methods, a new way of treating data was used in the present study and this method will be evaluated in the discussion.

**Parameters for the Skagerrak-Kattegatt harbour seal population**

(according to Härkönen & Heide-Jørgensen 1990)

Pupping usually starts in early June while mean pupping date in the period of 1979-1989 was June 20. Suckling pups can be seen immediately after birth and lactation then lasts for a period of less than four weeks. The average female ovulates July 17 and mating occurs in July-August. The pregnancy rate for mature animals (5-25) was close to 1 but decreased in the older age classes. Females reach sexual maturity at the mean age of 3.7 years and first parturition takes place when the average female is 4.6 years old. Males become sexually mature at the age of 4-6 years.

**Materials and methods**

**Study area**

The study was conducted in the archipelago of northern Bohuslän, on the Swedish west coast. Since the start of the data collection seven localities, Lysekil, Marstrand, Väderöarna, Segelskären, Ramsökalven, Ursholmen and Drammen, were surveyed (Fig. 1). For this study only data from 1990-1998 were used, and during these years only Väderöarna, Segelskären, Ramsökalven, Ursholmen and Drammen were surveyed.

The separate localities are characterised by rocky islands and skerries surrounded by shallow waters, but in order for a seal to swim from one locality to another it has to cross deep water. All the localities are at times rather exposed to wind and waves. Although a substantial part of
the study area is protected, seals are subjected to disturbance during the breeding season and at time of moult. This disturbance is caused by high intensity of recreational boat traffic.

Catching, branding and observations
(Carried out by Härkönen and coworkers. In detail in Härkönen et al.in 1999)

All handling of seals was carried out according to permits granted by the Ethical Board of the County Court of Göteborg, Sweden.

A majority of the 163 seals captured were caught at night during October and November. At this time pups-of-the-year are 4-5 months old and is the only age group that can be distinguished with certainty from older seals. The capturing procedure was therefore designed primarily for pups-of-the-year. Seals were caught with modified nets that were rigged in such a manner that an entangled seal would not drown. Caught seals were removed from the nets as soon as possible, strapped to a stretcher, and transported with boat, no more than 1 km, to the island of Ursholmen, where they were freeze branded. Unlike other marking techniques, e.g. dye branding and radiotagging, freeze branding is permanent and allows long term study of individual seals to be made. This technique renders in a marking much like the hot iron technique does on cattle, but without the risk of causing dangerous inflammation. The seals were given individual number codes on both shoulders. Initially the resulting brand marks measured 7,5 by 4,5 cm, but as the animals grew bigger the numbers increased in size as well. No sedation was necessary since firmly strapped animals calmed down, facilitating the handling and branding procedure.

Pups-of-the-year constituted 82% of the total catch, one-year olds 14%, and seals aged 2-4 years 4%. Females constituted 56% of the captured pups and 66% of the older animals. For seals older than pups, growth curves of males and females (Härkönen & Heide-Jorgensen 1990) were used for age estimation.

Observations of branded seals were made either from the island where the seals hauled out or from an adjacent island. The islands were always approached in such a way that the seals were disturbed as little as possible. Monocular telescopes (x 20-60) were used to identify branded animals. The distance between the observation point and the haul-out site of the seals usually ranged between 30 and 500 m. Occasionally branded seals were observed at distances greater than 500 m. In order to get momentary information about how the branded seals were distributed, each locality was covered within one day. When a marked seal was observed, date and locality were noted in a field book. At the end of the day the same person entered the information in a standard form. When the field season was over, all the information was gathered in a data base. This work was not necessarily done by the same person that carried out the field work.

Data treatment

In the period 1990-1998 the five localities (i.e. Väderöarna, Segelskären, Ramsökalven, Ursholmen and Drammen) were surveyed every summer (June 13-September 10) and therefore data from these years were appropriate for the analysis.

