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LARGE DECLINE IN HOODED SEAL (*CYSTOPHORA CRISTATA*) PUP PRODUCTION OFF OF NORTHEASTERN NEWFOUNDLAND IN 2012 AND 2017

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ABSTRACT

Accurate data on population abundance is needed to monitor trends through time, especially for species that are commercially harvested or vulnerable to climate change related impacts. Hooded seals (*Cystophora cristata*) in the Northwest Atlantic whelp on drifting sea ice in three areas: Davis Strait, the southern Gulf of St. Lawrence and off of northeastern Newfoundland ("Front"), Canada, with the majority of whelping (>90%) occurring at the Front. They are harvested in Canada and Greenland but have not been assessed since 2005. Aerial surveys for harp seals (*Pagophilus groenlandicus*) took place at the Front in 2012 and 2017. These surveys also captured the vast majority of hooded seal whelping patches in these years and so were used to estimate hooded seal pup production at the Front. Pup production was estimated from photo (2012 and 2017) and visual (2017 only) line-transect surveys. Staging data from 2004, 2005 and 2017 were used to correct these estimates for the proportion of pups not born on the survey days, resulting in total pup production estimates of 41,129 (SE = 7,374) and 39,021 (SE = 18,334) pups in 2012 and 2017, respectively. This is a large decrease from the previous estimate, being 38% and 36%, respectively, of the pup production estimated on the Front in 2005. Extensive reconnaissance that failed to locate whelping hooded seals in Davis Strait (2024) or outside the traditional whelping area at the Front (2012, 2017), along with low sea-ice coverage in the Gulf of St. Lawrence makes it unlikely that significant whelping was redistributed to other areas. The large decline in pup production after 2005 mirrors a similar decline and continued low level of pup production for hooded seals in the Greenland Sea that occurred between 1997 and 2005/07. Although the cause of the decline in the Northwest Atlantic is unknown, it is possible that negative impacts of ecosystem change on female fecundity and juvenile survival, as has been documented for harp seals in the Northwest Atlantic, are also impacting hooded seals.

Keywords: hooded seal, pup production, aerial survey, sea-ice decline, Newfoundland and Labrador Shelf

INTRODUCTION

Population abundance and changes in abundance through time are central pieces of information for the successful management and conservation of species. This is especially true for species that are commercially harvested or at risk from disturbance, bycatch or ecological impacts due to climate change (e.g. Hammill & Stenson, 2007; Laidre et al., 2015). Species in northern regions face an extra degree of risk as polar regions are warming faster than other areas of the globe, with numerous changes in species distribution and abundance documented to date (Fossheim et al., 2015; Huntington et al., 2020; Kovacs et al., 2011). Declining trends in sea-ice extent and concentration are a concern for species dependent on sea ice for critical parts of their life cycle (Kovacs et al., 2011; Laidre & Regehr, 2018; Post et al., 2013).

Hooded seals (*Cystophora cristata*) are a northern phocid that breeds on drifting sea ice during March and spends the rest of the year in mostly open water in the north Atlantic and adjacent Arctic regions (Kovacs, 2018). Although hooded seals from different areas cannot be distinguished genetically, they are managed as two stocks, the Northwest (NW) Atlantic stock and the Greenland Sea stock (Coltman et al., 2007). The NW Atlantic stock whelps on drifting sea ice during March in three areas, in the southern Gulf of St. Lawrence ("Gulf"), off of north-eastern Newfoundland or southern Labrador ("Front") and in Davis Strait (Figure 1). The majority of the population whelps at the Front, although the exact proportion in the three whelping areas may vary slightly over time. All three areas have been surveyed simultaneously only once in 2005, with over 90% of the whelping occurring at the Front in this year (Table 1; Stenson et al., 2006). After whelping, female hooded seals nurse their pups for an average of four days, with constant attendance by the mother until weaning (Bowen et al., 1985; Lydersen & Kovacs, 1999). Limited VHF tagging indicates that weaned pups spend time in the water in the days after weaning and leave the whelping patch sometime after seven days (Salberg et al., 2008). After breeding, NW Atlantic hooded seals disperse to feed before moulting off of southeast Greenland in July. Males and females have different space-use patterns during this period in terms of migration routes and areas where they concentrate their time (Andersen et al., 2013; Bajzak et al.,

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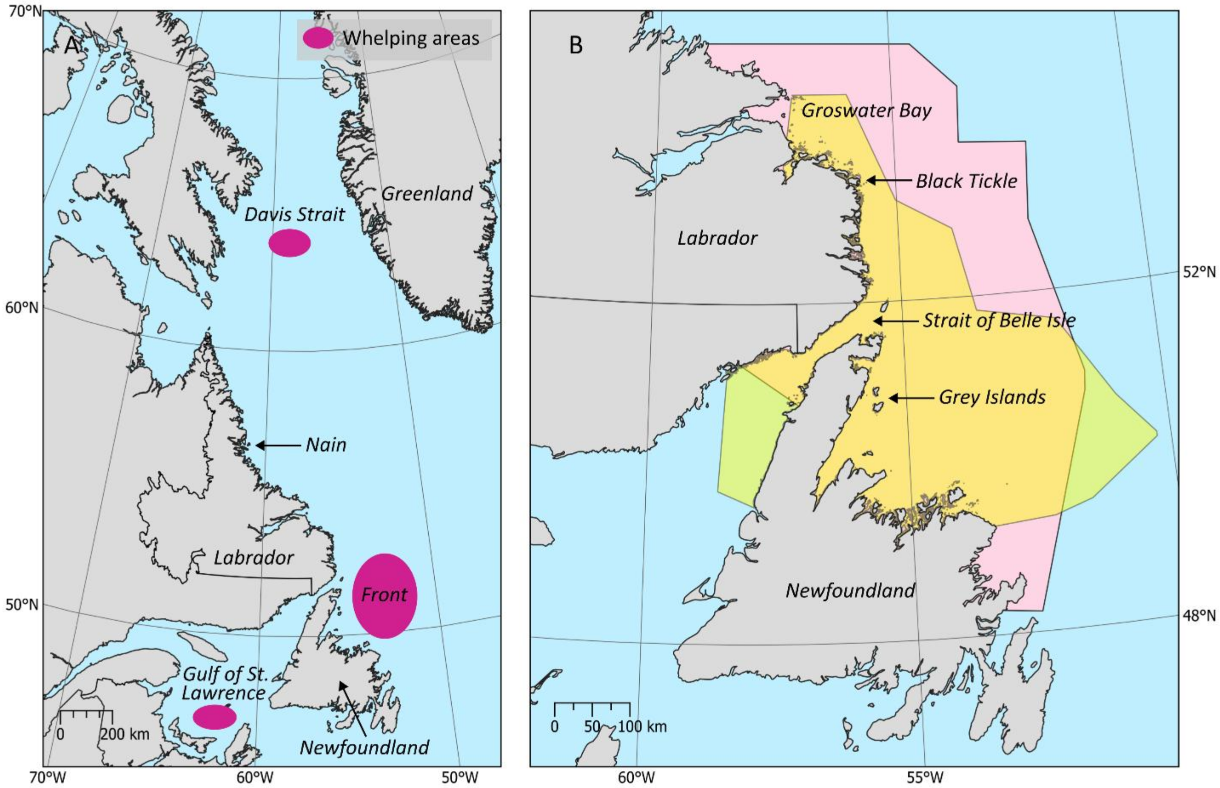

Figure 1. (A) Place names and whelping areas of hooded seals in the Northwest Atlantic and (B) area off of northeastern Newfoundland ("Front") covered by aerial surveys in 2012 and 2017 used for hooded seal pup production estimates. The areas covered by reconnaissance for the surveys are shown in pink (2012), green (2017) and yellow (both years).

2009; Vacquié-Garcia et al., 2024). Post-moult, hooded seals spend the remainder of the year in northern areas, generally over deep water (Andersen et al., 2009; Andersen et al., 2013; Sergeant, 1976a).

At the Front, hooded seals whelp on drifting sea ice similar to harp seals (*Pagophilus groenlandicus*) with the two species found in the same general area (Mansfield, 1967; Sergeant, 1991). The degree of separation between hooded and harp seals varies interannually depending on the sea-ice extent. Historically, hooded seals at the Front were found in slightly heavier ice and closer to the ice edge than harp seals (Lydersen & Kovacs, 1999; Mansfield, 1967; Stenson et al., 1991). However, in recent years the amount of separation has decreased with the two species being intermixed to variable extents in the whelping areas (Stenson et al., 2006).

Table 1. Pup production estimates and 95% confidence intervals from aerial surveys for hooded seals in the Northwest Atlantic for the three whelping areas.

Year	Front	Gulf	Davis Strait	Reference
1984	62,400 (43,700-89,400)		19,000 (14,000-23,000)	Bowen et al., 1987
1990	83,100 (58,208-107,992)	1,638 (725-2,551)		Hammill et al., 1992; Stenson et al., 1997
1991		2,006 (1,634-2,378)		Hammill et al., 1992
1994		3,978 (2,069-5,887)		Hammill et al., 1997
2004	123,862 (87,328-160,396)	1,388 (SE=298)		Stenson et al., 2006
2005	107,013 (92,199-121,827)	6,620 (3,288-9,952)	3,346 (414-7,731)	Stenson et al., 2006
2012	41,129 (26,676-55,582)			This paper
2017	39,021 (3,086-74,956)			This paper

Hooded seals have been subject to a commercial and subsistence hunt throughout their range. Catch data from 1895 onwards are available for the commercial harvest in Newfoundland and Labrador (ICES, 2023a; Sergeant, 1974; Stenson, 2006). Quotas were implemented for hooded seals at the Front in 1974 and the commercial catch of bluebacks (i.e. hooded seal pups up to two years old) was banned in 1987 (Stenson, 1994). Since the early 2000s, the quota was set using the Atlantic Seal Management Strategy (Hammill & Stenson, 2003). Starting in 2016, the Canadian quota for hooded seals has not been announced with the catch monitored by Fisheries and Oceans Canada through daily hail ins and compared to scientific recommendations (ICES, 2023a). During this time the catch decreased from tens of thousands in the early 1900's to less than 3,000 after 1982 (with four notable exceptions in 1991, 1996-1998) and lowered further to less than 160 since 2005 (mean = 27, SD = 41), after accounting for struck and loss (ICES, 2023a; Sergeant, 1974; Stenson, 2006). Catch history in Greenland is available from 1954 although recent catch reports are generally delayed by a few years. Catches were generally between 5,000-20,000 since 1975, decreasing to between 2,000-6,500 after 2007, after accounting for struck and loss (ICES, 2023a; Stenson, 2006). The majority of total NW Atlantic hooded seal catches have occurred in Greenland since 1983, with the exception of 1996 and 1998 (ICES, 2023a; Stenson, 2006).

