Harp seal populations in the northwestern Atlantic: modelling populations with uncertainty

by Prof. Stephen Harris, Carl D. Soulsbury & Graziella Iossa

School of Biological Science, University of Bristol, UK

Summary

- For the past six years, nearly 400,000 harp seals from the Northwest Atlantic population have been hunted annually by Canada and Greenland, the highest number since the 1950s. When such hunting pressure last occurred, the harp seal population declined rapidly by over 50%. With current levels of hunting pressure being so high, it is important to have accurate information about the total harp seal population size and the subsequent effects of differing hunting strategies. Therefore, in this report we evaluate the scientific model used by the Canadian Department of Fisheries and Oceans to estimate harp seal population size, set harp seal total allowable catches (TACs) and model the effect of different culling pressure.

- Two aspects make the Canadian harp seal population model unsafe: (i) it assumes that many variables such as the environment and food availability play no part in determining numbers of harp seals; and (ii) it assumes that all the input variables into the model are accurate.

- Significantly, the model fails to take into account many variables that can affect harp seal numbers. These include environment unpredictability, climate change and the bioaccumulation of anthropogenic toxins, which in turn reduce reproductive rates and increase mortality. When so many variables are unknown, a precautionary approach should be applied. However, no such measure is applied to the Canadian management plan.

- There is no direct way to measure harp seal populations; population estimates and TACs are modelled using three main input variables – annual pup production, pregnancy data and catch-at-age data (an indicator of mortality rates).

- Similarly, the total number of pups produced each year (pup production) cannot be counted directly. Instead, estimates from a small area (<2% of the breeding site) are extrapolated to give a total population estimate. Differing methods of counting pups may give large differences (60,000 – 160,000) in numbers for single breeding sites.

- Adult mortality rates used in the model do not take into account sex- or age-biases in mortality. In addition, data from Canadian kills are assumed to be representative of (i) the Greenland kill and (ii) fisheries bycatch; however, since the Canadian kill occurs at a different time of the year and in different areas, this is unlikely to be true. The estimated number of seals killed through fisheries bycatch is thought to be an underestimation.

- Pregnancy data are based on very few females, making information on pregnancy rates inaccurate. In other harp seal populations, pregnancy rate is related to female body condition; reduced food availability increases age at first reproduction and reduces population fecundity.

- Harp seal females begin to breed at ages 5 – 6; thus, the impact of culling so many pups will not be noticed in the population for 5 – 6 years.

- Currently the model used to estimate harp seal population size and used to assess TACs misses many important biological variables, is insensitive to rapid population changes and ignores many important threats to the population. Current levels of removals are as high or higher than the years before the population crashed.

- In their 2000 stock assessment for harp seals, the DFO predicted a decline in the population (from the estimated 5.2 million) over the following years as a result of high kill levels in the commercial seal hunt. This is not surprising considering that between one third and one half of all pups born in the population over the past ten years have been slaughtered. Yet four years later, the DFO estimated the Northwest Atlantic harp seal population at 5.9 million seals – an increase of 0.7 million. This contradicts the DFO's own predictions and highlights the unreliability of the model used to predict the size of the Northwest Atlantic harp seal population. This harp seal population may already be approaching the 70% level advocated by the Department of Fisheries and Oceans. The DFO says that it is committed to maintaining the population above this reference point.

- Several other Canadian fisheries have collapsed as a consequence of many variables, including environmental change and mismanagement. Despite the uncertainties surrounding the estimates of harp seal numbers and the uncertainty surrounding many other variables, the Canadian model does not apply a precautionary principle and so threatens the survival of seal populations.

The cull of harp seals in the northwest Atlantic

The biology of the harp seal

The harp seal (*Phoca groenlandica*) is a widespread species found in the northern Atlantic and Arctic oceans (Sergeant, 1991). Three distinct populations are recognised, one breeding in the Gulf of St Lawrence (Northwest Atlantic population), one breeding north of Jan Mayen Island in the Greenland Sea (Greenland Sea population) and one in the White Sea (White Sea population). Genetic evidence demonstrates that the Northwest Atlantic population is distinctly different from the other two populations, and little gene flow occurs between them (Perry *et al*., 2000). All three populations undergo an annual north-south migration of 6000-8000km. The Northwest Atlantic population spends the summer feeding in Hudson Bay, around Baffin Island and northwestern Greenland, before starting to return south in autumn. In spring, female harp seals aggregate in dense "whelping patches" on pack ice to give birth to a single pup. Pups are nursed for 12 days, after which they remain fasting on the pack ice for a further 2 weeks before finally taking to the water to feed. Adult females begin to breed at around 5-8 years of age, whilst for males reproductive maturity occurs at 8 years of age. They can live up to 30 years.