Data from six age groups of both sex were analysed (in total 12 groups). The seals were divided into 1, 2, 3, 4, 5 year old animals and animals that were six years or older (denoted as 5+). All seals marked as pups-of-the-year in the autumn were considered one year old the following summer, and consequently two years old the summer after that. The analysis of variance (two-way ANOVA) was performed with balanced age/sex groups and independent
observations (Fowler & Cohen 1997). For each individual seal, data from one or many years were available. For a data set to be independent, any individual must only contribute with one value. Individuals that had been observed at only one age could only be placed in this age group. However, seals observed in many years could represent anyone of several age groups. These animals were distributed among the groups in such a way that equal number of animals and equal number of males and females in each age group were acquired. Since a slightly smaller number of males have been branded, not all females were used in the analysis and the ones not used were excluded at random. Each age/sex group consists of 9 individuals and in total the movements of 54 females and 54 males were analysed.

For many individuals the maximum observed age was limited by the time span of the study. However, one of other possible explanations to why the animal was not observed at an older age was death. If this was caused by a decease there was a risk that the seals behaviour migh be unrepresentative for the age group corresponding to the seals maximum observed age. This problem was reduced by not setting all animals with the same maximum observed age to represent the same age group. For these individuals, values for different ages were used in the analysis.

For the 5+ group, data for more than one age (e.g. age 6, 7, 10 and 11) of the animal were available and possible to use. In this situation, one age was chosen randomly for each individual seal.

There were great differences in the number of days each locality were surveyed, both within and between years. To obtain values that were independent of the work effort, locality specific resighting frequencies ($P_{lt}$) of every seal were calculated according to eqn. 1 (which is a modification of the $P_{lt}$ calculated in Härkönen & Harding in press)

$$P_{lt} = \frac{R_{lt}}{N_{lt}}$$

where $R_{lt}$ is the number of days during summer (t) seal (i) was observed at locality (l), and $N_{lt}$ is the number of days locality (l) was surveyed summer (t). If a seal was not observed at a locality one summer the corresponding $P_{lt}$-value was zero, and if a seal was not sighted at all in the summer all the $P_{lt}$-values of that year equaled zero. In the analysis, only years with at least one $P_{lt}$-value greater than zero were used.

The proportion of time ($T_{lt}$) seal (i) spent at locality (l) in summer (t) was calculated as in eqn. 2:

$$T_{lt} = \frac{P_{lt}}{\sum_{i=1}^{5} P_{lt}}$$

$\sum_{i=1}^{5} P_{lt}$ is the sum of the $P_{lt}$ for the five localities. Seal (i) will produce five $T_{lt}$-values, which adds up to 1.

The $T_{lt}$-values were analysed, each locality separately, in a two-way ANOVA, making it possible to detect any age and/or sex specific differences in the use of each locality.
To see if groups of seals differed in their proportion of time spent at more distant localities \( (M_{it}) \) two calculations were made. This was done according to eqn. 3 and 4:

\[
M_{itR} = 1 - (T_{itUrsholmen} + T_{itRamsokalven}) \quad \text{eqn. 3}
\]

\[
M_{itS} = 1 - (T_{itUrsholmen} + T_{itRamsokalven} + T_{itSegelskären}) \quad \text{eqn. 4}
\]

The \( M_{it} \) -values in the equations are the proportion of time seal \((i)\), in the summer \((t)\), spent outside the localities for which \( T_{it} \)-values are given in the equation. No values on time spent outside Ursholmen were calculated as an analysis of these values would only show the opposite of the analysis of the \( T_{itUrsholmen} \)-values. For similar reasons, the \( T_{it} \)-values for Drammen were not excluded, since that equation would tell us how much of its time seal \( (i) \) spent on Väderöarna in the summer \((t)\), which is already known from eqn. 2. For each equation, \( M_{it} \)-values for all seals were tested in a two-way ANOVA.

The migration behaviour of seals of different age and sex were also tested by using another, rather unconventional, method (a modification of gradient analysis described in Krebs (1985)). A Migration Index (MI) was calculated for each seal:

\[
MI_{it} = \sum_{l=1}^{5} (T_{it} \times r_l) \quad \text{eqn. 5}
\]

where \( MI_i \) is the Migration Index for seal \((i)\) in the summer \((t)\) and \( r_l \) is a rank of the \( l \)-th locality. Since all seals were marked at Ursholmen it is possible to rank the localities according to the distance from Ursholmen. Väderöarna, which is the most distant locality was ranked as 4, Drammen as 3, Segelskären as 2, and Ramsökalven as 1. Ursholmen itself was ranked as 0, giving a seal that has a \( T_{itUrsholmen} = 1 \) (i.e. it has only been observed at Ursholmen at that age) a \( MI_i = 0 \). Thus, in the MI-value both the distance the animal has migrated and the proportion of time spent on the locality were considered. The MI-values of all seals were analysed in a two-way ANOVA.