Estimating the abundance of hooded seals is difficult as for most of the year hooded seals are dispersed over a large area. Large, predictable concentrations only occur during the whelping and moulting periods. In past decades, abundance of the NW Atlantic and the Greenland Sea stocks of hooded seals have been estimated from a combination of pup production surveys and population models (e.g. Biuw et al., 2022; Stenson et al., 2006; Øigård et al., 2014) The last range-wide survey for hooded seals in the NW Atlantic occurred in 2005 with an estimated total population size of 593,500 seals (95% CI: 465,600–728,300; Hammill & Stenson, 2006). At this time, 91.5% of pups were born at the Front (107,013 pups, SE = 7,558), 5.7% in the Gulf (6,620 pups, SE = 1,700) and 2.9% in Davis Strait (3,346 pups, SE = 2,237; Stenson et al., 2006). This was the only range-wide survey to occur for hooded seals in the NW Atlantic although portions of the range were surveyed in previous decades. Aerial surveys to estimate pup production occurred at the Front in 1984, 1990 and 2004, with 62,400, 83,100 and 123,900 pups, respectively, estimated (Bowen et al., 1987; Stenson et al., 1997; Stenson et al., 2006). In the Gulf, aerial surveys occurred in 1990, 1991, 1994 and 2004, with 1,638, 2,006, 3,978 and 1,388 pups estimated, respectively (Hammill et al., 1992; Hammill et al., 1997; Stenson et al., 2006). The 2004 estimate in the Gulf was considered negatively biased (Stenson et al., 2006). The Davis Strait whelping patch had previously been surveyed in 1984 with 19,000 pups estimated (Bowen et al., 1987). Pup production likely increased at the Front and in the Gulf but decreased in Davis Strait between the 1980s and 2005, although uncertainties in the degree of transfer of females among the different whelping patches makes it difficult to confirm trends. Tag returns and satellite tag data indicate that seals from the three NW Atlantic whelping areas use a common moulting area off of southeast Greenland, mix during the non-breeding period and that there is also limited mixing between the NW Atlantic and Greenland Sea stocks during the non-breeding period (Andersen et al., 2013; Stenson & Sjare, 1996). Genetic analysis using microsatellites did not find significant differences between whelping patches in the NW Atlantic indicating that some exchange may occur, but the magnitude of all exchange is currently unknown (Coltman et al., 2007).

Aerial surveys to estimate the pup production of harp seals occur approximately every five years in the NW Atlantic (e.g. Stenson et al., 2014; Stenson et al., 2022). As the degree of overlap between harp and hooded seal whelping patches varies interannually, the extent to which the harp seal survey covers the majority of hooded seal whelping patches may vary among survey years. For example, the harp seal surveys in 2012 and 2017 covered the vast majority of hooded seal whelping patches while the 2022 survey did not, due to a combination of unfavourable weather for flying surveys and logistical constraints. In years when harp and hooded seals do overlap, it may be possible to obtain reasonable estimates of hooded seal pup production from data collected during the harp seal surveys. Updated abundance information on hooded seals is needed as they are a commercially harvested species in Canada, have not been surveyed since 2005 and major changes in the NW Atlantic ecosystem have occurred. Using past harp seal aerial surveys, hooded seal pup production was estimated for the Front for 2012 and 2017 and compared to pup production estimates from 2005. The extent to which relocation from the Front to other whelping patches may have occurred was also examined by reconnaissance in Davis Strait.

MATERIALS AND METHODS

Aerial surveys

Surveys to assess harp seal pup production were conducted off of north-eastern Newfoundland ("Front") during March in 2012 and 2017. Hooded seals were also included in the aerial surveys and staging data were obtained for hooded seals when possible. These surveys are described in detail in Stenson et al. (2014; 2022). Briefly, reconnaissance of traditional whelping areas as well as areas further north up to Groswater Bay, Labrador using fixed-wing aircraft and helicopters was used to discover whelping patches in areas of drifting pack ice. VHF (2012 only) and GPS beacons (2012 and 2017) were deployed in the whelping patches in order to track the movement of the ice over time.

A visual survey of two hooded seal whelping patches was carried out in 2017 (March 22) and photographic surveys were conducted in both 2012 (March 14 and 16) and 2017 (March 14, 18 and 19). Both visual and photographic surveys were based on a systematic sampling design with a single random start and the sampling unit was a transect of variable length. The transects were spaced from 1.85-13.8 km (1-8 NM) depending on patch configuration with each area of homogenous transect distance treated as a separate survey.

For the visual survey, a Bell 429 helicopter was flown at a height of 61 m. Two observers seated in the right and left rear forward-facing seats counted all pups within a pre-measured strip of 30 m out of their respective side of the helicopter, for a total strip width of 60 m. Pup counts were recorded by each observer on a laptop using custom software which recorded a GPS-location and time for each pup sighted and whether it was with its mother (attended) or alone/presumed weaned (unattended/solitary).

For the photographic surveys, a fixed-wing aircraft was flown at 330 m altitude and 110 knots, giving an image footprint of 215 m along the flight line and 325 m across the flight line. Surveys were designed so that along a transect line there was no overlap between photographs with photograph coverage generally >90%. The resolution of the photographs was approximately 2.4 cm. Photographs were read in ArcGIS (2012; ESRI, Redlands, California) or qGIS (2017; https://www.qgis.org) with each hooded seal pup marked. Readers also noted if the pup was attended or unattended.

The photographic surveys on March 18 and 19, 2017 were treated as a single survey, as each day covered adjacent portions of the total surveyed area. To account for a small area of overlap between the two survey days, 8,872 m (74 photos and 13 pups) and 33,216 m (133 photos and 83 pups) were removed from the eastern side of the two southernmost transects on March 18, 2017. Abundance and variance were estimated for each area of homogenous transect spacing on each survey day as in Stenson et al. (2022).

Temporal distribution of births

The number of hooded seal pups counted on the ice needs to be corrected for pups that were not born yet at the time of the survey or that have already left the survey area after weaning. Two types of staging data were available for the 2012 and 2017 surveys. In 2012, hooded seal pups were staged as mother/pup pairs (attended) or solitary pups. In 2017, pups were staged in one of two ways; either staging in one of two classes (attended and solitary) or in one of four classes (newborn, thin, fat and solitary). Two-class staging data cannot be used to create a staging model to correct for pups born after the survey or that have left the survey area but can be used to give a rough understanding of whelping phenology. Previous hooded seal surveys used the four-class staging data to correct pup numbers for pups born after the survey or that have left the survey area (e.g. Bowen et al., 1987; Stenson et al., 2006; Øigård et al., 2014). However, the four-class staging data from 2017 were limited and began one day before the first survey, which caused difficulties in creating a staging model using only data from 2017. Four-class staging data were also available for the Front from hooded seal surveys in 2004 and 2005 (Stenson et al., 2006). Comparison of the available four-class staging data from 2004, 2005 and 2017 in addition to the two-class staging data from 2012, 2017 and the surveys themselves (which marked whether the pups were attended/solitary) did not indicate that any shift in whelping phenology occurred between 2004 and 2017. Near-yearly surveillance of harp and hooded seals in the Front in March also supports the premise that whelping phenology of hooded seals has not shifted (DFO, unpublished data). Therefore, the four-class staging data from 2004, 2005 and 2017 were combined and used to correct pup numbers for pups born after the survey in both 2012 and 2017 (Table 2). Combining the data not only increased the amount of staging data available but also increased the temporal coverage of the whelping and nursing period (2004: Mar 9-22; 2005: Mar 11-23; 2017: Mar 13-26; Stenson et al., 2006).

The combined four-class staging data from 2004, 2005 and 2017 were used in a Bayesian birth distribution model recently developed for grey seals in the NW Atlantic (*Halichoerus grypus*; Mosnier et al., 2023) and modified for hooded seals. The Bayesian birth distribution model was run in R version 4.3 (R Core Team, 2023). The Bayesian model for hooded seals has five stages, including stage 0 representing the birth period, three developmental stages during the lactation period (newborn, thin and fat) and a final stage representing solitary pups who leave the ice after a specified period of time. Gamma distributions were used to represent the temporal distribution of births and the durations of each stage. The Gamma distributions for stage durations all shared a shape parameter but had a separate rate parameter to reduce the number of parameters in the model. Priors for the shape and rate parameters were chosen based on Mosnier et al. (2023) and the duration of hooded seal stages in past work (Table 3). Bowen et al. (1987) estimated the duration of the thin (1.15 d, SE = 0.053) and fat (2.36 d, SE = 0.107) stages. Insufficient information was available for the newborn stage but observations from harp and grey seals suggest that it is approximately three hours long (Bowen et al., 1987). Based on a limited amount of tagging data, Salberg et al. (2008) estimated that solitary hooded seal pups leave the ice after approximately seven days.

The transitions between the different stages were described as the sum of the gamma distributions representing the temporal distribution of birth and stage durations. The Welch-Satterthwaite approximation was used to estimate parameters of the transition Gamma distributions (sum of Gamma distributions is also a Gamma distribution; Satterthwaite, 1946; Welch, 1947). The Bayesian model generates the proportion of pups in each stage over time based on the transition distributions. The Dirichlet-Multinomial link fits the time series produced by the model to the staging data available for the

Table 2. Total count of the number of hooded seals pups observed at the Front in each developmental stage in staging transects conducted in 2004, 2005 and 2017.

Date	Newborn	Thin	Fat	Solitary
Mar 9	10	125	14	2
Mar 10	18	128	25	5
Mar 12	1	613	68	31
Mar 13	6	35	10	9
Mar 14	0	383	75	44
Mar 16	0	37	193	200
Mar 17	13	656	313	441
Mar 18	0	145	75	125
Mar 19	0	25	100	295
Mar 20	12	331	255	377
Mar 22	0	185	391	2258
Mar 23	0	30	170	83
Mar 24	0	54	59	476
Mar 26	0	13	35	13

Table 3. Bayesian hooded seal staging model information including the prior shape and rates for the four stages and the model output including the estimated duration, shape and rate of the four stages and the sum of the first three stages (estimated duration of the nursing period).

Stage	Shape (prior)	Rate (prior)	Duration (d; mean ± SD; est)	Shape (mean ± SD; est)	Rate (mean ± SD; est)
1; Newborn	15	40	0.36 ± 0.10	14.98 ± 1.38	41.02 ± 1.53
2; Thin	15	13	1.72 ± 0.45	14.98 ± 1.38	8.72 ± 1.19
3; Fat	15	6.3	1.94 ± 0.47	14.98 ± 1.38	7.45 ± 1.10
4; Solitary	15	2.25	8.19 ± 13.28	14.98 ± 1.38	3.09 ± 1.83
Sum (Newborn – Fat)			4.02 ± 0.56		

survey time period. The Dirichlet-Multinomial link converts variability in the staging data into variance around the estimates. Three main sources of variability were present in the staging data used in the model herein: (1) variability among the observers; (2) spatial variability (variability among locations on the same date) and (3) any inter-annual variability in the combined dataset.

As the date of first birth was not observed, the day of first birth was estimated as March 7 based on the available staging data and visual observations. The day of first birth was a fixed model parameter to assist in model convergence.

The results from the Bayesian staging model were used to correct the pup counts on each survey day in both the 2012 and 2017 surveys. For the combined survey on March 18 and 19, 2017, the proportion born was calculated as a weighted mean based on the number of pups counted in photographs from each day. As the uncorrected pup abundance and staging results are independent estimates, the variance for the corrected pup abundance was calculated as per Mood et al. (1974) (see also Stenson et al., 2022). The total estimated pup abundance for 2012 and 2017 was based on a weighted mean of the estimates from each survey day, weighted by their respective variance (Stenson et al., 2022).

