Building time series of female reproductive parameters for Northeast Atlantic harp (*Pagohilus groenlandicus*) and hooded seals (*Cystophora cristata*)

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Introduction

Collaboration between Norwegian and Russian Scientists in seal research dates back at least a hundred years to the joint publication of "Bericht über die Lebensverhältnisse und den Fang der nordischen Seehunden" by Johan Hjort and Nikolai Knipovich in 1907.

The history of joint Norwegian-Russian exploitation of seals dates back even longer, but already in the early days of the Soviet Union, joint research plans were set up to provide guidance on the regulation of sealing effort in the White Sea area (Sivertsen, 1941). Joint research on seal biology was in fact one of the premises in the Soviet concessions to Norwegian sealers in the White Sea in the 1920s (Sivertsen, 1941).

In the mid 1950s, Soviet sealing vessels joined the Norwegian vessels on the sealing grounds in the Greenland Sea pack ice. Since then Norway and Russia have jointly exploited, monitored and managed the Greenland Sea populations of harp and hooded seals as well as the Barents Sea/White Sea harp seal population.

High postwar exploitation rates called for improvements in the understanding of harp and hooded seal population dynamics (Sergeant, 1991). Thus, driven by need and inspired by a new method for age determination of mammals based on teeth (Scheffer, 1950; Laws, 1952), both Russian and Norwegian scientists initiated sampling of age specific reproductive data in the late 1950s. In the following years, Russian and Norwegian scientists made many contributions to the scientific literature on the reproductive biology of seals (e.g. Popov, 1960; Øritsland, 1964; Jakovenko and Nazarenko, 1967; Khuzin, 1972). Regular sampling of teeth and ovaries has continued until recently resulting in accumulation of long-term data series on female reproductive traits such as mean age at maturity (MAM). This type of data is needed for models converting pup censuses into total population sizes (e.g. ICES, 2004) and the dynamics of MAM itself may be used as an indicator of per capita resource levels (Eberhardt and Siniff, 1977).

Obtaining representative samples from the wide-ranging Northeast Atlantic stocks of harp and hooded seals requires a considerable sampling effort. It is therefore desirable to combine data sets, which in turn requires a common understanding of procedures for sampling, laboratory analyses and statistical analyses. This common understanding has developed over the years through cooperation in various fora such as the scientific committee of the Norwegian-Soviet Sealing Committee operating from 1959 to 1984 (Bjordal et al, 2004).

From 1991 onwards, the Joint ICES-NAFO working group on harp and hooded seals (WGHARP) has been the principal scientific advisory body for management. WGHARP comprises scientists from Russia, Norway, Canada, Greenland, the USA and the EU and thus represents a multilateralisation of seal management advice reflecting the transatlantic distribution of both harp and hooded seals.

Political changes in Russia in the late 1980s facilitated direct scientific collaboration and lead to an increase in joint publications on various aspects of seal biology including distribution (e.g. Haug et al, 1994), diet (Nilssen et al, 1995; Potelov et al, 2000) and reproductive biology (Frie et al, 2003). This paper reviews results from recent years Russian-Norwegian cooperation on harp and hooded seal reproductive biology and also provides some transatlantic and future perspectives on this research.

Harp seals

Due to their high abundances, the Barents Sea/White Sea harp seal stock (~2 million animals) and the Greenland Sea harp seal stock (~600000 animals) are important components of their respective ecosystems (ICES, 2004). They are significant predators on krill, amphipods and smaller forage fish such as capelin (*Mallotus Villosus*), polar cod (*Boreogadus saida*) and herring (*Clupeus harengus*) and are themselves preyed upon by polar bears and hunted by humans (Nilssen et al, 2000; Derocher et al, 2002; ACIA, 2005).