In the study, the site fidelity of harbour seals in the Skagerrak was estimated. The locality specific average haul out frequencies of the age/sex groups were converted to actual numbers of individuals hauling out at a locality. This often resulted in an underestimation. The deviation between the true and the calculated number of seals was divided by the true number of seals at the locality. The acquired value describes the strength of the seals site fidelity. The calculations were carried out according to eqn. 6.

\[
F_{lg} = (N_{lg} - T_{lg} \times 9) / N_{lg} \quad \text{eqn. 6}
\]

In eqn. 6, \( F_{lg} \) is the site fidelity for seals of age/sex group \((g)\) at locality \((l)\), \( N_{lg} \) is the true number of individuals of age/sex group \((g)\), \( T_{lg} \) is the average haul out frequency at locality \((l)\) of age/sex group \((g)\) and 9 is the number of animals in each age/sex group. The \( F_{lg} \)-value is an average value for seals of age/sex group \((g)\) and it correlates negatively to the strength of the site fidelity (i.e. a small \( F_{lg} \) indicates a strong site fidelity).
Fig. 1. Map, showing the study area. The two southernmost localities, Lysekil and Marstrand, were not included in the study. The catching and branding procedures were carried out at Ursholmen.
Results

Fig. 2 and Fig. 3 show the average proportion of time ($T_{il}$) each age/sex group spent at a locality. The results from the statistical analysis (two-way ANOVA) reveals that females use Ursholmen and Ramsökalven significantly more than males. At Segelskären and Drammen males spend significantly more time. No difference in the use of Väderöarna was found. Age group 5 was observed to spend significantly less time at Ursholmen than age group 1 (Student-Newman-Keuls). At Ramsökalven age group 1 spent a significantly smaller proportion of time than age group 5+ did (Student-Newman-Keuls). These results, along with some trends (Fig. 2 and Fig. 3) will be interpreted in Discussion.

![Ursholmen](image1)

![Ramsökalven](image2)

Fig 2. Average proportion of time seals, of different age and sex, spent at Ursholmen and Ramsökalven.
Fig. 3. Average proportions of time seals, of different age and sex, spent at Segelskären, Drammen and Väderöarna.
Fig. 4. Average proportions of time seals, of different age and sex, spent outside Ursholmen and Ramsökalven.

Fig. 5. Average proportions of time seals, of different age and sex, spent outside Ursholmen, Ramsökalven and Segelskären.

The results from the tests made on the Migration Indexes (MI) from equations 3 and 4 show that there was a significant sex difference in how much the seals migrated. The test revealed that males spent more time at localities outside Ursholmen and Ramsökalven (M_{UR}), and also outside Ursholmen, Ramsökalven and Segelskären (M_{URS}).

When testing the Migration Indexes (MI) for all 108 seals it was found that males had significantly higher values than did females. No age group differed from any else in time spent at more distant localities. Average MI-values for each age/sex group are shown in figure 6.
The $F_{lg}$-values calculated in eqn. 6 describe the site fidelity that seals of each age/sex group show toward separate locations. A smaller $F_{lg}$-value indicates a stronger site fidelity. In Table 1 the $F_{lg}$-values for females of all age groups are presented. The corresponding values for male seals are shown in Table 2. The average $F_{lg}$-values for each locality (Table 3) reveal how the site fidelity differ between animals hauling out at different localities.

The $F_{lg}$-values calculated in eqn. 6 describe the site fidelity that seals of each age/sex group show toward separate locations. A smaller $F_{lg}$-value indicates a stronger site fidelity. In Table 1 the $F_{lg}$-values for females of all age groups are presented. The corresponding values for male seals are shown in Table 2. The average $F_{lg}$-values for each locality (Table 3) reveal how the site fidelity differ between animals hauling out at different localities.

Table 1. True number of females of each age group observed at each locality, and the site fidelity these animals exhibit ($F_{lg}$-value). A smaller $F_{lg}$-value indicates a stronger site fidelity. The column to the far right (Location $F_{lf}$-value) indicates the site fidelity of females in general at each locality. Values in the bottom row show the site fidelity each age female group exhibit in general.