During breeding, harp seals form large aggregations which makes them easy to exploit by humans. Historically, all three populations have been hunted; both the Greenland and the Northwest Atlantic population have been overhunted, leading to dramatic population crashes (Sergeant, 1991). This led to the near cessation of hunting and the gradual recovery of the populations. Both the Greenland and the Northwest Atlantic populations are currently hunted for commercial purposes, principally for their pelts, but also for meat and blubber. Harp seal pups are the main component of Canadian kills. Pups are hunted as either ragged jackets (12-25 days old) or as beaters (1-13 months). Seals can be legally killed using rifles, shotguns, clubs and hakapiks.

The Canadian Department of Fisheries and Oceans (DFO) sets total allowable catches (TACs) within a three-year period for the Northwest Atlantic population. Greenland also exploits this population, and their annual kill (circa 100,000 animals) is not incorporated into the Canadian TACs. To set quotas requires an accurate knowledge of the population size and the complex underlying processes driving changes in breeding and mortality rates. Direct counting of seals is not feasible; hence the population size is modelled to estimate sustainable hunting levels. The ability of the models used in population estimation and the ability to simulate uncertainties in the natural population are unclear.

Estimating harp seal populations

Modelling harp seal populations

In recent years, different methods have been used to estimate the size of the Northwest Atlantic harp seal population. These include aerial surveys, tagging, survival indices and population models (Lett & Benjamin, 1977; Ugland, 1985). The DFO now uses a population model fitted to field estimates of pup production to estimate the harp seal population size and to model the effect of different harvest strategies (Shelton *et al*., 1996). The model, known as the Cadigan-Shelton model, requires three sets of field data: annual pup production, catch-at-age data and age specific pregnancy rates (Cadigan & Shelton, 1993; Shelton *et al*., 1996).

Annual pup production data

Estimates of the numbers of pups produced each year (pup production) have been carried out at regular intervals since the late 1970s. The data appear to indicate that pup production has been increasing (Stenson *et al*., 2002; Table 1).

Table 1. Estimated pup production with standard error (±SE) of the Northwest Atlantic population of harp seals. Methods refer to capture-mark-recapture techniques (CMR), visual (V) or photography (P) surveys.

Year	Estimated Pups	SE	Method	Reference
1978	497,000	± 34,000	CMR	Roff & Bowen (1986)
1979	478,000	±35,000	CMR	Roff & Bowen (1986
1980	475,000	± 47,000	CMR	Roff & Bowen (1986)
1983	475,000	± 33,000	CMR	Warren *et al*. (1997)
1990	577,900	± 38,800	V, P	Stenson *et al.* (2003)
1994	708,400	± 67,000	V, P	Stenson *et al*. (2003)
1999	997,900	± 102,200	V, P	Stenson *et al.* (2003)
2004	991,400	± 58,200	V, P	Stenson *et al.* (2005)

The most important variable in the Cadigan-Shelton model is the estimate of pup production. Two methods have been used from the 1990s to estimate pup abundance: aerial surveys using photographs along strip transects, and visual counts by observers in helicopters. Several sources of error in the strip transects tend to lead to the underestimation of pup numbers; these include missing unborn pups, pups hidden by ice and missing whelping concentrations (Myers & Bowen, 1989). The methods used to estimate pup production give cause for concern. However, while photographs can be reanalysed, visual counts are a one-off, and are not subject to any quantified error rate, such as misidentification of pups. Where both methods are used, estimates can be similar or may vary by up to 160,000 pups at individual sites (visual estimates 284,959 versus 124,409 made by photographic estimates). Visual estimates are based on subjective counts, and although a pre-defined strip is searched, maintaining a count within a set strip width over a relatively featureless landscape is difficult. Thus the inclusion of more pups outside the defined strip is likely to be a problem in visual counts and lead to an overestimation of the pup production. Photographic methods provide a better method of estimating pup production.