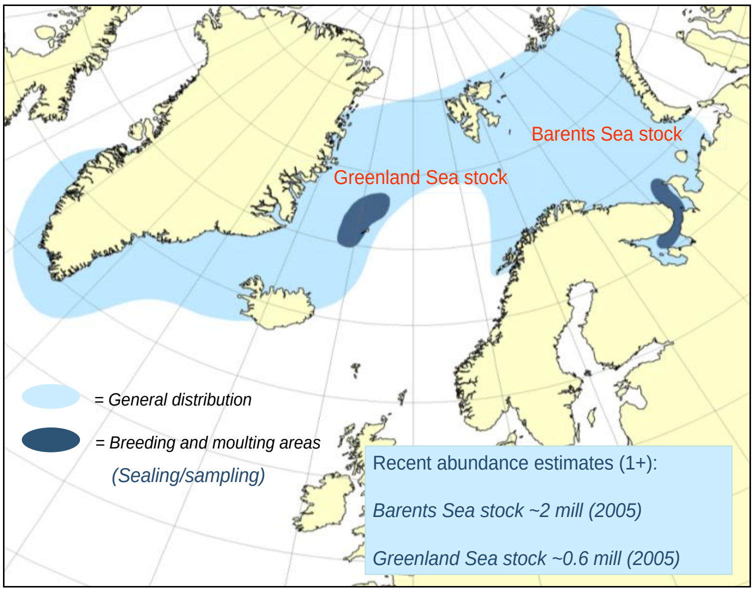


Figure 1. Distribution of Northeast Atlantic harp seals.

The so-called harp seal invasions during the Barents Sea capelin crash in 1986-1988 increased the public and scientific focus on harp seal ecology and population dynamics and a number of studies were initiated, many of them funded by the Norwegian Fisheries Research Council under the Marine Mammal Research Programme running from 1988-1994 (See Blix et al, 1995). During this period, there was also a renewed interest in harp seal reproductive studies. Based on different data sets and analytical approaches, researchers from Norway and Russia found a considerable reduction in reproductive rates of female Barents Sea/White Sea harp seals from the 1960s to the late 1980s (Kjellqwist et al, 1995; Timoshenko, 1995). Both studies related their findings to the decrease in abundance of winter forage fish such as capelin, herring and polar cod in the southern Barents Sea. Yurij Timoshenko titled his paper "Harp seals as indicators of the Barents Sea ecosystem, and was thus an early advocate of the ecosystem approach.

Kjellqwist et al (1995) estimated mean age at maturity of Barents Sea/White Sea harp seals based on age specific accumulations of ovarian corpora and found an increase in MAM from 5.5 years in 1963-1972 to 8.1 years in 1988-1993. The term ovarian corpora refers to various stages of the *Corpus luteum* - a hormone producing structure formed annually at ovulation. Regressing stages of *Corpora luteae* usually remain visible in the ovaries for several years after formation.

The estimated values of MAM in the late 1980s are considerably higher than the previous record for the species of 6.1 years estimated for Northwest Atlantic harp seal stock (Bowen et al, 1981) and the results caused some discussion in WGHARP. Were the observed inter-stock differences real biological differences or results of methodological differences? Had a similar increase in MAM occurred in the Greenland Sea stock?

These questions were later addressed in a joint Norwegian-Russian-Greenlandic publication analysing combined Norwegian and Russian reproductive data from the Barents Sea/White Sea harp seal stock and Russian data from the Greenland Sea harp seal stock (Frie et al, 2003). This time MAM was estimated from age specific proportions mature by a method similar to the one previously used in the Northwest Atlantic, thus allowing direct comparisons of estimates.

For the Barents Sea/White Sea stock, the analysis of MAM (Figure 2) showed very similar results for Norwegian and Russian data sets indicating inter-laboratory consistency of routines on age determination and ovary analysis. The values of MAM derived by the new method were also very similar to the values previously found by Kjellqwist et al (1995).