<table>
<thead>
<tr>
<th>Females</th>
<th>Age</th>
<th>Location</th>
<th>$F_{lg}$-value</th>
<th>$F_{lf}$-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ursholmen</td>
<td>True number</td>
<td>7</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>Ramsökalven</td>
<td>True number</td>
<td>3</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>Segelskären</td>
<td>True number</td>
<td>3</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>Drammen</td>
<td>True number</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Väderöarna</td>
<td>True number</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
</tbody>
</table>

Group $F_{lg}$-value | 0.3 | 0.3 | 0.2 | 0.2 | 0.1 | 0.2 |
Table 2. True number of males of each age group observed at each locality, and the site fidelity these animals exhibit ($F_{lg}$-value). A smaller $F_{lg}$-value indicates a stronger site fidelity. The column to the far right (Location $F_{lm}$-value) indicates the site fidelity of males in general at each locality. Values in the bottom row show the site fidelity each male age group exhibit in general.

<table>
<thead>
<tr>
<th>Males</th>
<th>Location</th>
<th>Age</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>5+</th>
<th>$F_{lm}$-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ursholmen</td>
<td>True number</td>
<td>6</td>
<td>5</td>
<td>5</td>
<td>6</td>
<td>1</td>
<td>2</td>
<td></td>
<td>0.3</td>
</tr>
<tr>
<td></td>
<td>$F_{lg}$-value</td>
<td>0.3</td>
<td>0.6</td>
<td>0.7</td>
<td>0.6</td>
<td>0.5</td>
<td>0.8</td>
<td>0.6</td>
<td></td>
</tr>
<tr>
<td>Ramsökalven</td>
<td>True number</td>
<td>2</td>
<td>4</td>
<td>1</td>
<td>3</td>
<td>3</td>
<td>5</td>
<td></td>
<td>0.3</td>
</tr>
<tr>
<td></td>
<td>$F_{lg}$-value</td>
<td>0.3</td>
<td>0.8</td>
<td>0.8</td>
<td>0.6</td>
<td>0.4</td>
<td>0.1</td>
<td>0.5</td>
<td></td>
</tr>
<tr>
<td>Segelskären</td>
<td>True number</td>
<td>2</td>
<td>4</td>
<td>3</td>
<td>5</td>
<td>5</td>
<td>2</td>
<td></td>
<td>0.4</td>
</tr>
<tr>
<td></td>
<td>$F_{lg}$-value</td>
<td>0.4</td>
<td>0.7</td>
<td>0.3</td>
<td>0.3</td>
<td>0.1</td>
<td>0.1</td>
<td>0.3</td>
<td></td>
</tr>
<tr>
<td>Drammen</td>
<td>True number</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td></td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>$F_{lg}$-value</td>
<td>0</td>
<td>0.4</td>
<td>0.4</td>
<td>0.4</td>
<td>0.4</td>
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<td></td>
</tr>
<tr>
<td>Väderöarna</td>
<td>True number</td>
<td>0</td>
<td>3</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
<td>#</td>
</tr>
<tr>
<td></td>
<td>$F_{lg}$-value</td>
<td>#</td>
<td>0.2</td>
<td>0.2</td>
<td>#</td>
<td>#</td>
<td>#</td>
<td>#</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Group $F_{lg}$-value</td>
<td>0.2</td>
<td>0.5</td>
<td>0.4</td>
<td>0.4</td>
<td>0.4</td>
<td>0.2</td>
<td>0.2</td>
<td></td>
</tr>
</tbody>
</table>

Table 3. Average $F_{lg}$-values, indicating the site fidelity of seals in general at each locality. A smaller $F_{lg}$-value indicates a stronger site fidelity.

<table>
<thead>
<tr>
<th>Location</th>
<th>Ursholmen</th>
<th>Ramsökalven</th>
<th>Segelskären</th>
<th>Drammen</th>
<th>Väderöarna</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average $F_{l}$-value</td>
<td>0.4</td>
<td>0.4</td>
<td>0.2</td>
<td>0.1</td>
<td>0.1</td>
</tr>
</tbody>
</table>

Discussion

At Ursholmen and Ramsökalven there were significant female biased haul out frequencies ($T_{bf}$), and the $F_{l}$-values ($F_{lf}$ and $F_{lm}$) indicates that females show a greater fidelity to the area where they were branded than males do.