Davis Strait Reconnaissance

Reconnaissance flights to locate whelping hooded seals in Davis Strait and determine if a major redistribution of hooded seal whelping has occurred, took place from March 17-21, 2024, to match when whelping patches in Davis Strait have been discovered in previous decades (Bowen et al., 1987; Sergeant, 1974, 1976b, 1977; Stenson et al., 2006). A King Air aircraft equipped with a WESCAM MX-10 EO/IR camera system with a continuous, long-distance zoom was used to fly the reconnaissance. The sea-ice edge from 60-66.5° N and six transects across the ice edge were flown at a mean altitude of 900 m (range = 130–1550 m) to check for whelping hooded seals. Lower altitudes were flown as needed to descend beneath cloud cover. Experienced marine mammal observers also inspected the ice out the port and starboard windows to locate seals when the altitude was less than 457 m, with ~30% of the survey covered with both methods. The higher altitude was preferred to increase the area that could be covered on each flight given the distance to the nearest Canadian airport (515-635 km) and the aircraft's range.

RESULTS

2012

Sea-ice conditions in 2012 were below the long-term average (1968-2011; Stenson et al., 2014). Hooded seal mother pup pairs were first observed at the Front on March 6 northeast of Black Tickle (~53° N, 55° W) and off the northern tip of Newfoundland (~51.5° N, 54° W). GPS beacons were deployed in the areas where whelping seals were found and used to track the movement of the ice south. The locations of the beacons on March 14 and 16 verified that the entire whelping area as well as the surrounding area were surveyed on both dates (Figure 2). On March 14, 28 transects were flown with 7,480 m (4 NM) spacing, with 531 pups counted on 8,395 photos (Figure 2). This resulted in an estimated pup production of 12,663 pups (SE = 1,603, CV = 0.13; Table 4). On March 16, 20 transects were flown with 11,112 m (6 NM) spacing (Figure 2). 827 pups were counted on 6,220 photographs, resulting in an estimated pup production of 29,653 pups (SE = 6,909, CV = 0.23; Table 4).

2017

The coverage of first year ice in southern Labrador in 2017 was similar to coverage observed in 2012 (Stenson et al., 2022). The main hooded seal whelping patch was first observed on March 6 near the Grey Islands (51.00° N, 55.00° W, Figure 1B). GPS beacons were deployed throughout the patch and were used to track its movement as it drifted and its area expanded. The main hooded seal whelping patch was located near the centre of all areas surveyed (beacons I, J, K and P; Figure 3). The locations of the beacons confirmed that the main hooded seal patch as well as the surrounding areas were surveyed three times, March 14 (photographic), March 18/19 (photographic) and March 22 (visual). March 18 and 19 are considered as a single survey as they covered adjacent areas of the larger patch, with a minimal amount of overlap.

On March 14, 12 transects were flown with 7,408 m (4 NM) spacing, with 788 pups counted on 5,028 photos (Figure 3). This resulted in an estimated pup production of 16,733 pups (SE = 6,092, CV = 0.36; Table 4). Seventeen transects were flown with two spacings (7,408 m (4 NM) and 3,704 m (2 NM)) on March 18. After a total of 207 photos were removed from the eastern edge of the two southernmost transects to account for overlap in the photographed area between March 18 and 19, 195 pups

Table 4. Overview of the photographic and visual line transect surveys to estimate hooded seal pup production at the Front in 2012 and 2017.

Year	Date	Survey type	Number of transects	Transect spacing (m)	Number of pups	Number of photos	Proportion attended	Estimated number of pups
2012	Mar 14	Photographic	28	7,408	531	8,395	91%*	12,663 (SE = 1,603; CV =0.13)
	Mar 16	Photographic	20	11,112	827	6,220	91%*	29,653 (SE=6,909; CV=0.23)
2017	Mar 14	Photographic	12	7,408	788	5,028	86%	16,733 (SE=6,092; CV=0.36)
	Mar 18	Photographic	17	3,704; 7,408	195	5,740	78%	3,652 (SE=689; CV=0.19)
	Mar 19	Photographic	11	14,816	722	5,945	71%	31,060 (SE=15,473; CV=0.50)
	Mar 18/19				917	11,685	73%	34,712 (SE=15,488; CV=0.45)
	Mar 22	Visual	39	1,852; 3,704	489	-	45%	25,866 (SE=3,169; CV=0.12)

*Proportion attended based on a sub-sample of pups from each day. March 14: 342 of 531 (64%) pups; March 16: 605 of 827 (73%) pups with attended/unattended data.

were counted on 5,740 photos, resulting in an estimated pup production of 3,652 pups (SE = 689, CV = 0.19; Table 4, Figure 3). On March 19, 11 transects were flown at 14,816 m (8 NM) spacing, with 722 pups counted on 5,945 photographs (Figure 3). This resulted in an estimated pup production of 31,060 pups (SE = 15,473, CV = 0.50, Table 4). Combining the estimates from March 18 and 19 resulted in a pup production of 34,712 pups (SE = 15,488, CV = 0.45; Table 4). On March 22, a total of 39 visual survey transects were flown at two different whelping patches at spacings of 3,704 m (2 NM) and 1,852 m (1 NM). The observers counted a total of 489 pups, resulting in an estimated pup production of 25,866 pups (SE = 3,169, CV = 0.12; Table 4).

Temporal distribution of births

Staging data were available for 14 days between March 9 and 26 after combining the available four-class staging data from 2004, 2005 and 2017, which covers the vast majority of the whelping and nursing period at the Front (Table 2). Solitary pups reached around 50% of staged pups just after mid-March but this showed some variability towards the end of March with the majority of staged pups being attended pups (stages 1 to 3) on March 23 and 26. These two dates also had a smaller number of pups surveyed than the surrounding dates when solitary pups were the largest proportion of the pups staged (Table 2).

The Bayesian model estimated that the duration of the nursing period (newborn, thin and fat stages) was 4.02 d (SD = 0.56 d; Table 3) and that 50% of pups were born by March 14 (95% CI: March 11–19; Figure 4). The Bayesian model estimated that the proportion born on the March 14 to 22 surveys days ranged from 49% (95% CI: 19%–77%) to 92% (95% CI: 69%–99%; Table 5, Figure 4). These proportions were used to correct the pup production estimates to account for the pups not yet born when the survey took place (Table 5). The proportion of attended or unattended pups on the different survey days (Table 4) were generally inside the confidence intervals from the Bayesian model of the proportion of pups in the different stages on the respective day (Figure 4).

Total pup production

For 2012, a total pup production of 41,129 pups (SE = 7,374, CV= 0.18) was estimated from a weighted average of the March 14 and 16 estimates after correcting for the temporal distribution of births (Table 5). For 2017, a total pup production of 39,021 pups (SE = 18,334, CV = 0.47) was estimated from a weighted average of the March 14, 18/19 and 22 estimates after correcting for the temporal distribution of births (Table 5).

Davis Strait Reconnaissance

Six reconnaissance flights were flown from March 17–21, 2024 to look for whelping hooded seals in Davis Strait (Figure 5). Three flights were flown to cover the sea-ice edge from 61–66.5° N on March 17-18. An additional three flights were used to complete six transects across the sea-ice edge at 62–65.5° N latitude at 0.5° increments on March 20–21. Overall, a distance of 2,250 km was surveyed for hooded seals, covering an area of ~23,500 km^2. No hooded seals or traces of whelping patches were seen on any of the flights.

DISCUSSION AND CONCLUSIONS

Hooded seal pup production at the Front was estimated as 41,129 (SE = 7,374) and 39,021 (SE = 18,334) pups in 2012 and 2017, respectively, which are the two lowest estimates of pup production at the Front since surveys began in 1984. This is a large decrease from the 107,013 pups (SE = 7,558) estimated to have been born at the Front in 2005 (Stenson et al., 2006), with the 2012 and 2017 estimates being 38% and 36% of the 2005 estimates, respectively. The new estimates are also less than the pup production at the Front estimated in 1984 (62,400) and in 1990 (83,100) (Bowen et al., 1987; Stenson et al., 1997). Although it is possible that a small number of hooded seals at the Front were missed, it is believed that these numbers represent a true decrease in hooded seal pup production at the Front, where the vast majority of whelping in the NW Atlantic occurs. Whelping hooded seals were also observed during the harp seal survey at the Front in 2022 and while it was not possible to get a numerical estimate of pup production, experienced observers considered the number to be similar to that seen in 2012 and 2017, suggesting that the lower pup production has persisted. The sharp decline is similar to trends observed for hooded seals in the Greenland Sea where pup

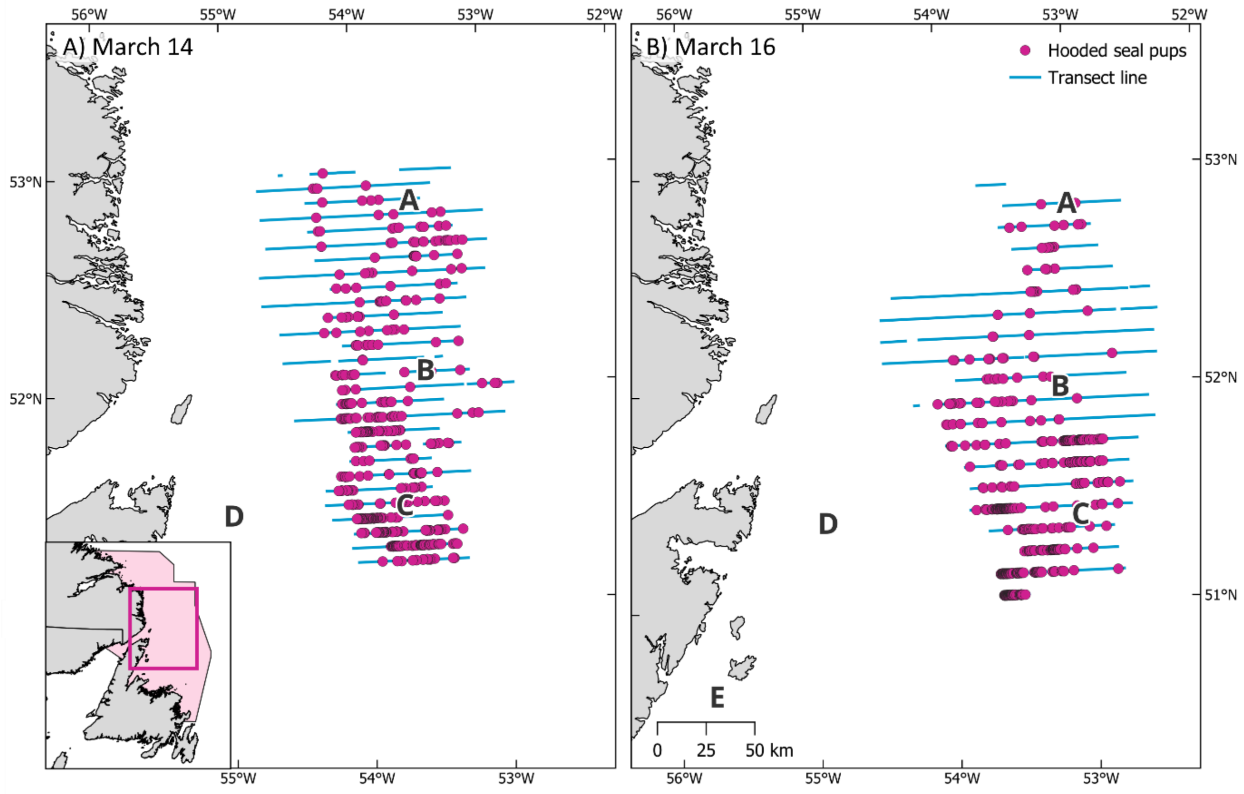

Figure 2. Hooded seal pup production surveys on the Front in 2012 showing the transect lines and locations of photographed hooded seal pups on (A) March 14 and (B) March 16. The letters on the maps denote the locations of the GPS beacons on each survey day. The light pink polygon in the locator map shows the area covered by reconnaissance.

production sharply declined between 1997 and 2005/2007, remaining at a low level up to the last survey in 2022 (ICES, 2023a).