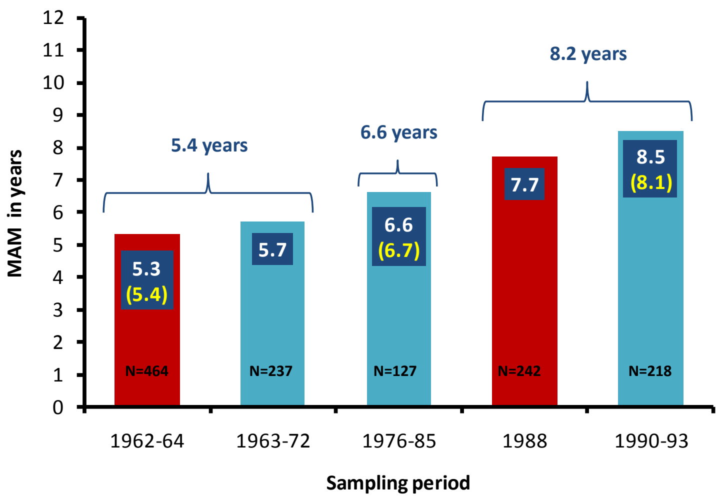


Figure 2. Estimates of MAM for moulting patch samples of White Sea/Barents Sea harp seals. White numbers in blue squares indicate MAM estimated from age specific proportion mature according to Frie et al (2003). Yellow numbers in blue squares indicate MAM as estimated by Kjellqwist et al (1995) based on quantification of ovarian scars. Parentheses show groupings of samples based on maximum likelihood tests and numbers above parentheses indicate MAM estimated from the most parsimonious model as described in Frie et al, 2003. Black numbers on the bars indicate sample sizes.

The Greenland Sea material differed from the White Sea/Barents Sea material in that there was no clear long term trend in MAM, and the values of MAM were significantly lower than for the Barents Sea/White Sea harp seal stock in the late 1980s (Figure 3). The data show a rather clear ecological differentiation between the two Northeast Atlantic harp seal stocks, indicating that young seals from the two stocks are likely to rely on different prey bases. This, together with observed differences in the seasonal timing of breeding, supports the current delineation of management units even though population genetic studies so far have not found evidence for population subdivision between the two areas (Perry et al, 2000).

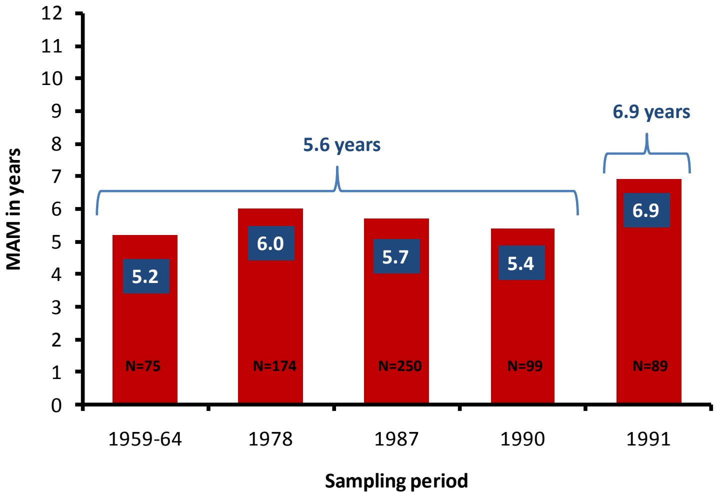


Figure 3. Estimates of MAM for Russian moulting patch samples of Greenland Sea harp seals. White numbers in blue squares indicate MAM estimated from sigmoid maturity curves fitted to age specific proportion mature according to Frie et al (2003). Parentheses show groupings of samples based on maximum likelihood tests and numbers above parentheses indicate MAM estimated from the most parsimonious model as described in Frie et al, 2003. Black numbers on the bars indicate sample sizes.