The number of pups is estimated using standard strip transect methods (Burnham & Anderson, 1984; Buckland *et al*., 1993; Stenson *et al.*, 2002). However, a source of statistical error missed by the authors is spatial autocorrelation (Legendre, 1993). Spatial autocorrelation occurs when a spatial measurement in a given locality is not independent, but is likely to be linked to measurements close by. Seals on ice show marked spatial autocorrelation, even across large geographic distances, because seals may congregate in groups or near areas with similar environmental conditions (Ferguson & Bester, 2002). Autocorrelation therefore is an important consideration when estimating abundances of animals (Ferguson & Bester, 2002). One possible way of compensating for this is to count groups rather than individuals (Kingley, 1989; Trenkel *et al.*, 1997; Hedley & Buckland, 2004). Population estimates are then based on observed group size (e.g. Mizuno *et al*., 2002). However, harp seals form large dispersed groups at whelping sites. Current methods for density estimation are ill equipped to cope with such a spatial pattern (Buckland *et al*., 1993), unless they incorporate spatial modelling methods linking geographical and environmental variables to their estimates (e.g. Hedley & Buckland, 2004). Failure to take spatial autocorrelation into account can lead to reduced accuracy in population estimates (Khaemba & Stein, 2001).

Age specific pregnancy rates

Long-term data show that fertility rates of females are not related to population density. Significant interannual variance in pregnancy rates suggests that ecological and environmental factors may be important, and that changing oceanographic conditions may negatively affect harp seal reproductive rates (Kjellqwist *et al*., 1995; Frie *et al*., 2003). One problem arises from the data used in the models: namely sample sizes. Female ages are separated into year categories (3, 4, 5, 6, 7, and 8+) and when the data are examined interannually, samples sizes are too low to examine age specific reproduction (Table 2).

Table 2. Sample sizes (number of females) used in the estimation of age-specific pregnancy rates 1994 – 2001 (data from Sjare *et al*., 2004).

	3 years	4 years	5 years	6 years	7 years	8 + years
1994	23	16	14	7	5	36
1995	10	13	4	5	0	24
1996	8	6	4	1	0	35
1997	6	4	10	2	2	34
1998	6	10	9	4	9	26
1999	6	7	18	15	9	50
2000	1	9	6	5	6	37
2001	2	0	2	3	3	36

Low samples significantly reduce the accuracy and confidence of age-specific fertility rates. In particular, having more samples from older age groups, which have a higher proportion of breeding females, will overestimate the overall population pregnancy rate. Age-specific comparisons of harp seal reproduction demonstrate that females from the Northwest Atlantic population breed at a younger age than females from the White Sea and Greenland Sea populations. In the Northwest Atlantic, female harp seal reproduction begins on average at 4.6- 5.8 years in contrast to 5.5- 8.1 years and 6.6 years in the White Sea and Greenland Sea populations respectively (Kjellqwist *et al*., 1995; Frie *et al*., 2003). This itself may be a result of higher hunting pressure. All studies on female harp seal reproduction note a high degree of interannual variability in age at first reproduction and overall reproductive rates. Pooling data across years does not represent an accurate measure of age-specific reproduction, nor of overall reproductive rates. An overestimation of breeding at younger ages is an important source of error in the Cadigan-Shelton model: older age at first breeding suggests lower fecundity in the population. Changes in pregnancy rates have a profound affect on population trajectory (Warren *et al*., 1997).

Mortality

Mortality rates of harp seal pups are unknown. In population models, variation in juvenile survival is the main factor determining recruitment, and is more important than adult survival (Gaillard *et al*., 1998). The Cadigan-Shelton model is run using three possible variables: juvenile mortality is (i) equal to adult mortality, (ii) threefold higher or (iii) fivefold higher. The threefold higher variable is used as the primary population estimate. The only adequate data from harp seals observed 3% mortality in the first three weeks of life. However, detailed studies have not estimated 1st year survival. In other seals, juvenile mortality in particular is sensitive to environmental variation: poor maternal condition can reduce juvenile survivorship (Hastings *et al*., 1999). Assuming a stable mortality rate is clearly not an accurate measure of mortality. Significant yearly variation in natural mortality may lead to significant over-culling of an individual cohort. For example, in 1998, 2000 and 2002, natural pup mortality was up to fivefold higher as a result of poor ice conditions, and so during these years the TACs were higher than the replacement yield (i.e. the number of pups required to maintain a stable population size).

Previous work criticised the fact that not all mortality sources for adults were incorporated into model simulations (Lavigne, 1999; Johnston *et al*., 2000). Later simulations take into account other mortality sources such as the Greenland hunt, struck and lost animals (the proportion of seals killed but not recovered and hence not recorded in official statistics) and fishery-related mortality (seals caught as bycatch other fisheries). However, there is concern as to how these mortality sources have been incorporated. For instance, Canadian scientists noted that the level of struck and lost varied considerably with hunter experience and this is not being taken into account (Anon., 2001). Moreover, struck and lost rates varied not only with age class but also with season, weather conditions and killing method. This can lead to an underestimation of the number of animals killed. There is a high degree of uncertainty in the estimates used to incorporate fishery-related mortality into the model (Johnston & Santillo, 2005), mainly because the number of seals caught as bycatch is under-reported.

