Trends in the harvest of Brünnich's guillemots Uria lomvia in Newfoundland: effects of regulatory changes and winter sea ice conditions

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Original article

Trends in the harvest of Brünnich's guillemots *Uria lomvia* in Newfoundland: effects of regulatory changes and winter sea ice conditions

Anthony J. Gaston & Gregory J. Robertson

The harvest of Brünnich's guillemots (thick-billed murres) *Uria lomvia* off Newfoundland and Labrador is the only legal hunt of seabirds by non-natives in Canada and the United States. Ringing programmes at Arctic breeding colonies have been used to track changes in numbers and age composition of harvested birds. In recent years, the numbers of rings reported by hunters have fallen steeply. We examined recoveries by hunters of rings from a colony in northern Hudson Bay during 1984-2006 to assess the possible reasons for the decline in recoveries. Because recoveries of common guillemots have remained stable over the same period, it seems unlikely that a change in reporting rates is involved. Instead, it appears that a combination of a reduction in hunting pressure and a change in the behaviour of the birds due to more northerly termination of the winter pack-ice boundary account for the observed reduction in recovery rates. The pattern of first year recovery rates, in particular, appears consistent with an explanation based on accommodation to ice conditions. Recovery rates of older birds appear less affected by ice conditions and in recent years, have, in any case, been very low. Our study demonstrates that under conditions of changing weather and climate, harvest management decisions may not always have the impact expected.

Key words: Brünnich's guillemot, eastern Canada, Uria lomvia, age, harvest regulations, sea ice, NAO

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The harvest of seabirds is a traditional activity in northern regions across the globe (Merkel & Barry 2008). In North America, most bird hunting is focused on waterfowl and upland game birds. However, there is one large seabird harvest in Newfoundland and Labrador. Following the terms of union with Canada in 1949, which technically made the harvest of seabirds by non-Aboriginals illegal under the Migratory Bird Convention Act, provisions were made to allow for Newfoundlanders to hunt guillemots (Brünnich's *Uria lomvia* and common *U. aalge*), but not other seabirds (Elliot et al. 1991, Chardine et al. 2008). This was largely justified for cultural and subsistence reasons, as the harvest of guillemots provided a crucial source of protein in the winter months for rural Newfoundlanders (Elliot 1991). With the advent of faster boats and better firearms, annual harvests of guillemots ranged up to 750,000 birds in the late 1970s (Wendt & Cooch 1984). At that time, the hunting season extended from 1 September to 31 March, and there were no bag limits. This harvest was considered unsustainable and a variety of hunting regulations were subsequently introduced, designed to reduce the harvest to about half the levels seen in the 1970s (Chardine et al. 1999).

Brünnich's guillemots make up the majority of the harvested guillemots (Elliot et al. 1991) in the

Newfoundland and Labrador hunt and originate from breeding colonies throughout the eastern Canadian Arctic, West Greenland, Iceland and as far east as Spitsbergen (Tuck 1961, Kampp 1988, Gaston & Hipfner 2000). Monitoring of the guillemot harvest in Newfoundland and Labrador has been carried out through periodic guillemot hunter surveys (Chardine et al. 1999). In addition, guillemot populations are monitored to detect trends at several breeding colonies in the eastern Canadian Arctic, especially at Coats Island, northern Hudson Bay and at Prince Leopold Island (Gaston 2002a). Ringing of nestling Brünnich's guillemots has been carried out annually at Coats Island since 1984 and ring returns from hunters (recoveries) have been used to assess changes in hunting pressure and the proportion of different age classes in the kill (Donaldson et al. 1997, Gaston 2002b).

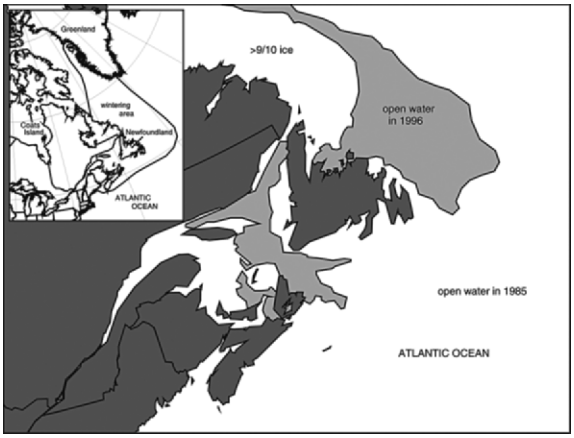

Figure 1. Map of eastern Canada, showing the position of the Brünnich's guillemot breeding colony at Coats Island and the position of the pack ice front off Newfoundland and Labrador on 1 February 1985 and 1996.

Ring returns from hunters are a fundamental tool for monitoring harvests of many game bird species. The probability of a hunter reporting a ring is related to the probability of killing the bird, the probability of retrieving a dead bird and the probability of reporting the ring to authorities (Brownie et al. 1985). Changes in any or all of these probabilities can lead to changes in ring recovery rates, and need to be considered when interpreting any trends in recovery rates.