For both females and males there are rather clear age patterns in the haul out behaviour. Most one year old females stay at Ursholmen. On an average, this group spend 60% of their time at the locality where they spent some time the previous autumn. The percentage decreases successively the first few years, but at the age of four or five the females return to Ursholmen and use this location for haul out more frequently again. Individuals in the oldest age class spend about 40% of their time at Ursholmen. This trend was also observed by Härkönen and Hårding (in press).
The decrease in time spent at Ursholmen occurring during the early stages of the female life does not seem to result in any extensive migration but merely in increased haul out at Ramsökalven. This is supported by the observed negative correlation of Ramsökalven and Ursholmen (Fig. 1). One year old females only spend about 10% of their time at Ramsökalven. As the seals grow older, they haul out more and more at this locality, reaching a peak value of 65% at the age of five. The 5+ age group spends, on an average, 47% of their time at Ramsökalven, which is only slightly more than at Ursholmen. Young females exhibit a weak fidelity toward Ramsökalven, but as they reach maturity the fidelity turns stronger. The negative correlation for the female use of Ursholmen and of Ramsökalven indicates that there is an age dependent movement between these two localities.

At the three remaining localities it is difficult, and would probably be erroneous, to interpret any trends in the female haul out behaviour.

At Segelskären and Drammen males were observed to haul out significantly more frequently than females. At Drammen this result was highly significant and as Fig. 2 shows only two year old females were observed to haul out at Drammen at any degree.

Males are rather stationary at the age of one, spending most of their time at Ursholmen (Fig. 1) and little time at three other locations (Fig. 1 and Fig 2). Of the nine one year old males in the study, four hauled out exclusively at Ursholmen. None were observed at Väderöarna. As the males grow older, the choice of haul out site tends to shift from Ursholmen to Segelskären. Two and three year old males also migrate to Väderöarna. The oldest males (age 5+) haul out at Ramsökalven approximately as frequently (50%) as females of the same age, and also show a strong fidelity toward this locality. Five year old males exhibit approximately the same haul-out frequency and amount of fidelity at Segelskären. Males of all ages were found to haul out at Drammen roughly the same amount of time and, except for age group 2, the seals here used this locality exclusively.

In the study, not only the use of each locality was of interest but also to what extent age/sex classes differed in their amount of dispersal. As shown by the test results, males predominate at Segelskären and Drammen, but the study also suggests that males spend significantly more time in the area outside Ursholmen and Ramsökalven as a whole, indicating a greater rate of dispersion for males than females. This conclusion is supported by the fact that males have a significantly higher Migration Index (MI) than females, revealing that males spend more time at more distant localities. Observations of male biased dispersal rates are also common among other species of mammals (Sussman 1992, Phillipsonroy et al. 1992, Lukyanov 1993, Kunkele & von Holst 1996, McNutt 1996), including the southern elephant seal (Mirounga leonina)(Wilkinson & Bester 1990).

Although the time spent on Väderöarna were not found to differ significantly it should be noted that two and three year old males tended to migrate all the way to this location more than any other group. Three of the two year old and four of the three year old males visited Väderöarna during the summer. Males of age group 3 were also observed to have the highest average MI. Subadult males can therefore be considered to be the most mobile individuals. Also, as indicated by the high $F_g$-value, at this age males haul out at several localities. Bideau et al. (1993) found a similar age related migration pattern for European roe deer (Capreolus capreolus).

Godsell (1988) observed adult females to be very stationary during the breeding period. Accordingly, the average MI-values in the present study indicate that females older than five years, as well as one year old females, disperse the least. One year old males migrate slightly more than these two female groups, while males in age class 2, 4, 5 and 5+ have MI-values
approximately 0.8-1.1 lower than three year old males. The large error bars in the diagram reveal that there are great variation within some of the groups.