Catch-at-age data are an important component of the model as they are used to describe the age composition and mortality rate of the adult population. One bias associated with catch-at-age data is that they assume that the age samples collected are representative of the age structure of the entire population (Ugland, 1985), but as with all hunt data, age- and sex-biases can occur with location and season. For example, trawling mortality for Cape fur seals (*Arctocephalus pusillus*) was sex- and age-biased (Miller *et al*., 1996), whilst commercial sealing and gill net data indicate female-biased mortality in harp seals from the Barents Sea (Kjellqwist *et al*., 1995). No incorporation of sex-specific mortality is made in Canadian adult seal culls, whilst age data from the Canadian cull are assumed to be the same as the Greenland cull. This ignores the fact that the Canadian cull consists mainly of pups and juveniles, whilst the Greenland hunt is a significant source of adult mortality. In the same way, no data are incorporated into age data of bycatches or other mortality sources. It is unclear if catch-at-age data for the Canadian cull are representative of the age- and sex-structure of the population as a whole, or whether they are representative of the mortality from other sources.

Sex ratio

Calculation of total population size is based on calculating the number of females. It is then assumed that the adult sex ratio is 1:1 (males to females). As yet there are no reliable data to support this assumption. Like many seals, harp seal sex ratio at birth is equal (Stewart & Lavigne, 1980). However, many species show considerable sex biased mortality for juveniles. For example, survival is three-fold higher in first year female grey seals (*Halichoerus grypus*) (Hall *et al*., 2001), and significantly higher in Weddell seals (*Leptonychotes weddellii*) (Hastings *et al*., 1999). Estimating adult seal sex ratio is much harder, as season affects the prevalence of individuals in any given area (Øritsland, 1971; Harkonen *et al.*, 1999; Vincent *et al.*, 2005) and catch methods may give a false impression of the presence or absence of sex biases within a population (e.g. Kjellqwist *et al*., 1995). Given the uncertainty surrounding the sex ratio of the adult harp seal population, possible effects of varying sex ratio should be incorporated into the population model.

Population management

Population management with unknown variables

Under the current management the main objective of the harp seal cull is to increase the number of seals killed, while maintaining the harp seal population above a precautionary reference point set at 70% (3.85 million seals) of the current population level. Explicitly the model assumes that the age structure of the Canadian and Greenland harvest does not change and that natural mortality and pregnancy rates do not change. Current management policy aims to reduce the harp seal population towards the 70% reference point.

As highlighted previously, there are many uncertainties not incorporated into the harp seal population model, which may affect population size estimates. The same is also true for modelling current and future population trends, particularly in the presence of hunting pressure. Explicit in any management is the assessment of risk, and in particular risk associated with uncertainties and unknown variables. This approach, known as the precautionary principle, has been used by the EU in such measures as to protect the ozone layer or reduce the rate of climate change (Commission of the European Communities, 2000). The management of the Canadian seal population does not follow the precautionary principle as it fails to take into account many uncertainties.

Other unknown variables

The population estimates and simulations are run under one basic assumption: other factors that may influence the harp seal population remain stable. These include environmental conditions such as ice cover and food availability. There is considerable evidence of the impact of these factors on harp seal biology. For example, marked temporal changes in age at sexual maturity for females has been linked to *per capita* food rate; a reduction in food leads to decreased growth rates and later sexual maturity (Frie *et al*., 2003). Large declines in food availability can lead to a general decline in body condition and dispersal away from traditional breeding sites (Nilsson *et al*., 1997; Lucas & Daoust, 2002). Reduced food availability may also increase the mortality of juveniles, as breeding females may be in poorer condition (Hastings *et al.* 1999). While these parameters are known to affect the harp seal population, no contingency is made in the population model for such variables.

There is growing evidence that global climate change is affecting sea ice dynamics in northern and eastern Canada (Johnston *et al*., 2005). Light ice years may cause unquantified risks to harp seals; increased crowding caused by a reduction in breeding sites may increase neonatal mortality, decrease food availability and increase the risk of a disease epizootic (Johnston *et* *al*., 2005). As noted by Canadian government scientists, poor ice conditions in 1998, 2000 and 2002 led to almost complete cohort failure, something that has happened in the past. In addition, the long-term trend of decreasing ice coverage and depth (Johnston *et al*., 2005) can affect the long-term population trends. For example, for ringed seals (*Phoca hispida*) from the Hudson Bay area, reduced ice coverage and depth has lead to a significant decrease in recruitment into the adult population and a long-term population decline (Ferguson *et al*., 2005). Uncertainty surrounding climatic variation and the insensitivity of the model to changing mortality rates are of concern when setting killing quotas.