It is unlikely that large whelping patches at the Front were missed during the 2012 and 2017 surveys. Weather permitting, daily, systematic reconnaissance took place from the coastal to seaward edge of the ice pack over the course of the entire survey effort, covering the traditional whelping areas at the Front (northeast coast of Newfoundland) and extending north of the traditional whelping area to Groswater Bay, Labrador in both years (Figure 1). Over the survey period, much of this ice was examined multiple times to account for drifting ice that originated north of the reconnaissance area. In 2010, when sea-ice extent was less than in 2012 and 2017, a harp seal whelping patch, but no hooded seals, was found north of traditional whelping areas but in 2012 and 2017 extensive reconnaissance found no evidence of pupping north of traditional whelping areas by hooded or harp seals. A variable and sometimes high proportion of hooded seals can also whelp outside of the main whelping patches, with estimates ranging from 17% to 43% depending on survey year (e.g. Bowen et al., 1987; Stenson et al., 1997). To ensure that scattered hooded seals were not missed, the survey designs in 2012 and 2017 covered large areas outside of the main concentrations of seals at the Front (Stenson et al., 2014, 2022) (Figures 2 & 3).

The NW Atlantic stock of hooded seals whelps in three locations, the southern Gulf of St. Lawrence, the Front and in Davis Strait. Traditionally, the Front has had the largest proportion of hooded seal pups, with over 90% of total pup production occurring here in 2005. Understanding the relative proportions in the three whelping areas and how this may have changed over time is however constrained by the limited number of times more than one whelping patch was surveyed in the same year (Table 1) (Stenson et al., 2006). The degree to which the three whelping areas are connected is currently unknown, but it is unlikely that the lower pup production at the Front in 2012 and 2017 is due to a large number of pregnant hooded seals relocating to the other two whelping areas. The number of hooded seals that pup in the Gulf has always been small which is what led to a ban on hunting in the area since 1964 (Table 1). Seal researchers working in the Gulf have not observed any large increase in the number of hooded seals in the area (GBS, M. Hammill, personal communication). Sea-ice extent has drastically decreased in the Gulf of St. Lawrence. There is evidence to indicate that harp seals that used to whelp in the southern Gulf of St. Lawrence have moved to the Front in some years, with the proportion of harp seals born in the southern Gulf of St. Lawrence declining from 25-30% historically to less than 2% in 2017 (Stenson, Haug, & Hammill, 2020). It is possible that the same phenomenon may have occurred for hooded seals with extensive reconnaissance of suitable ice in the Gulf during March 2017 observing no hooded seals although small numbers of hooded seal pups were observed after 2017 (DFO, unpublished data). Although future surveys will be needed to provide an accurate estimate of the number of hooded seals currently whelping in the Gulf, there is no evidence that it has substantially increased to account for the decline in pupping at the Front.

Although sea ice in Davis Strait appears to be suitable for whelping, it is unlikely that the majority of whelping in the NW Atlantic now occurs in this northern whelping area. Pup production in Davis Strait decreased from ~19,000 in 1984 to only 3,346 pups in 2005. It is unlikely that the 2005 pup production was greatly underestimated as reconnaissance in Davis Strait in 2003 also found only a limited number of hooded seals in the area (DFO, unpublished data). Furthermore, no hooded seals were seen during reconnaissance of Davis Strait in 2024 in an effort to determine if large numbers of hooded seals had relocated to this whelping area. Although it is possible that the 2024 reconnaissance may have missed some small groups of hooded seals, the lack of sightings makes it very unlikely that a redistribution of pregnant females and attendant males of the magnitude needed to account for the loss of 60,000 pups from the Front has occurred. It is also unlikely that hooded seal whelping has relocated north of the traditional whelping areas along the Front to along the Labrador coast. Extensive reconnaissance for the 2012 and 2017 surveys occurred up to Groswater Bay, Labrador and did not find hooded seals north of the traditional area. Reconnaissance from the north-east coast of Newfoundland to Nain, Labrador that occurred in March 2024 in preparation for the opening of the commercial seal harvest also did not find any hooded seals north of the traditional whelping area at the Front (DFO, unpublished data). Future reconnaissance efforts will be needed in these areas to validate the lack of sightings in 2024. It is also highly unlikely that whelping females from the Front relocated to the Greenland Sea whelping patch as there are no signs of increased pup production in this latter area after 2005. Pup production in the Greenland Sea greatly decreased between 1997 and 2005/2007 and has remained at a low level, between 10,000 and 15,000 pups, in the three surveys that occurred between 2012 and 2022 (Biuw et al., 2022, ICES, 2023a).

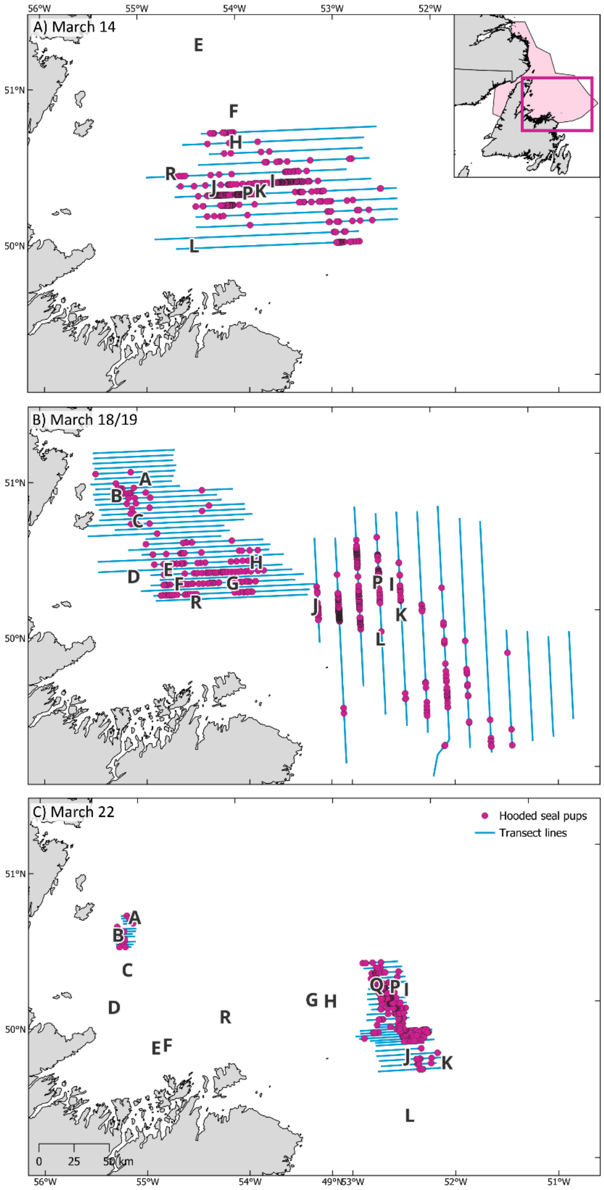

Figure 3. Hooded seal pup production surveys on the Front in 2017 showing the transect lines and locations of hooded seals pups on (A) March 14, (B) March 18 and 19 and (C) March 22. The letters on the maps denote the locations of the GPS beacons on each survey day. The light pink polygon in the locator map shows the area covered by reconnaissance.

The final estimate of hooded seal pup production is sensitive to the staging curve and the proportion of births assumed to have occurred on the different survey dates. Available four-class staging data for 2012 and 2017 were absent and limited, respectively, which caused difficulties in making a separate staging model for each year. Staging data were also only available from March 13 in 2017 (one day before the first survey), which caused issues in estimating the proportion of pups born on the March 14 survey date when using only staging data from 2017. Staging data were also available from the 2004 and 2005 hooded seals surveys at the Front, beginning on March 9 (Stenson et al., 2006). Comparison of data from 2004, 2005 and 2017 suggested that whelping phenology did not display a shift in this 13-year time interval, enabling the staging data from the 2004, 2005 and 2017 surveys to be grouped for use in the staging model herein. In the absence of four-stage staging data for 2012, it is assumed that the temporal birth distribution could be described using the combined data from 2004, 2005 and 2017 and so the staging model was also applied to the 2012 survey. The available attended/unattended proportions from the four years, both from the staging data and the surveys, were generally inside the confidence intervals of the staging model. This increased confidence in the assumption that whelping phenology was similar over the 13-year time period and that it was reasonable to use a model that included data from the three years. Determining the degree of interannual variation in the timing of births will require additional surveys. If the assumption of similar phenology between 2004 and 2017 was incorrect, then the corrected estimates of pup production are either positively or negatively biased. If more pups had been born by the survey dates then estimated by the staging model (i.e. whelping started earlier in 2017 than in 2004), an overestimate in total pup production would result and the decline in pup production would be greater than shown herein. Similarly, if less pups had been born by the survey dates (i.e. whelping started later in 2017 than in 2004), then the estimated total pup production would be an underestimate and the decline in pup production after 2005 would be of a smaller magnitude. However, given the scale of decline (~65%) noted in this study, a large shift in phenology would be needed to change the trajectory to either stable or increasing pup production and while the staging data from 2012 and 2017 are limited, they suggest that such a sizeable shift in phenology has not occurred. The presence of a large proportion of attended pups on March 23 and 26 suggests that a second pulse of whelping may have occurred around mid-March.

However, the staging data on March 23 and 26 included only 283 and 61 pups in total, respectively, while the larger samples of staging data on March 22 (2,384 pups) and 24 (589 pups) are both dominated by solitary pups. Whether the higher proportion of attended pups on March 23 and 26 is due to the small sample size, a limited second pulse of whelping or to solitary pups beginning to leave the whelping area and thus no longer being detected is unclear.

Although a shift in the timing of pupping has been found for grey and harbour seals (*Phoca vitulina*) in the NW Atlantic over the last three decades, the timing of birth of harp seals has not changed (Bowen et al., 2003; Bowen et al., 2020; Stenson, Haug, & Hammill, 2020). Harp seals in the Gulf historically whelp approximately one week earlier than at the Front (Sergeant, 1991; Stenson et al., 2022). While some early whelping has been observed at the Front over the past decade, this appears to be due to the redistribution of harp seals from the Gulf to the Front in response to absent or very low sea-ice concentration in the Gulf rather than a shift in phenology. No difference in the timing of whelping for hooded seals between the Gulf and Front has ever been documented.