According to a study performed in the Wash, England, pups migrate extensively (Bonner & Witthames 1974). As recoveries were mainly made from dead animals, that might have drifted considerable distances, the degree of migration may have been overestimated. However, Härkönen & Härding (in press) found that one year old females and adult males were the most mobile classes, which is quite contrary to observations made in the present study. The difference in results is probably due to differences in calculations made and in the formulation of the null hypothesis. Härkönen et al. expected the migration of age/sex groups to be correlated to the stable age structure. In this paper a quantitative comparison of age and sex related migration was made and therefore all age/sex groups were expected to migrate to the same extent. In accordance with the present study, Walker and Bowen (1993) observed subadult males to be more mobile than adult males during the entire breeding season.

The result from the MI-method agrees well with the migration behaviour indicated by previous results in this paper. Therefore, the method can be a useful tool in estimating dispersion and migration rates in populations. One problem could be that a simple ranking of the localities might not be suitable for the purpose of the study. The ranking used in this study can then be exchanged for a set of numbers that represent the localities position in relation to the parameters of interest. As an example, the same locality could be represented by two different figures when examining gene flow between two adjacent populations and when the purpose is to investigate how a source of pollution outlet affects a population. The use of the method is restricted to areas where subareas are feasible to distinguish, thus making them possible to rank. When the ranking is solved, the simplicity of the method makes it easy to use and the results are readily evaluated.

It is important to point out that because many seals use more than one locality for haul out, the average haul out frequencies can not be assumed to represent the true number of animals that haul out at the specific locality. If this is done there is a great risk that the numbers will be underestimated. Only when seals haul out exclusively at one locality, which might be the case at more isolated locations, is this conversion possible. Interestingly, the difference between the actual number of animals and the number of animals acquired in a conversion, estimates the fidelity of seals hauling out at a particular location. A smaller difference indicates a stronger fidelity. In the area studied, an application of this method shows that animals hauling out at more isolated localities show a stronger site fidelity in the summer than seals at Ursholmen and Ramsökalven. Apparently, since seals in the area of Ursholmen and Ramsökalven do not have to transport themselves long distances in order to haul out at another location, they tend to move around more. This is, to a lesser extent, also true for animals at Segelskären.

In the present study, the varying degree of work effort among the localities is a problem that might not be as considerable as it first appears. At the more distant locations, e.g. Väderöarna, many of the observed seals are found to haul out exclusively at this location. Obviously, the behaviour of a seal hauling out at a well-studied locality, like Ursholmen, Ramsökalven and, to some extent, Segelskären, is determined with greater accuracy, but as seals that spend all their time at Väderöarna have not been observed at any of these well-studied localities it can be established with rather good probability that these individuals have actually only hauled out at Väderöarna.

Conclusively, this study of the Skagerrak harbour seal population shows that male seals migrate more than females, which is in concordance with the results Härkönen & Härding (in press) reached in their study. As the present study encompasses the whole summer it is not possible to say whether the observed male behaviour is representative for the mating period, occurring in July-August (Härkönen & Høide-Jørgensen 1990). If it is representative, the fact
that males migrate more than females would result in a greater dispersal of male genes. On the other hand, adult males were found to be only slightly more mobile than adult females, and if these males also decrease their range size (Thompson et al. 1989, Van Parijs et al. 1997) and haul out near the females, which has been found for grey seal (Halichoerus grypus) (Twiss et al. 1994), at the start of the mating season, the difference in male and female gene flow will be smaller than indicated by this study.

The age and sex related variations in the migration behaviour are also likely to influence the population structure at the localities within the study area. Juveniles and adult females were found to be the most stationary individuals, adult males migrated some more, while subadult males were the most mobile ones. If this migration pattern, found for seals presumably born at Ursholmen, is not counterbalanced by an equal behaviour performed by seals born at the other locations, deviations in the age structure of sub-populations will arise. Such counterbalance is not likely to occur for two reasons, the migration behaviour is probably influenced by the position of the locality, as indicated by this study, and also, the pup production is greater at Ursholmen and Ramsökalven than at the other locations (Härkönen & Hårding, in press). In the Wadden Sea, the majority of the migrantes originated from 7 out of 38 sub-areas (Ries et al 1994). Therefore, during the summer the age structure at separate localities are expected to differ, which is also argued by Härkönen & Hårding (in press).

Finally, the MI-method that was practised parallel to more conventional methods proved to be useful as the results were in concordance with each other.

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References


Härkönen, T. & Hårding, K. in press. Spatial structure amongst harbour seals (*Phoca vitulina*): consequences on population dynamics, ecology, epidemiology and genetics.