Harp seals are also at the top of the food chain and there is a lot of information on the anthropogenic origin of chemicals found in harp seal blubber. Xenobiotics (i.e. chemical compounds foreign to the body) such as PCBs, DDT, DDE and heavy metals such as lead and zinc are all found in the blubber of seals in concentrations exceeding the threshold levels for adverse affects on reproductive and immune systems (Addison, 1989; Kleivane *et al*., 1997; Zitko *et al*., 1998; Anon., 2005; Shaw *et al*., 2005). The overall impact of the bioaccumulation of such toxins is not clear, but negative effects include reproductive failure, infertility and reduced individual survivorship (Hutchinson & Simmonds, 1994; Moor *et al*. 1997; Jepson *et al*., 2005). Xenobiotics, therefore, represent a serious but unknown threat to seal populations.

The delayed impact

As female harp seals first begin to breed at around 5-6 years of age, any killing of pups will take 5-6 years to impact the breeding population (Stenson *et al*., 2003). This raises a question about the sensitivity of the model. As highlighted, unquantified variables may reduce pup survivorship. These would not affect the adult population for another 5-6 years, excluding the continuing TACs allowed during the intervening years. When such a long time delay occurs, making assessments of future population trends is uncertain. At the same time, the insensitivity of the populating model means there is a low probability of detecting population changes, unless the change is large (Johnston *et al*., 2000).

Total allowable catches (TACs)

The TACs are calculated from the population estimates. However, as noted by several authors, the reported total catch is not the total number of individuals killed (Johnston & Santillo, 2005). For example, in 1999 the TAC set by the Canadian government was 275,000 harp seals. However, incorporating all mortality sources (hunted, struck and lost, fisheries related mortality), total anthropogenic removal was 483,000 harp seals, of which 281,000 were pups. Given the dramatic unreliability of harp seal population estimates, the uncertainty surrounding environmental related mortality and two non-cooperating fisheries (Canada and Greenland), such high levels of removals are unsustainable. This has been noted in previous scientific meetings, where total catches were higher than replacement yields. Previously, when total removals were so high – around 350,000 seals per annum – the harp seal population crashed dramatically to below 1,800,000 and only recovered when total removals were reduced significantly.

The precautionary principle

It is clear that the management of the Canadian seal population is not carried out using a precautionary approach. Simplistic modelling assumes stability of many biological parameters, while at the same time ignoring the many other variables that may have a deleterious effect on harp seal numbers. In addition, a 2003 harp seal workshop attended by Canadian scientists concluded that uncertainty in estimating maximum population size of seal populations meant this should not be used when setting precautionary reference points. The current Canadian management strategy continues to use the uncertain population estimates to set precautionary reference points.

The current population size of the harp seal population

In 2000, the Northwest Atlantic harp seal population was estimated to be 5.2 million seals (95% confidence interval 4.0-6.4 million). Following this, Canadian scientists simulated current culling levels, and predicted a population decline, yet in 2005 the DFO announced that the Northwest Atlantic harp seal population had risen to 5.9 million seals (95% C.I. 4.6-7.2 million). In both cases, confidence estimates mean the seal population may be up to 1.3 million lower than reported and already approaching the 70% level advocated by the DFO. In addition these estimate are contrary to expected predictions, and highlight the insensitivity of the model to populations changes. The population model used to estimate the population size of the Northwest Atlantic harp seal population does not incorporate enough biological data to make accurate predictions about both population size and the effect of different hunting strategies.

Canadian management of other fisheries and the precautionary principle

The history of Canadian fishery management has recorded many failures. Management strategies have at one time lead to the collapse of cod (*Gadus morhua*), sharks, walleye (*Sander vitreus*), salmon (*Oncorhynchus* spp.), Pacific herring (*Clupea pacificus*) and harp seal populations (Taylor *et al.*, 1994; Myers *et* al., 1997; Hurley, 1998; Pitcher *et al.*, 2002; Baum *et al.,* 2003; Sullivan, 2003). The principle problem with any management strategy is the degree of uncertainty incorporated into the management plan. Unknown environmental variables (e.g. water temperature for snow crabs), uncertainty of population parameters (e.g. survival rates for cod) and structural uncertainty, may all cause the collapse of a population (Charles, 1998). Given such a level of uncertainty, the precautionary principle should be applied and in poor ice years, no hunting should be allowed. Instead, maximum exploitation of the harp seal population seems to prevail when setting quotas. Past evidence from several fisheries collapses continues to be ignored in the current management of harp seal populations.