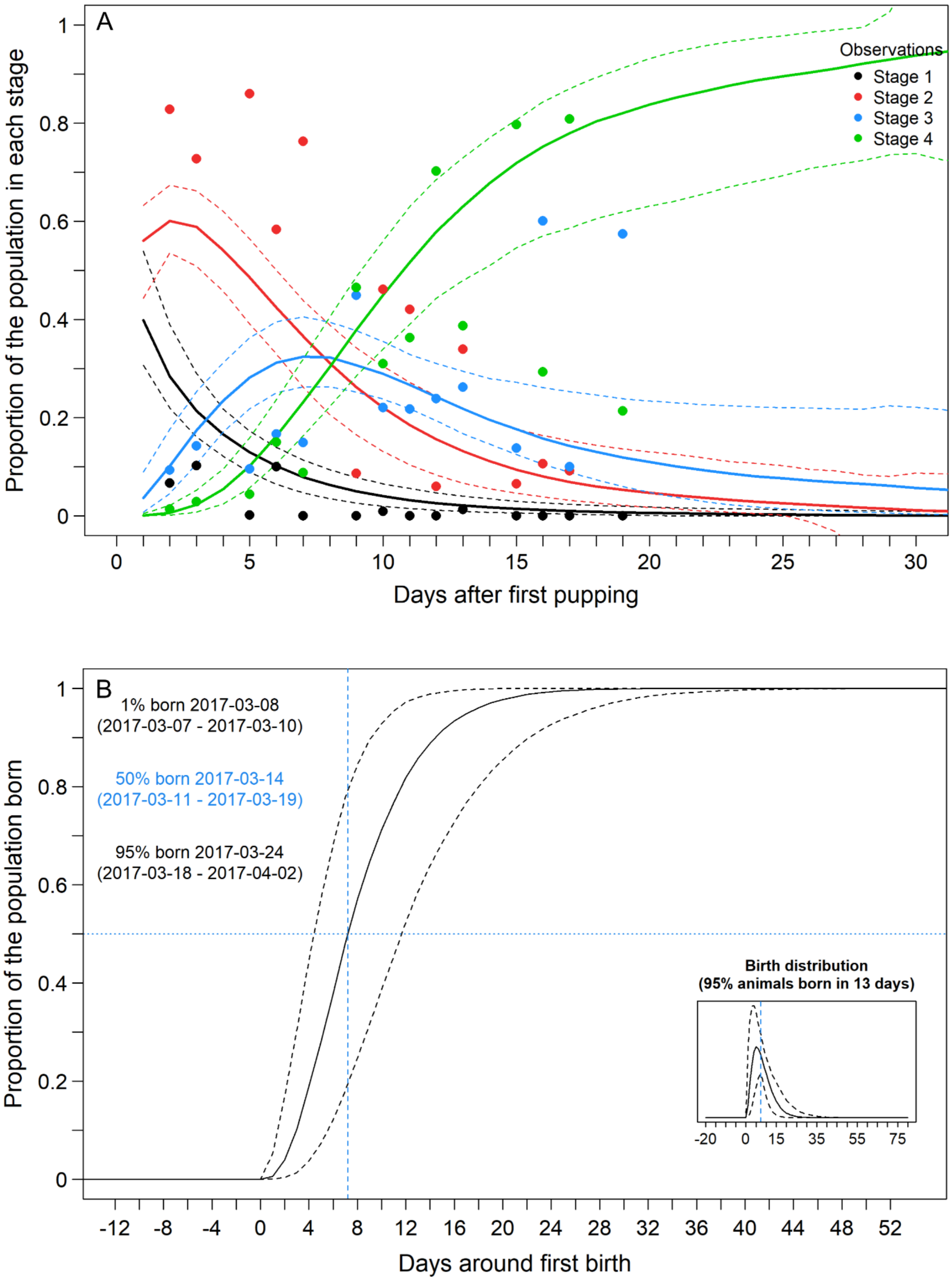

Figure 4. Output of the Bayesian staging model for hooded seal pup production at the Front showing (A) the proportion of pups in each stage after the day of first pupping (March 7) including staging data (observations) and model estimates and (B) the proportion of the population born after the day of first birth (March 7).

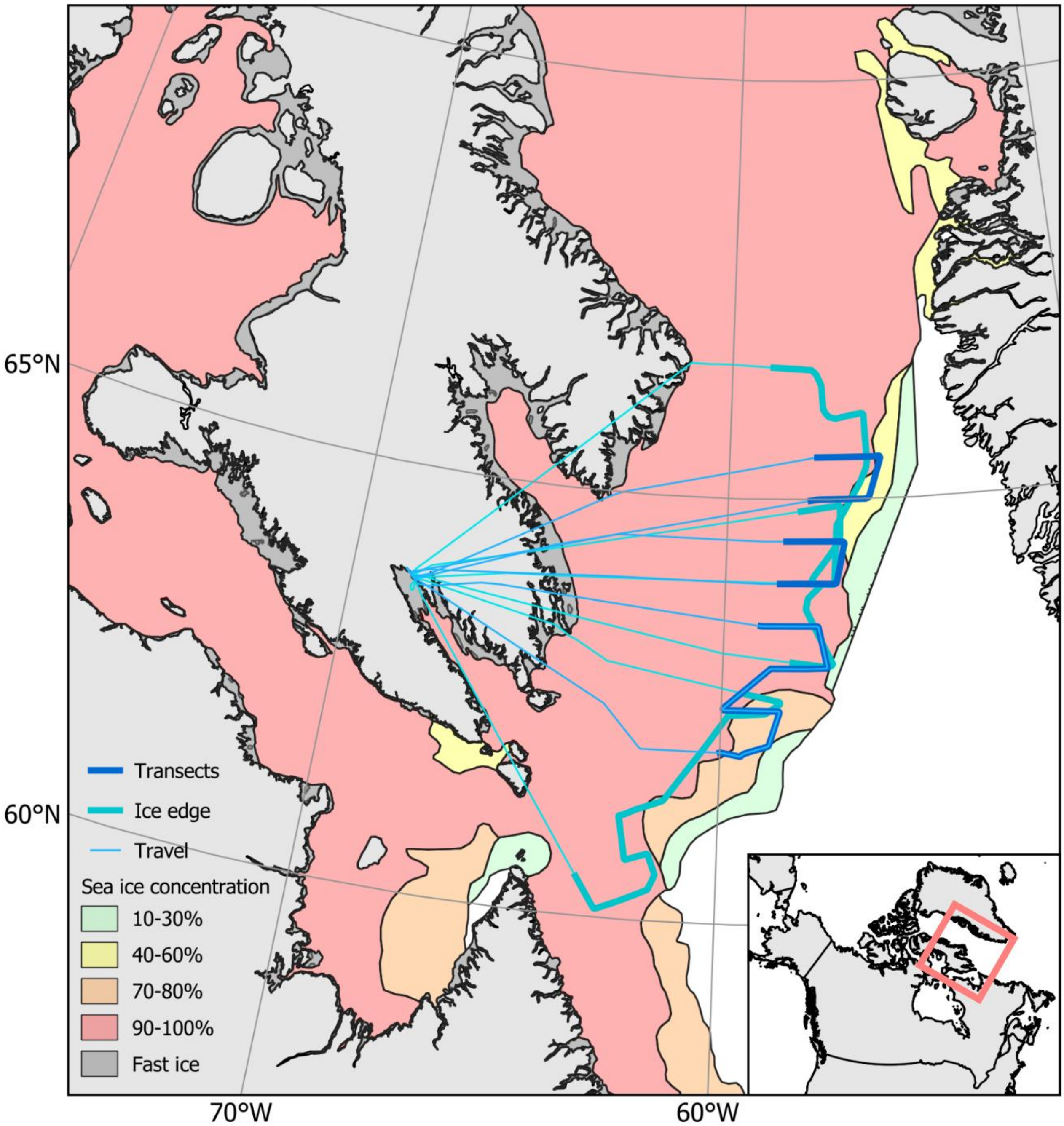

Figure 5. Map showing the reconnaissance flights taken in Davis Strait to find hooded seal whelping patches in March 2024 along with the weekly sea-ice concentration for March 18, 2024. The light blue lines show the flights taken along the ice edge and the dark blue lines show the transects flown across the ice edge with thicker lines indicating areas of active search and thinner lines indicating travel.

The results herein suggest that hooded seal pup production has likely declined by over 50% between 2005 and 2012 at the Front and then remained at a lower level, leading to similar estimates for 2012 and 2017. Observations from the harp seal survey in 2022 at the Front suggest that pup production remained low past 2017. Although it is possible that small groups of hooded seals were missed in the surveys at the Front or that small numbers of hooded seals may have redistributed away from the Front, it is unlikely that they can account for the large decline observed at the Front which is the main whelping area for the NW Atlantic stock. Possible explanations for this decline include a decline in overall hooded seal abundance after 2005, a decline in the proportion of mature females giving birth or a combination of the two factors.

A reason for a large decline in hooded seal abundance is not obvious. Harvesting of hooded seals in Canada and Greenland is unlikely to be a major cause of the decline in pup production reported herein. With the exception of a few years (1987, 1991, 1996-1998) and accounting for assumed levels of struck and loss, annual harvests in Canada have been less than 3,000 hooded seals since 1982. Since 2006, annual takes have been a mean of 28 (SD=42, range=0-158) seals (Stenson, 2006; ICES, 2023a). Harvesting bluebacks in Canada has been illegal since

Table 5. Estimated total pup production of hooded seals on the Front in 2012 and 2017. The total pup production is corrected for the estimated proportion of pups born at the time of the survey.

Year	Survey date	Estimated number of pups	Proportion born (mean ± 95% CI)	Estimated total pup production
2012	Mar 14	12,663 (SE=1,603; CV=0.13)	0.49 (0.19-0.77)	25,843 (SE=8,462, CV=0.33)
	Mar 16	29,653 (SE=6,909; CV=0.23)	0.65 (0.32-0.90)	45,974 (SE=15,032, CV=0.33)
	Mean			41,129 (SE=7,374, CV=0.18)
2017	Mar 14	16,733 (SE=6,092; CV=0.36)	0.49 (0.19-0.77)	34,149 (SE=16,153, CV=0.47)
	Mar 18/19	34,712 (SE=15,488; CV=0.45)	0.81 (0.52-0.97)	42,674 (SE=19,980, CV=0.47)
	Mar 22	25,866 (SE=3,169; CV=0.12)	0.92 (0.69-0.99)	28,269 (SE=4,173, CV=0.15)
	Mean			39,021 (SE=18,334, CV=0.47)

1987. The majority of harvest of the NW Atlantic stock occurs in Greenland but this harvest also does not appear to be high enough to have been a major factor behind the decline. Although catches were in the 10,000-20,000 range during the 1980s and 1990s, they have declined to a mean of 3,816 seals, (SD=1,899) after 2006, after accounting for struck and loss (ICES, 2023a; Stenson, 2006). Bycatch is also unlikely to be a large contributing factor to stock declines. There is no reported bycatch of hooded seals in Canada and either no bycatch of seals or a low risk of bycatch in Greenlandic fisheries, including in the Greenland halibut (*Reinhardtius hippoglossoides*) fishery (Government of Greenland, 2017; ICES, 2023b).