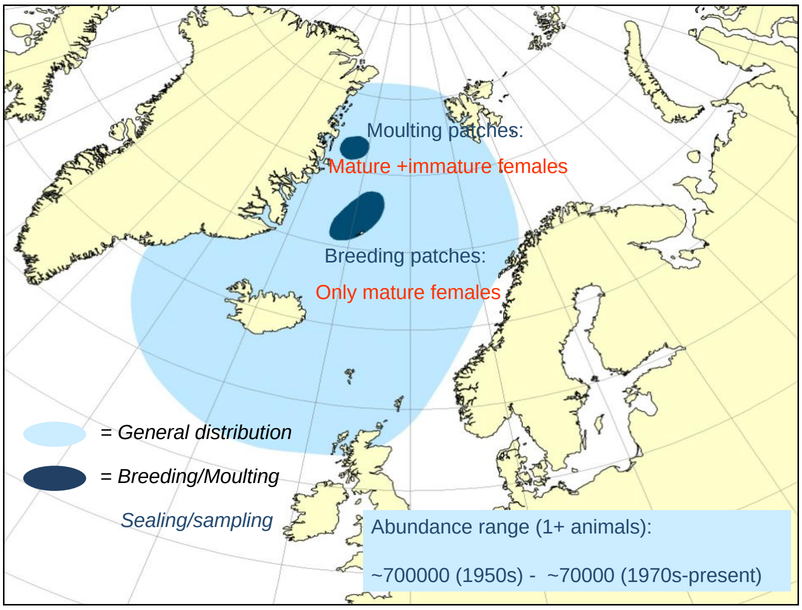
Using MAM as an indicator of per capita resource levels, it is noteworthy that the Barents Sea/White Sea harp seal stock with a maximum observed abundance of around 2 million animals has displayed a significantly higher MAM than the Northwest Atlantic stock with a maximum observed abundance of around 5.5 million animals (DFO, 2005). This probably indicates significant differences in carrying capacity between the Barents Sea and the Northwest Atlantic but the results could also be at least partly due to potential differences in sampling probabilities of mature and immature seals between areas or systematic differences in age determinations between Canadian and Russian/Norwegian labs.

Ongoing and planned harp seal satellite tagging programs on both sides of the Atlantic are likely to shed more light on questions regarding spatial and/or temporal differences in distribution patterns of mature and immature harp seals and which (if any) effect this has on the estimation of reproductive rates. So far, satellite tagging in the Northeast Atlantic has primarily focused on mature animals (Folkow et al, 2004), but for the understanding of population dynamic factors, the distribution of immature animals, particularly females, is equally important. Hopefully a joint IMR/PINRO satellite tagging project planned to start in 2008 will provide this type of information.

The role of age determination biases is currently being evaluated based on results from an Internordic/Russian/Canadian age determination workshop held at the Institute of Marine Research in Bergen in 2006. The workshop included a blind-reading experiment based on images of more than 100 tooth sections from known age harp seals, which have been tagged as pups during joint Norwegian –Russian tagging operations in the period 1977-1991. Age readers from all laboratories regularly engaging in age determination of harp seals participated in the experiment and considerable inter-reader variability was found. Simulation studies are underway to assess the possible effect of age reading errors on age related parameters. This workshop reflects a general trend towards closer integration of monitoring methodology between institutes participating in WGHARP. Continued collaboration aimed at identification and reduction of methodological biases, will facilitate future ecosystem level comparisons of seal population dynamics across all of the North Atlantic.

Hooded seals

Like harp seals, hooded seals are ice-breeding seals distributed on both sides of the North Atlantic (Coltman et al, 2006) (Figure 4). The Greenland Sea hooded seal stock breeds and moults in the Greenland Sea pack ice, while the Northwest Atlantic hooded sea stock primarily breeds in the Labrador Sea and moults in the Denmark Strait (Sergeant, 1991). Almost all published data on reproductive rates of hooded seals are from the Northwest Atlantic Stock and have indicated a remarkably early age at maturity in females (2-4 years) and pregnancy rates close to 100% (Øritsland, 1964; Born, 1982).