Conclusions

The population model used by the DFO to assess the population size of the Northwest Atlantic harp seal population has three flaws. It assumes that the data inputted into the model are accurate which is not true; it ignores or lacks important biological data such as pup mortality rates and adult sex ratio; and it assumes that variables such as changing ice cover, food abundance and pollutants have no affect on the population and population parameters. Given the level of uncertainty surrounding the variables either included or not included in the model, the estimates produced by the population model must be deemed unsafe. Harp seal population estimates produced in 2005 show 95% confidence intervals of 2.6 million seals, indicating exactly how imprecise the model actually is.

Based on the model output, varying TACs are set with then long-term aim of reducing the harp seal population to 70% of the current estimated population size. However, difficulty in estimating current population size makes setting a 70% level unsafe. In addition, given the uncertainties surrounding harp seal populations, a precautionary approach should be applied. Since the current management strategies used by the Canadian government are based on an uncertain population estimate, and do not use a precautionary approach, they therefore threaten the Northwest Atlantic harp seal population.

References

Addison, R.F. (1989) Organochlorines and marine mammal reproduction. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 360- 368.

Anon (2001) Report of the eminent panel on seal management. *Fisheries and Oceans Canada* Fs23-405/2001E.

Anon. (2005) The tip of the iceberg: chemical contamination in the Arctic. WWF International Arctic Programme.

Baum, J.K., Myers, R.A., Kehler, D.G., Worm, B., Harley, S.J. & Doherty, P.A. (2003) Collapse and conservation of shark populations in the northwest Atlantic. *Science*, **299**, 389- 392.

Buckland, S.T. Anderson, D.R., Burnham, K.P. & Laake, J.L. (1993) *Distance sampling: Estimating abundance of biological populations.* Chapman & Hall, London.

Burnham, K.P. & Anderson, D.R. (1984) The need for distance data in transects counts. *Journal of Wildlife Management*, **48**, 1248- 1254.

Cadigan, N.G. & Shelton, P.A. (1993) SAS programs for fitting a seal population dynamics model. *Canadian Technical Report of the Fisheries and Aquatic Science*, **1927**, 1- 34.

Charles, A.T. (1998) Living with uncertainty in fisheries: analytical methods, management priorities and the Canadian groundfishery experience. *Fisheries Research*, **37**, 37- 50.

Commission of the European Communities (2000) Communication from the Commission on the precautionary principle. http://europa.eu.int/comm/dgs/health_consumer/library/pub/pub07_en.pdf

Ferguson, J.W.H. & Bester, M.N. (2002) The treatment of spatial autocorrelation in biological surveys: the case of line transect surveys. *Antarctic Science*, **14**, 115- 122.

Ferguson, S.H., Stirling, I. & McLoughlin, P. (2005) Climate change and ringed seal (*Phoca hipida*) recruitment in western Hudson bay. *Marine Mammal Science*, **21**, 121- 135.

Frie, A.K., Potelov, V.A., Kinglsey, M.C.S. & Haug, T. (2003) Trends in age-at-maturity and growth parameters of female Northeast Atlantic harp seals, *Pagophilus groenlandicus* (Erxleben, 1777). *ICES Journal of Marine Science*, **60**, 1018- 1032.

Gaillard, J-M., Festa-Bianchet, M. & Yoccoz, N.G. (1998) Population dynamics of larger herbivores: variable recruitment with constant adult survival. *Trends in Ecology and Evolution*, **13**, 58-63.

Hall, A.J., McConnell, B.J. & Barker, R.J. (2001) Factors affecting first-year survival in grey seals and their implications for life history strategy. *Journal of Animal Ecology*, **70**, 138-149.

Härkonen, T., Hårding, K.C. & Lunneryd, S.G. (1999) Age and sex specific behaviour in harbour seals *Phoca vitulina* leads to biased estimates of vital population parameters. *Journal of Applied Ecology*, **36**, 825- 841.

Hastings, K.K., Testa, J.W. & Rexstad, E.A. (1999) Interannual variation in survival of juvenile Weddell seals (*Leptomychotes weddellii*) from the McMurdo Sound, Antarctica*:* effects of cohort, sex and age. *Journal of Zoology*, **248**, 307- 323.

Haug, T., Stenson, G.B., Corkeron, P.J. & Nilssen, K. (2006) Estimation of harp seal (*Pagophilus groenlandicus*) production in the North Atlantic completed: results from surveys in the Greenland Sea in 2002. *ICES Journal of Marine Science*, **63**, 95- 104.