The significant decline in pup production and apparent lack of recovery reported in this paper is similar to what has been documented for hooded seals in the Greenland Sea (Biuw et al., 2022; ICES, 2023a). Pup production of hooded seals in the Greenland Sea also declined sharply between 1997 and 2005/2007 and has remained low in the following years (Biuw et al., 2022; ICES, 2023a). Modelling indicates that the hooded seal population in the Greenland Sea has stabilized at a level less than 10% of the estimated abundance in 1946 (Øigård et al., 2014). Hunting is also not thought to be responsible for the decline of Greenland Sea hooded seals and pup production has remained at a low level despite a moratorium on hunting since 2007. Although the cause remains unknown, it is proposed that ecological changes are responsible for the decline and lack of recovery of Greenland Sea hooded seals (Biuw et al., 2022).

Large-scale ecological changes that occurred in the NW Atlantic in the late 1980's and early 1990's resulted in a regime shift from a groundfish dominated system to an ecosystem dominated by invertebrates (e.g. Buren et al., 2014; Koen-Alonso & Cuff, 2020). Capelin (*Mallotus villosus*), a key forage fish in the NW Atlantic, which is preyed upon by hooded seals, also collapsed at the same time (Buren et al., 2014, 2019; Hammill & Stenson, 2000;). Hammill & Stenson (2006) estimated that hooded seal pup production continued to increase after 1990 and did not begin to decline prior to 2005. This suggests that the collapse that occurred in a number of groundfish stocks and capelin did not have immediate impacts upon hooded seal pup production although it is possible that longer-term ecosystem changes did negatively impact pup production.

The high degree of ecosystem variability and generally warmer conditions observed since the mid-1990s may have impacted hooded seals through a variety of different pathways including direct impacts on pup survival through stability of the sea-ice platform or indirect impacts on survival or body condition through prey availability for juveniles and adults. Global warming has been linked to decreased sea-ice concentration and earlier melting of sea ice in the spring across the Arctic, with declining sea-ice trends expected to continue in the coming decades (Laidre et al., 2015; Stroeve & Notz, 2018). Years with low sea-ice cover in the spring in the NW Atlantic are linked to incidences of high pup mortality in harp seals as females will give birth on ice, which is not thick enough to support the pups, resulting in high mortality levels when the ice breaks beneath their weight or is broken apart by storms and waves (Stenson & Hammill, 2014). Hooded seals breed in the same ice habitat at the same time of the year as harp seals. Historically, hooded seals whelped on slightly heavier ice than harp seals but in recent decades the two species have begun to be found on the same type of ice at the Front. The very short lactation period of hooded seals is thought to be an adaptation to their unstable ice environment, but similar to harp seals, young hooded seals may be susceptible to ice breakup even after they are weaned. Hooded seal pups and adults are also heavier than harp seals which likely increases the chance of the ice breaking apart (Bowen et al., 1985; Lydersen & Kovacs, 1999). In May 2005, approximately 2,000 white coat harp seals and young blueback hooded seals washed ashore along the west coast of Newfoundland. Based upon their pelage and size, they were estimated to have drowned during a storm that broke up the ice during the whelping period in mid-March. This shows that low sea-ice cover directly impacts juvenile survival of hooded seals as has been found for harp seals (Stenson & Hammill, 2014), although the magnitude and interannual variability of this impact is currently unknown.

The Newfoundland and Labrador Climate Index (NCI) (Cyr & Galbraith, 2021) aims to describe the state of the environment in the NW Atlantic using 10 climate variables. For harp seals, the NCI has been linked to both female fecundity and juvenile survival (Tinker et al., 2023). Limited mid-winter ice cover and low capelin biomass (i.e. positive NCI) negatively impacts female fecundity. These environmental factors are linked to low female body condition which is related to higher rates of lateterm abortions in harp seals (Stenson et al., 2016; Stenson, Buren, & Sheppard, 2020). Declines have been documented in female fertility of NW Atlantic hooded seals in the 1990s compared to the 1970s and 1980s, likely related to ecosystem changes (Frie et al., 2012), but current information on female fertility is not available. More research is needed to investigate current trends in female fecundity to explore whether ecosystem changes are negatively impacting female fecundity as has been documented for harp seals.

Ecosystem change may also be impacting juvenile and adult body condition, growth or survival through potential changes in the distribution or abundance of hooded seals' prey. Hooded seals range widely over the NW Atlantic, mainly concentrating their time in northern areas including along the Labrador Shelf, in Davis Strait and the western Greenland Sea (Andersen et al., 2009; 2013). Although recent diet work on this species is limited, a wide variety of prey types have been identified (Hammill & Stenson, 2000; Haug et al., 2000, 2004, 2007; Kapel, 2000; Potelov et al. 2000; Tucker et al., 2009; Enoksen et al., 2017) Many of these prey types lack data on trends in abundance due to their northern distributions or lack of importance to the commercial fishing industry. Others have contrasting trends in different areas. Arctic cod (*Boreogadus saida*), squid (*Gonatus fabricii*), redfish (*Sebastes* spp.), capelin, Greenland halibut, Atlantic argentine (*Argentina silus*), amphipods and euphausiids have been identified as important prey for hooded seals in past diet work (e.g. Hammill & Stenson, 2000; Tucker et al., 2009; Enoksen et al., 2017). Arctic cod and squid have unknown status in the northern areas where hooded seals spend the majority of the year and capelin have been at a low biomass around Newfoundland and southern Labrador since the early 1990's (Buren et al., 2019; Gardiner & Dick, 2010; Walkusz et al., 2019). Atlantic argentine have increased in biomass over the last two decades around Iceland but have unknown trends along the Labrador coast or around Greenland (MFRI, 2024). Redfish also have unknown status in Davis Strait but have increased in biomass since 2010 on the Newfoundland and Labrador Shelves (DFO, 2020; 2022). Euphausiid biomass decreased in many areas of the Labrador Sea during the 2000s and remained low thereafter while hyperiid amphipod abundance was low during much of the early 2000s but subsequently increased (Ringuette et al., 2022). Greenland halibut have decreased since 2010 in the Gulf of St. Lawrence but have remained stable from 1997-2017 in Davis Strait and since 2005 in southeast Greenland and around Iceland (DFO, 2023; Treble et al., 2022; Úbeda et al., 2023). Although the stock structure of Greenland halibut is uncertain, available evidence suggests that the stock in the NW Atlantic (Davis Strait/Baffin Bay) is separate from the West Nordic stock (Southeast Greenland and Iceland) although the West Nordic Stock may be composed of two populations (Úbeda et al., 2023). If this is the case, there is the possibility that the stable biomass in the West Nordic Stock since 2005 is hiding underlying changes in either or both populations as the surveys in southeast Greenland show decreases in abundance since the early 2000s (Úbeda et al., 2023). Limited recent data on hooded seal body condition or fecundity and opposite trends or lack of data for important prey make it difficult to link declines in pup production to changes in the distribution or abundance of important prey species.

Potential additional threats to hooded seals include underwater noise, contaminants and parasites, which may be having impacts on hooded seal survival or body condition. Underwater noise has increased throughout hooded seals' range from anthropogenic sources (PAME, 2021). In general, the impact of noise on marine mammals is poorly understood but it has been linked to increased levels of hormones linked to the stress response in cetaceans and behavioural responses in pinnipeds (Costa et al., 2003; Rolland et al., 2012; Romano et al., 2004). The impact on foraging behaviour or efficiency of deep diving species such as hooded seals should be a topic of further research. Mercury or other contaminants may also be a threat to hooded seals. Hooded seals collected in Davis Strait between 2000-2015 were at high risk of mercury mediated health effects (Dietz et al., 2019). High levels of DDT, PCBs, chlordanes and PBDEs have also been recorded with concentrations varying over time, with evidence that OH-PCBs may be impacting the thyroid homeostasis of hooded seal mothers and pups (Hobbs et al., 2002; Rotander et al., 2012; Villanger et al., 2013; Wolkers et al., 2006). More research on the tissue-specific concentration and potential impacts of mercury and other contaminants is warranted. Female hooded seals collected in the Gulf of St. Lawrence in 2005 were also positive for *Toxoplasma gondii* and *Sarcocystis* sp. parasites. It is unknown how widespread exposure to these parasites has been in hooded seals or the impact parasites and contaminants may be having on the seals' health (Reiling et al., 2019).

The extent to which population abundance of hooded seals in the NW Atlantic has declined since 2005 is currently unknown. Although it was possible to estimate hooded seal pup production from data collected during the 2012 and 2017 harp seal surveys, population abundance cannot be estimated for hooded seals for these years using the hooded seal population model used in 2005 (Hammill & Stenson, 2006) or a newer modelling approach such as the one developed for NW Atlantic harp seals (Hammill et al., 2021; Tinker et al., 2023) as the data required for the models, such as age specific pregnancy rates or mortality rates, are lacking. Such data will be needed before population abundance estimates from future surveys can be determined.

Conclusion

Pup production of hooded seals in the NW Atlantic at the Front in 2012 (41,129 pups, SE = 7,374) and 2017 (39,021 pups, SE = 18,334) has sharply decreased since 2005, estimated at 38% and 36% of the 2005 pup production. This mirrors a similar large decline and continued low production of hooded seals pups in the Greenland Sea that occurred between 1997 and 2005/07. Harvesting and immediate impacts of the large ecosystem shift that occurred in the Newfoundland and Labrador Shelf in the late 1980s/early 1990s are not likely to be responsible for this decline due to low harvest numbers and a mismatch with timing. More likely explanations relate to the direct and indirect impacts of climate and ecosystem change on female fertility and juvenile survival, via a similar mechanism as has been documented for harp seals in the NW Atlantic (e.g., Stenson & Hammill, 2014; Stenson et al., 2016). However, negative impacts from other factors such as contaminant concentrations or parasites cannot be ruled out. Future research will be needed to investigate the potential causal mechanisms of the decline in pup production documented herein.

ADHERENCE TO ANIMAL WELFARE PROTOCOLS

The research presented in this article has been done in accordance with the institutional and national animal welfare laws and protocols applicable in the jurisdictions in which the work was conducted.