Despite a relatively large sampling effort, no stock specific estimates of reproductive rates have actually been available for the Greenland Sea hooded seal stock in the past and modeling has therefore relied on data for the Northwest Atlantic stock. In 2005, the total pup production of Greenland Sea hooded seals was estimated at 15000 pups (CV=24%), which is only about half of the amount caught annually by sealers in the 1950s and 1960s (ICES, 2007). Modeling suggests that the reduction in pup production may represent a 10-fold decrease in total abundance from the 1950s to 2005 (ICES, 2007).

While high exploitation levels are likely to have driven most of the decline, the apparent lack of recovery, following a significant decrease in hunting pressure in the 1980s, is somewhat surprising and unlike the development in the Northwest Atlantic stock (ICES, 2007). This situation has highlighted the need for stock specific population parameters (ICES, 2007) both for historical population models and current management models. In order to maximise data quantity and quality, joint Norwegian -Russian analyses of all available historical material are currently being conducted and some preliminary results can be presented.

A common MAM of 4.8 years (see Figure 5) could be fitted to Russian moulting patch samples from the period 1990-94 regardless of month of sampling. This is the highest MAM on record for hooded seals. Using the same methods to fit MAM to two Northwest Atlantic data sets from 1956-60 (Øritsland, 1964) and 1970-71 (Born, 1982) a common value of 3.1 years is found (ICES, 2007).

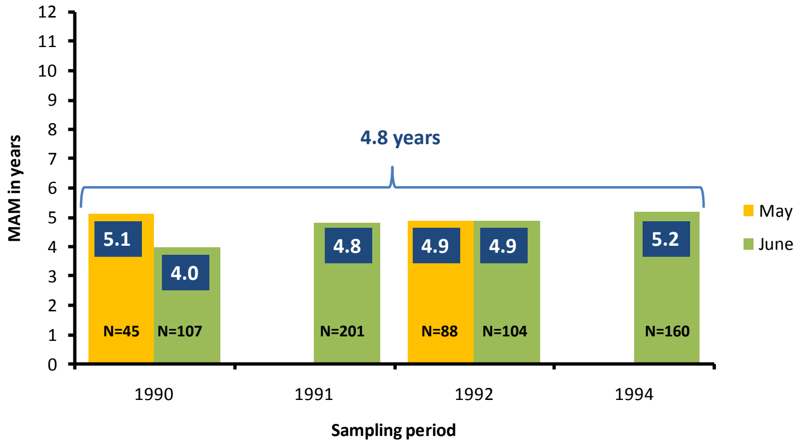


Figure 5. Estimates of MAM for Russian moulting patch samples of Greenland Sea hooded seals. White numbers in blue squares indicate MAM estimated from age specific proportions mature according to Frie et al (2003). Parentheses show grouping of samples based on maximum likelihood tests and numbers above parentheses indicate MAM estimated from the most parsimonious model following principles described in Frie et al (2003). Black numbers on the bars indicate sample sizes.

The difference in MAM between Greenland Sea samples and Northwest Atlantic samples is both statistically and biologically significant, but as the sampling periods are 20-30 years apart, it is impossible to determine, if the split represents a spatial or a temporal difference. Nevertheless, the high MAM found for Greenland Sea hooded seals seems to suggest, that the stock experienced suboptimal resource availability during a period of historically low abundance in the late 1980s and early 1990s and that a reduction in food availability may be playing a role in preventing recovery of the stock.

The hooded seal is a deep diving species thought to forage to a large extent on meso-and bathypelagic prey species such as redfish (*Sebastes spp.*), Greenland halibut (*Rheinhardtius hippoglossoides*), blue whiting (*Micromesistius poutassou*), herring and the squid *Gonatus fabricii* (Folkow et al, 1996, Haug et al, 2007). In drift ice areas, polar cod , capelin and sand eel (*Ammodytes spp*.) are the most important prey species in addition to *Gonatus fabricii (*Haug et al, 2007).

Several of these prey species have shown very dynamic abundance and distribution patterns over the past 50 years, but our understanding of the relative importance of prey species for hooded seals is still too limited to establish any likely relationships between prey dynamics and hooded seal reproductive rates.