Hedley, S.L. & Buckland, S.T. (2004) Spatial models for line transect sampling. *Journal of Agricultural, Biological, and Environmental Statistics*, **9**, 181- 199.

Hurley, P.C.F. (1998) A review of the fishery for pelagic sharks in Atlantic Canada. *Fisheries Research*, **39**, 107- 113.

Hutchinson, J.D. & Simmons, M.P. (1994) Organochlorine contamination in pinnepids. *Review of Environmental Contamination and Toxicology*, **136**, 123- 167.

Jepson, P.D., Bennett, P.M., Deaville, R., Allchin, C.R., Baker, J.R. & Law, R.J. (2005) Relationship between polychlorinated biphenyls and health status in harbor porpoises (*Phocoeca phocoena*) stranded in the United Kingdom. *Environmental Toxicology and Chemistry*, **24**, 238- 248.

Johnston, D.W., Frienlaender, A.S., Torres, L.G. & Lavigne, D.M. (2005) Variation in sea ice cover on the east coast of Canada from 1969 to 2002: climate variability and implications for harp and hooded seals. *Climate Research*, **29**, 209- 222.

Johnston, D.W., Meisenheimmer, P. & Lavigne, D.M. (2000) An evaluation of management objectives for Canada's commercial harp seal hunt, 1996 – 1998. *Conservation Biology*, **14**, 729- 737.

Johnston, P. and Santillo, D. (2005) The Canadian hunt: no management and no plan. Greenpeace http://www.greenpeace.org/international/press/reports/canadian-seal-hunt-no-managem

Khaemba, W.M. & Stein, A. (2001) Spatial statistics for modelling of abundance of wildlife species in the Masai Mara ecosystem, Kenya*. Environmental and Ecological Statistics*, **8**, 345- 360.

Kingsley, M.C.S. (1989) The distribution of hauled-out ringed seals and an interpretation of Taylor's law. *Oecologica*, **79**, 106- 110.

Kjellqwist, S.A., Haug, T. & Øritsland, T. (1995) Trends in age-composition, growth and reproductive parameters of Barents Sae harp seals, *Phoca groenlandica*. *ICES Journal of Marie Science*, **52**, 197- 208.

Kleivane, L., Espeland, O., Fagerheim, K.A., Hylland, K., Polder, A. & Skaare, J.U. (1997) Organochlorine pesticides and PCBs in the East ice harp seal (*Phoca groenlandica*) populations. *Marine Environmental Research*, **43**, 117- 130.

Kovacs, K.M., Lavigne, D.M. & Stewart, R.E.A. (1985) Early postnatal mortality in Northwest Atlantic harp seals (*Phoca groenlandica*). *Journal of Mammalogy*, **66**, 556- 558.

Lavigne, D.M. (1999) Estimating total kill of northwest Atlantic harp seals, 1994-1998. *Marine Mammal Science*, **15**, 871- 878.

Legendre, P., Dale, M.R.T., Fortin, M.J., Gurevitch, J., Hohn, M. & Myers, D. (2002) The consequences of spatial structure for the design and analysis of ecological field surveys. *Ecography*, **25**, 601- 615.

Lett, P.F. & Benjamin, T. (1977) A stochastic model for the management of the Northwestern Ataltnic harp seal population (*Pagophilus groenlandicus*) population. *Journal of the Fisheries Research Board of Canada,* **34**, 1155- 1187.

Lucas, Z. & Daoust, P-Y. (2002) Large increases of harp seals (*Phoca groenlandica*) and hooded seals (*Cystophora cristat*) on Sable Island, Nova Scotia, since 1995. Polar Biology*,* **25**, 562- 568.

Mizung, A.W., Wada, A., Ishinazaka, T., Hattori, K., Watanabe, Y. & Ohtaishi, N. (2002) Distribution and abundance of spotted seals *Phoca largha* and ribbon seals *Phoca fasciata* in the southern Sea of Okhotsk. Ecological Research, **17**, 79- 96.

Myers, R.A. & Bowen, W.D. (1989) Estimating bias in aerial surveys of harp seal pup production. *Journal of Wildlife Management*, **53**, 361- 372.

Myers, R.A., Hutchings, J.A. & Barrowman, N.J. (1997) Why do fish stocks collapse? The example of cod in Atlantic Canada. *Ecological Applications*, **7**, 91-106.

Nilssen, K.T., Haug, T., Grotnes, P.E. & Potelov, V. (1997) Seasonal variation in body condition of adult Barents seas harp seals (*Phoca groenlandica*). *Journal of Northwest Atlantic Fisheries Science*, **22**, 17- 25.