AUTHOR CONTRIBUTION STATEMENT

Conceptualisation: CH, PG, SL, GS

Formal Analysis: CH, PG, GS

Methodology: CH, PG, AM, GS

Investigation: CH, PG, SL, AM, GS

Writing-original draft: CH

Writing-review & editing: CH, PG, SL, AM, GS

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REFERENCES

Andersen, J. M., Wiersma, Y. F., Stenson, G., Hammill, M. O., & Rosing-Asvid, A. (2009). Movement patterns of hooded seals (*Cystophora cristata*) in the Northwest Atlantic Ocean during the post-moult and pre-breed seasons. *Journal of Northwest Atlantic Fishery Science, 42*, 1-11. https://doi.org/10.2960/J.v42.m649

Andersen, J. M., Wiersma, Y. F., Stenson, G. B., Hammill, M. O., Rosing-Asvid, A., & Skern-Maurizen, M. (2013). Habitat selection by hooded seals (*Cystophora cristata*) in the Northwest Atlantic Ocean. *ICES Journal of Marine Science, 70,* 173-185. https://doi.org/10.1093/icesjms/fss133

Bajzak, C. E., Côté, S. D., Hammill, M. O., & Stenson, G. (2009). Intersexual differences in the postbreeding foraging behaviour of the Northwest Atlantic hooded seal. *Marine Ecology Progress Series*, *385,* 285-294. https://doi.org/10.3354/meps08015

Biuw, M., Øigård, T. A., Nilssen, K. T., Stenson, G., Lindblom, L., Poltermann, M., … Haug, T. (2022). Recent harp and hooded seal pup production estimates in the Greenland Sea suggest ecology-driven declines. *NAMMCO Scientific Publications, 12*. https://doi.org/10.7557/3.5821

Bowen, W. D., Oftedal, O. T., & Boness, D. J. (1985). Birth to weaning in 4 days: remarkable growth in the hooded seal, *Cystophora cristata*. *Canadian Journal of Zoology, 63,* 2841-2846. https://doi.org/10.1139/z85-424

Bowen, W. D., Myers, R. A., & Hay, K. (1987). Abundance estimation of a dispersed, dynamic population: hooded seals (*Cystophora cristata*) in the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences, 44,* 282-295. https://doi.org/10.1139/f87-037

Bowen, W. D., Ellis, S. L., Iverson, S. J., & Boness, D. J. (2003). Maternal and newborn life-history traits during periods of contrasting population trends: implications for explaining the decline of harbour seals (*Phoca vitulina*), on Sable Island. *Journal of Zoology, London, 261,* 155-163. https://doi.org/10.1017/S0952836903004047

Bowen, W. D., den Heyer, C. E., Lang, S. L. C., Lidgard, D., & Iverson, S. J. (2020). Exploring causal components of plasticity in grey seal birthdates: effects of intrinsic traits, demography, and climate. *Ecology and Evolution, 10,* 11507-11522. https://doi.org/10.1002/ece3.6787

Buren, A. D., Koen-Alonso, M., Pepin, P., Mowbray, F., Nakashima, B., Stenson, G., … Montevecchi, W. A. (2014). Bottom-up regulation of capelin, a keystone forage species. *PLoS ONE, 9,* e87589. https://doi.org/10.1371/journal.pone.0087589

Buren, A. D., Murphy, H. M., Adamack, A. T., Davoren, G. K., Koen-Alonso, M., Montevecchi, W. A., … Varkey, D. (2019). The collapse and continued low productivity of a keystone forage fish species. *Marine Ecology Progress Series, 616,* 155-170. https://doi.org/10.3354/meps12924

Coltman, D. W., Stenson, G., Hammill, M. O., Haug, T., Davis, C. S., & Fulton, T. L. (2007). Panmictic population structure in the hooded seal (*Cystophora cristata*). *Molecular Ecology, 16,* 1639-1648. https://doi.org/10.1111/j.1365-294X.2007.03229.x

Costa, D. P., Crocker, D. E., Gedamke, J., Webb, P. M., Houser, D. S., Blackwell, S. B., … Le Boeuf, B. J. (2003). The effect of a low-frequency sound source (acoustic thermometry of the ocean climate) on the diving behavior of juvenile northern elephant seals, *Mirounga angustirostris. The Journal of the Acoustical Society of America, 113,* 1155-1165. https://doi.org/10.1121/1.1538248

Cyr, F., & Galbraith, P. S. (2021). A climate index for the Newfoundland and Labrador shelf. *Earth System Science Data, 13,* 1807-1828. https://doi.org/10.5194/essd-13-1807-2021

DFO. (2020). Stock Status of redfish in NAFO SA 2 + divs. 3K. (Advisory Report 2020/021). Canadian Science Advisory Secretariat.

DFO. (2022). Assessment of redfish in the Northwest Atlantic Fisheries Organization (NAFO) subarea 0, October 2016. (Advisory Report 2022/008). Canadian Science Advisory Secretariat.

DFO. (2023). Assessment of the Gulf of St. Lawrence (4RST) Greenland halibut stock in 2022. (Advisory Report 2023/022). Canadian Science Advisory Secretariat.

Dietz, R., Letcher, R. J., Desforges, J.-P., Eulaers, I., Sonne, C., Wilson, S., … Víkingsson, G. (2019). Current state of knowledge on biological effects from contaminants on arctic wildlife and fish. *Science of the Total Environment, 696,* 133792. https://doi.org/10.1016/j.scitotenv.2019.133792

Enoksen, S., Haug, T., Lindstrøm, U., & Nilssen, K. T. (2017). Recent summer diet of hooded *Cystophora cristata* and harp *Pagophilus groenlandicus* seals in the drift ice of the Greenland Sea. *Polar Biology, 40,* 931-937. https://doi.org/10.1007/s00300-016-2002-2

Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R. B., Aschan, M. M., & Dolgov, A. V. (2015). Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nature Climate Change, 5,* 673-677. https://doi.org/10.1038/nclimate2647

Frie, A. K., Stenson, G. B., & Haug, T. (2012). Long-term trends in reproductive and demographic parameters of female Northwest Atlantic hooded seals (*Cystophora cristata*): population responses to ecosystem change? *Canadian Journal of Zoology, 90,* 376-392. https://doi.org/10.1139/z11-140

Gardiner, K., & Dick, T. A. (2010). Arctic cephalopod distributions and their associated predators. *Polar Research, 29,* 209-227. https://doi.org/10.1111/j.1751-8369.2010.00146.x

Government of Greenland. (2017). *Review of existing knowledge on marine mammal by-catch in Greenland* (SC/24/BYC/14). Nuuk, Greenland: The Government of Greenland Ministry of Fisheries and Hunting.

Hammill, M. O., Stenson, G. B., & Myers, R. A. (1992). Hooded seal (*Cystophora cristata*) pup production in the Gulf of St. Lawrence. *Canadian Journal of Fisheries and Aquatic Sciences, 49,* 2546-2550. https://doi.org/10.1139/f92-281

Hammill, M. O., Lydersen, C., Kovacs, K. M., & Sjare, B. (1997). Estimated fish consumption by hooded seals (*Cystophora cristata*), in the Gulf of St. Lawrence. *Journal of Northwest Atlantic Fishery Science, 22,* 249-257.

Hammill, M. O., & Stenson, G. B. (2000). Estimated prey consumption by harp seals (*Phoca groenlandica*), hooded seals (*Cystophora cristata*), grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) in Atlantic Canada. *Journal of Northwest Atlantic Fishery Science, 26,* 1-23.

Hammill, M. O., & Stenson, G. B. (2003). Application of the precautionary approach and conservation reference point to the management of Atlantic seals: a discussion paper. (Research Document 2003/067). Canadian Science Advisory Secretariat.

Hammill, M. O., & Stenson, G. (2006). Abundance of Northwest Atlantic hooded seals (1960-2005). (Research Document 2006/068). Canadian Science Advisory Secretariat.

Hammill, M. O., & Stenson, G. B. (2007). Application of the precautionary approach and conservation reference points to management of Atlantic seals. *ICES Journal of Marine Science, 64,* 702-706. https://doi.org/10.1093/icesjms/fsm037

Hammill, M. O., Stenson, G. B., Mosnier, A., & Doniol-Valcroz, T. (2021). Trends in abundance of harp seals, *Pagophilus groenlandicus*, in the Northwest Atlantic, 1952-2019. (Research Document 2021/006). Canadian Science Advisory Secretariat.

Haug, T., Nilssen, K. T., & Lindblom, L. (2000). First independent feeding of harp seal (*Phoca groenlandica*) and hooded seal (*Cystophora cristata*) pups in the Greenland Sea. *NAMMCO Scientific Publications, 2,* 29-39. https://doi.org/10.7557/3.2969

Haug, T., Nilssen, K. T., & Lindblom, L. (2004). Feeding habits of harp and hooded seals in drift ice waters along the east coast of Greenland in summer and winter. *Polar Research, 23,* 35-42. https://doi.org/10.3402/polar.v23i1.6264

Haug, T., Nilssen, K. T., Lindblom, L., & Lindstrøm, U. (2007). Diets of hooded seals (*Cystophora cristata*) in coastal waters and drift ice waters along the east coast of Greenland. *Marine Biology Research, 3,* 123-133. https://doi.org/10.1080/17451000701358531

Hobbs, K. E., Lebeuf, M., & Hammill, M. O. (2002). PCBs and OCPs in male harbour, grey, harp and hooded seals from the Estuary and Gulf of St Lawrence, Canada. *The Science of the Total Environment, 296,* 1-18. https://doi.org/10.1016/S0048-9697(01)01074-9

Huntington, H. P., Danielson, S. L., Wiese, F. K., Baker, M., Boveng, P., Citta, J. J., … Wilson, C. (2020). Evidence suggests potential transformation of the Pacific Arctic ecosystem is underway. *Nature Climate Change, 10,* 342-348. https://doi.org/10.1038/s41558-020-0695-2

ICES. (2023a). Report of the joint ICES/NAFO/NAMMCO working group on harp and hooded seals (WGHARP). *ICES Scientific Reports, 5,* 96. https://doi.org/10.17895/ices.pub.24306100

ICES. (2023b). Northwestern Working Group (NWWG). Greenland halibut (Iceland and Faroes grounds, West of Scotland, North of Azores, and East of Greenland). *ICES Scientific Reports, 5:64,* 471-508. https://doi.org/10.17895/ices.pub.23267153

Kapel, F. O. (2000). Feeding habits of harp and hooded seals in Greenland waters. *NAMMCO Scientific Publications, 2,* 50-64. https://doi.org/10.7557/3.2971

Koen-Alonso, M., & Cuff, A. (2020). Status and trends of the fish community in the Newfoundland Shelf (NAFO Div. 2J3K), Grand Bank (NAFO Div. 3LNO) and southern Newfoundland Shelf (NAFO Div. 3Ps) Ecosystem Production Units. (Research Document 18/070). NAFO Scientific Council.

Kovacs, K. M., Lydersen, C., Overland, J. E., & Moore, S. E. (2011). Impacts of changing sea-ice conditions on Arctic marine mammals. *Marine Biodiversity, 41,* 181-194. https://doi.org/10.1007/s12526-010-0061-0

Kovacs, K.M. (2018). Hooded seal: *Cystophora cristata*. In B. Würsig, J. G. M. Thewissen, & K. M. Kovacs (Eds.), *Encyclopedia of Marine Mammals* (3rd Ed.) (pp. 477-480). London, United Kingdom: Academic Press.

Laidre, K. L., Stern, H., Kovacs, K. M., Lowry, L., Moore, S. E., Regehr, E. V., … Ugarte, F. (2015). Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. *Conservation Biology, 29,* 724-737. https://doi.org/10.1111/cobi.12474

Laidre, K. L., & Regehr, E.V. (2018). Arctic Marine Mammals. In B. Würsig, J. G. M. Thewissen, & K. M. Kovacs (Eds.), *Encyclopedia of Marine Mammals* (3rd Ed.) (pp. 34-40). London, United Kingdom: Academic Press.