Unfortunately this Russian data set is the only moulting patch data available for Greenland Sea hooded seals and therefore no long-term trends in MAM can be extracted. However, long-term ovary data from breeding patches exist and are currently being analysed by us. Breeding patch material only comprises data from mature females, and analyses therefore rely on quantification of age specific accumulation of ovarian corpora. This type of analysis is more prone to reader biases than simple classifications of females as either mature or immature and to ensure comparability of data in time and space, calibrations of ovary readings between readers are to be conducted before the analyses can be completed.

Future Perspectives

There is currently an urgent need for updates on female reproductive rates for both harp and hooded seals in the Northeast Atlantic. In recent years, high quality pup production surveys have been carried out for all three stocks but the conversion to absolute population abundances unfortunately have to rely on outdated reproductive data from the early 1990s (ICES, 2004; ICES, 2007). Sensitivity analyses of the currently used population models

(ICES, 2005), suggest this may have a significant impact on the total abundance estimates, which are the basis for catch quota calculations and estimation of seal prey consumption.

Harp seals are the most abundant mammals in the Barents Sea and they are resident year round (Haug et al, 1998). Understanding the dynamics of harp seal prey consumption is therefore a key element in ecosystem research and management in the Barents Sea. This is acknowledged in a recent advisory report to the Norwegian government on ecosystem management of the Barents Sea listing total abundance of harp seals as well as MAM as relevant ecosystem indicators in the Barents Sea (Quillfeldt et al, 2005).

In the past, harp and hooded seals have sustained high catch levels and hunting mortality has widely been regarded as the primary driving factor for population growth rates (Stortingsmelding 27, 2004). In the past 2-3 decades, hunting pressures have been historically low for the Northeast Atlantic stocks of harp and hooded seals, but the population trajectory seen in Greenland Sea hooded seals suggests that other factors than the catches may significantly affect population growth rates. The importance of environmental conditions is also highlighted by the scenarios for global warming, which is expected to have a negative impact on the population dynamics of arctic seal species through loss of breeding habitat (ACIA, 2005). Climate change is also likely to affect resource availability for harp and hooded seals but the population dynamic effect of this is harder to predict. Implementing the precautionary approach to management, WGHARP recommends updates of pup production estimates and reproductive parameters every 5 years. Otherwise a given stock is characterised as data poor and recommended catch options will be restricted (ICES, 2004).

Some new reproductive material has been collected from Northeast Atlantic harp and hooded seals in recent years, but based on previous experience, sample sizes are not yet sufficient to derive reliable estimates of MAM. For harp seals, sampling of reproductive data can be carried out at relatively low cost from Norwegian sealing vessels operating in the moulting period (April-May). For hooded seals, on the other hand, dedicated cruises are necessary to obtain samples from moulting patches as all regular hunting takes place in the breeding season.

In addition to the classical monitoring of age at maturity, extraction of actual age specific late term pregnancy rates, would greatly enhance population dynamic models. However, this would either require expensive dedicated sampling efforts in the period immediately prior to the breeding season or development of reliable methods for indirect estimation of pregnancy rates based on sampling at other times of the year. Together with Canadian and Greenlandic colleagues, Norwegian and Russian researchers are currently seeking funding for research projects aimed at increasing our understanding of reproductive processes in female seals and identification of morphological and/or biochemical characteristics, which will allow us to record the most important reproductive events from a variety of sample types.

Continuation of the existing time series on MAM and age specific corpora accumulation is valuable in its own right, because they represent long term indicators of habitat quality for harp and hooded seals in different ecosystems and under changing environmental conditions. The level of sophistication of such analyses of course depends on the amount of synoptic information on seal abundance, distribution and prey availability. The abundance of these types of information has increased over time and will hopefully continue to do so in the future. By continuing long-term data series along with this larger suite of ecosystem data, we're likely to learn a lot more about the parameter dynamics, which will also be of use to retrospective analyses. To make full use of MAM and corpora accumulation rates in this context, the comparability of results in space and time must be tested by regular calibration of methods between laboratories.

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