Øritsland, T. (1971) The status of Norwegian studies of harp seals in Newfoundland. *International Commission for the Northwest Atlantic Fisheries Redbook, Part III,* 185-209.

Perry, E.A., Stenson, G.B., Bartlett, S.E., Davidson, W.S. & Carr, S.M. (2000) DNA sequence analysis identifies genetically distinguishable populations of harp seals *Pagophilus groenlandicus*, in the northwest and northeast Atlantic. *Marine Biology*, **137**, 53- 58.

Pitcher, T.J., Buchary, E.A. & Sumaila, U.R. (2002) A synopsis of Canadian Fisheries. http://www.fisheries.ubc.ca/publications/reports/canada-syn.pdf

Potelov, V.A., Golikov, A.P. & Bondarev,V.A. (2003) Estimate pup production of harp seals (*Pagophilus groenlandicus*) in the White Sea, Russia, in 2000. *ICES Journal of Marine Science*, **60**, 1012- 1017.

Roff, D.A. & Bowen, W.D. (1986) Further analysis of population trends in the northwest Atlantic harp seal (*Phoca groenlandica*) from 1967 to 1985. *Candian Journal of Fisheries and Aquatic Science*, **43**, 553- 564.

Sergeant, D.E. (1991) Harp seals, man and ice. *Canadian Special Publications of Fisheries and Aquatic Sciences*, **114**, 1- 153.

Shaw, S.D., Brenner, D., Bourakovsky, A., Mahaffey, C.A. & Perkins, C.R. (2005) Polychlorinated biphenyls and chlorinated pesticides in harbor seals (*Phoca vitulina concolor*) from the northwestern Atlantic coast. *Marine Pollution Bulletin*, **50**, 1069- 1084.

Shelton, P.A., Stenson, G.B., Sjare, B. & Warren, W.G. (1996) Model estimates of harp seals numbers-at-age for the Northwest Atlantic. *NAFO Scientific Council Studies*, **26**, 1- 14.

Stenson, G.B., Hammill, M.O., Kingsley, M.C.S., Sjare, B., Warren, W.G. & Myers, R.A. (2002) Is there evidence of increase pup production in northwest Atlantic harp seals, *Pagophilus groenlandicus*. *ICES Journal of Marine Science*, **59**, 81- 92.

Stenson, G.B., Myers, R.A., Hammill, M.O., Ni, I-H., Warren, W.G. & Kingsley, M.C.S. (1993) Pup production of harp seals, *Phoca groenlandica*, in Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Science*, **50**, 2429- 2439.

Stenson, G.B., Riest, L.-P., Hammill, M.O., Gosselin, J.F. & Sjare, B. (2003) Estimating pup production of harp seals, *Pagophilus groenlandicus*, in the Northwest Atlantic. *Marine Mammal Science*, **19**, 141- 160.

Stewart, R.E.A. & Lavigne, D.M. (1980) Neonatal growth of northwest Atlantic harp seals, *Pagophilus groenlandicus*. *Journal of Mammalogy*, **61**, 670- 680.

Sullivan, M.G. (2003) Active management of walleye fisheries in Alberta: dilemmas of managing recovering fisheries. *North American Journal of Fisheries Management*, **23**, 1343- 1358.

Tayler, D.M., O'Keefe, P.G. & Fitzpatrick, C. (1994) A snow crab, *Chionoecetes opilio* (Decapoda, Majidae), fishery collapse in Newfoundland. *Fishery Bulletin*, **92**, 412- 419.

Trenkel, V.M., Buckland, S.T., McLean, C. & Elston, D.A. (1997) Evaluation of aerial line transect methodology for estimating red deer (*Cervus elaphus*) abundance in Scotland. *Journal of Environmental Management.* **50**, 39- 50.

Ugland, K.I. (1985) Abundance estimation of the Northwestern Atlantic harp seal population, *Polar Biology*, **4**, 187- 198.

Vincent, C., Fedak, M.A., McConnell, J.B., Meynier, L., Saint-Jean, C. & Ridoux, V. (2005) Status and conservation of the grey seal, *Halichoerus grypus*, in France. *Biological Conservation*, **126**, 62- 73.

Warren, W.G., Shelton, P.A. & Stenson, G.B. (1997) Qunatifying some of the major sources of uncertainty associated with harp seal prey consumption Part I: Uncertainty in the estimates of harp seal population size. *Journal of the Northwest Atlantic Fineries Science*, **22**, 289- 302.

Zitko, V., Stenson, G. & Hellou, J. (1998) Levels of organocholrine and polycyclic aromatic compounds in harp seal beaters (*Phoca groenlandica*). *The Science of the Total Environment,* **221**, 11- 29.