Lydersen, C., & Kovacs, K. M. (1999). Behaviour and energetics of ice-breeding, North Atlantic phocid seals during the lactation period. *Marine Ecology Progress Series, 187,* 265-281. https://doi.org/10.3354/meps187265

Mansfield, A. W. (1967). Seals of arctic and eastern Canada. *Bulletin of the Fisheries Research Board of Canada, 137,* 1-30.

Marine and Freshwater Research Institute (MFRI), Iceland. (2024). Greater silver smelt *Argentina silus* Technical Report. Retrieved from https://www.hafogvatn.is/static/extras/images/19-gss_techreport_en.html

Mood, A. M., Graybill, F. A., & Boes, D. C. (1974). *Introduction to the Theory of Statistics* (3rd Ed.). Toronto, Ontario, Canada: McGraw-Hill.

Mosnier, A., den Heyer, C. E., Stenson, G. B., & Hammill, M. O. (2023). A Bayesian birth distribution model for grey seals and an evaluation of timing of the harvest. (Research Document 2023/052). Canadian Science Advisory Secretariat.

Øigård, T. A., Haug, T., & Nilssen, K. T. (2014). Current status of hooded seals in the Greenland Sea. Victims of climate change and predation? *Biological Conservation, 172,* 29-36. https://doi.org/10.1016/j.biocon.2014.02.007

PAME. (2021). *Underwater noise pollution from shipping in the Arctic Report*. Protection of the Arctic Marine Environment Working Group (PAME). Tromsø, Norway: Arctic Council.

Post, E., Bhatt, U. S., Bitz, C. M., Brodie, J. F., Fulton, T. L., Hebblewhite, M., … Walker, D. A. (2013). Ecological consequences of sea-ice decline. *Science, 341,* 519-524. https://doi.org/10.1126/science.1235225

Potelov, V., Nilssen, K. T., Svetochev, V., & Haug, T. (2000). Feeding habits of harp (*Phoca groenlandica*) and hooded seals (*Cystophora cristata*) during late winter, spring and early summer in the Greenland Sea. *NAMMCO Scientific Publications, 2,* 40-49. https://doi.org/10.7557/3.2970

R Core Team. (2023). R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Reiling, S. J., Measures, L., Feng, S., Boone, R., Merks, H., & Dixon, B. R. (2019). *Toxoplasma gondii*, *Sarcocystis* sp. and *Neospora caninum*-like parasites in seals from northern and eastern Canada: potential risk to consumers. *Food and Waterborne Parasitology, 17,* e00067. https://doi.org/10.1016/j.fawpar.2019.e00067

Ringuette, M., Devred, E., Azetsu-Scott, K., Head, E., Punshon, S., Casault, B., & Clay, S. (2022). Optical, chemical and biological oceanographic conditions in the Labrador Sea between 2014 and 2018. (Research Document 2022/021). Canadian Science Advisory Secretariat.

Rolland, R. M., Parks, S. E., Hunt, K. E., Castellote, M., Corkeron, P. J., Nowacek, D. P., … Kraus, S. D. (2012). Evidence that ship noise increases stress in right whales. *Proceedings of the Royal Society B, 279,* 2363-2368. https://doi.org/10.1098/rspb.2011.2429

Romano, T. A., Keogh, M. J., Kelly, C., Feng, P., Berk, L., Schlundt, C. E., … Finneran, J. J. (2004). Anthropogenic sound and marine mammal health: measures of the nervous and immune systems before and after intense sound exposure. *Canadian Journal of Fisheries and Aquatic Sciences, 61,* 1124-1134. https://doi.org/10.1139/F04-055

Rotander, A., van Bavel, B., Polder, A., Rigét, F., Auðunsson, G. A., Gabrielsen, G. W., … Dam, M. (2012). Polybrominated diphenyl ethers (PBDEs) in marine mammals from Arctic and North Atlantic regions, 1986-2009. *Environmental International, 40,* 102-109. https://doi.org/10.1016/j.envint.2011.07.001

Salberg, A.-B., Haug, T., & Nilssen, K. T. (2008). Estimation of hooded seal (*Cystophora cristata*) pup production in the Greenland Sea pack ice during the 2005 whelping season. *Polar Biology, 31,* 867-878. https://doi.org/10.1007/s00300-008-0425-0

Satterthwaite, F. E. (1946). An approximate distribution of estimates of variance components. *Biometrics, 2,* 110-114. https://doi.org/10.2307/3002019

Sergeant, D. E. (1974). A rediscovered whelping population of hooded seals *Cystophora cristata* Erxleben and its possible relationships to other populations. *Polarforschung, 44,* 1-7. https://doi.org/10.2312/polarforschung.44.1.1

Sergeant, D.E. (1976a). History and present status of populations of harp and hooded seals. *Biological Conservation, 10,* 95-118. https://doi.org/10.1016/0006-3207(76)90055-0

Sergeant, D. E. (1976b). Research on hooded seals *Cystophora cristata* Erxleben in 1976. (Research Document 76/X/126). International Commission for the Northwest Atlantic Fisheries.

Sergeant, D. E. (1977). Research on hooded seals in the western North Atlantic in 1977. (Research Document 77/XI/57). International Commission for the Northwest Atlantic Fisheries.

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

Stenson, G.B. (1994). The status of pinnipeds in the Newfoundland region. *NAFO Scientific Council Studies, 21,* 115-119.

Stenson, G. B. (2006). Hunt induced mortality in Northwest Atlantic hooded seals. (Research Document 2006/066). Canadian Science Advisory Secretariat.

Stenson, G. B., Ni, I.-H., Myers, R. A., Hammill, M. O., Warren, W. B., & Kingsley, M. C. S. (1991). Aerial survey estimates of pup production of harp seals (*Phoca groenlandica*) in the Gulf of St. Lawrence and off Newfoundland during March 1990. (Research Document 91/83). Canadian Science Advisory Secretariat.

Stenson, G. B., & Sjare, B. (1996). Newfoundland hooded seal tag returns in the Northeast Atlantic. *Northwest Atlantic Fisheries Organization Scientific Council Studies*, *26*, 115-118.

Stenson, G. B., Myers, R. A., Ni, I.-H., & Warren, W. G. (1997). Pup production and population growth of hooded seals (*Cystophora cristata*) near Newfoundland, Canada. *Canadian Journal of Fisheries and Aquatic Sciences, 54 (Supplement 1*), 209-216. https://doi.org/10.1139/f96-168

Stenson, G. B., Hammill, M. O., Lawson, J., & Gosselin, J. F. (2006). 2005 pup production of hooded seals, *Cystophora cristata,* in the Northwest Atlantic. (Research Document 2006/067).

Stenson, G. B., & Hammill, M. O. (2014). Can ice breeding seals adapt to habitat loss in a time of climate change? *ICES Journal of Marine Science, 71,* 1977-1986. https://doi.org/10.1093/icesjms/fsu074

Stenson, G. B., Hammill, M. O., Lawson, J. W., & Gosselin, J.-F. (2014). Estimating pup production of Northwest Atlantic harp seals, *Pagophilus groenlandicus*, in 2012. (Research Document 2014/057).

Stenson, G. B., Buren, A. D., & Koen-Alonso, M. (2016). The impact of changing climate and abundance on reproduction in an ice-dependent species, the Northwest Atlantic harp seal, *Pagophilus groenlandicus*. *ICES Journal of Marine Science, 73,* 250-262. https://doi.org/10.1093/icesjms/fsv202

Stenson, G. B., Buren, A. D., & Sheppard, G. L. (2020). Updated estimates of reproductive rates in Northwest Atlantic harp seals and the influence of body condition. (Research Document 2020/057). Canadian Science Advisory Secretariat.

Stenson, G. B., Haug, T., & Hammill, M. O. (2020). Harp seals: monitors of change in differing ecosystems. *Frontiers in Marine Science, 7,* 569258. https://doi.org/10.3389/fmars.2020.569258

Stenson, G. B., Gosselin, J.-F., Lawson, J. W., Buren, A., Goulet, P., Lang, S. L. C., … Hammill, M. O. (2022). Pup production of harp seals in the Northwest Atlantic in 2017 during a time of ecosystem change. *NAMMCO Scientific Publications, 12.* https://doi.org/10.7557/3.6214

Stroeve, J., & Notz, D. (2018). Changing state of Arctic sea ice across all seasons. *Environmental Research Letters, 13,* 103001. https://doi.org/10.1088/1748-9326/aade56

Tinker, M. T., Stenson, G. B., Mosnier, A., & Hammill, M. O. (2023). Estimating abundance of Northwest Atlantic harp seal using a Bayesian modelling approach. (Research Document 2023/068). Canadian Science Advisory Secretariat.

Treble, M. A., Nogueira, A., & Hedges, K. J. (2022). Assessment of the Greenland Halibut stock component in NAFO Subarea 0 + 1 (offshore). (Research Document 22/022).

Tucker, S., Bowen, W. D., Iverson, S. J., Blanchard, W., & Stenson, G. B. (2009). Sources of variation in diets of harp and hooded seals from quantitative fatty acid signature analysis (QFASA). *Marine Ecology Progress Series, 384,* 287-302. https://doi.org/10.3354/meps08000

Úbeda, J., Nogueira, A., Tolimieri, N., Vihtakari, M., Elvarsson, B., Treble, M., & Boje, J. (2023). Using multivariate autoregressive state-space models to examine stock structure of Greenland halibut in the North Atlantic. *Fisheries Management and Ecology, 30,* 521-535. https://doi.org/10.1111/fme.12639

Vacquié-Garcia, J., Spitz, J., Hammill, M., Stenson, G. B., Kovacs, K. M., Lydersen, C., …Jeanniard du Dot, T. (2024). Foraging habits of Northwest Atlantic hooded seals over the past 30 years: Future habitat suitability under global warming. *Global Change Biology*, *30*, e17186. https://doi.org/10.1111/gcb.17186

Villanger, G. D., Gabrielsen, K. M., Kovacs, K. M., Lydersen, C., Lie, E., Karimi, M., … Jenssen, B. M. (2013). Effects of complex organohalogen contaminant mixtures on thyroid homeostasis in hooded seal (*Cystophora cristata*) mother-pup pairs. *Chemosphere, 92,* 828-842. https://doi.org/10.1016/j.chemosphere.2013.04.036

Walkusz, W., Atchison, S., Hedges, K., & Deslauriers, D. (2019). Assessment of potential impacts of bycatch mortality on the Arctic cod (*Boreogadus saida*) populations from the Northern (*Pandalus borealis*) and striped (*Pandalus montagui*) shrimp fisheries in Shrimp Fishing Areas 1, 2, and 3. (Research Document 2019/073).

Welch, B. L. (1947). The generalization of 'student's' problem when several different population variances are involved. *Biometrika, 34,* 28-35. https://doi.org/10.1093/biomet/34.1-2.28

Wolkers, H., Hammill, M. O., & van Bavel, B. (2006). Tissue-specific accumulation and lactational transfer of polychlorinated biphenyls, chlorinated pesticides, and brominated flame retardants in hooded seals (*Cystophora cristata*) from the Gulf of St. Lawrence: applications for monitoring. *Environmental Pollution, 142,* 476-486. https://doi.org/10.1016/j.envpol.2005.10.031