Since the mid-1990s, the numbers of ringed guillemots reported by hunters, in relation to numbers ringed, have been much lower than during earlier decades. We examine possible causes for this change, concentrating on the role of changes in annual sea ice cover in the wintering area (Fig. 1). Sea ice affects the distribution of guillemots by denying them access to feeding areas, forcing them to move to areas of open water (Elliot 1991). There have been significant changes in sea-ice cover in the north-western Atlantic over the past two decades (Grumet et al. 2001). In addition to ice cover, we examined the effects on recovery rates of large-scale climate patterns, using the North Atlantic Oscillation Index (NAO, Hurrell 1995a), as this index has been found to affect ice cover (Sterne & Heide-Jørgensen 2003), marine ecosystems (Planque & Taylor 1998) and seabird reproduction and survival in the North Atlantic (Thompson & Ollason 2001, Grosbois & Thompson 2005, but see Sandvik & Erikstad 2008). We also considered changes in the hunting pressure in Newfoundland and Labrador, as indexed by the number of hunting permits sold in the province, and examined whether the large regulatory changes introduced in 1993 (shorter seasons and bag limits) influenced recovery rates. Information obtained on these relationships can be used to predict harvest levels in Newfoundland, and to understand the relative roles of hunting regulation changes and natural events in determining guillemot harvest levels.

Methods

Study area

At Coats Island (62°57'N, 82°00'W), Brünnich's guillemots breed on two cliffs separated by about 1.5 km (Gaston et al. 1993). All of the ringing and observations described here were performed at the western cliff, which supports about 18,000 breeding pairs.

Ringing recoveries

Ringing of nestlings at Coats Island took place in 1981 and annually during 1984-2002, with 1,331-2,686 ringed each year (see Gaston & Donaldson 1994, Donaldson et al. 1997 for methods). Adult guillemots were ringed from 1984 onwards, with a mean (± SE) of 107 ± 13 (range: 34-346) ringed annually. The current analysis considers only those birds recovered (i.e. shot and reported) by hunters in Newfoundland and Labrador from cohorts ringed between 1984-2006. More than 90% of all recoveries of Brünnich's guillemots ringed at Coats Island came from Newfoundland and Labrador, of which more than 95% were shot (Donaldson et al. 1997).

As the focus of our study was factors influencing the probability of guillemots being shot, recovery rates (the proportion of ringed birds that were reported as recovered to the Bird Banding Office) were analysed using the traditional Brownie parameterization (f; Brownie et al. 1985). Direct recovery rates (shot in the hunting season immediately following ringing) of juveniles alone can be modelled with standard generalized linear models with a binomial distribution. Older cohorts should be analysed using specific approaches normally used in ring recovery analyses, such as those in Program MARK (White & Burnham 1999), to address the issue that survival becomes part of the probability of being recovered in years subsequent to the original ringing. Because second and third year guillemots were not marked as part of our study, it was not possible to estimate direct recovery rates of these cohorts using standard recovery analysis methods. Therefore, indirect (recovered in a hunting season after the year of ringing) recovery rates (number of recoveries over the total number of chicks ringed in that cohort) of these cohorts were also analysed with generalized linear models. Recovery rates for these older cohorts are more difficult to interpret than direct juvenile recovery rates, as they represent the product of juvenile survival (and the second year survival for the third year cohort) and the year-specific recovery rate of that cohort. For adult recovery rates, guillemots ringed as chicks and as adults were included in a standard recovery analysis (f; Brownie et al. 1985). Once birds reached their fourth year, they were treated as adults, so recovery rates for adults were estimated using birds marked as adults and juveniles recovered in their fourth and older years.

Our inability to estimate second and third year survival and recovery rates (and therefore juvenile survival) coupled with a paucity of adult recoveries (restricting our ability to estimate adult survival), created severe restrictions on the models that could be investigated for adults. Specifically, many parameters in highly parameterised models could not be estimated or models would simply not converge. Even reduced parameter models suffered similar problems, or constrained models in ways that raised concerns about the interpretation of recovery rate estimates (e.g. constraining juvenile survival to a constant). Consequently, tables of AIC values for competing models, and other related statistics are not presented. Instead, we simply left all survival rates unconstrained and allowed recovery rates to vary annually and independently across the four-age classes. Therefore, our focus was on obtaining unconstrained adult recovery rates and subsequently modeling of these recovery rates with covariates of interest. Relationships between various covariates and recovery rates were examined by extracting relevant β values (i.e. slopes), their standard errors and 95% confidence limits. β values that did not include zero within their 95% confidence limits were considered indicative of relationships. P-values, as such, were not considered in the paper (Anderson et al. 2001), as they basically provide the same information as 95% confidence limits.

Climatic covariates included the southern extent of sea ice, measured on 1 February. A winter NAO index, based on data from December to March, was extracted from Hurrell (1995b). The NAO is an index of pressure differences between Iceland and the Azores, in its negative phase, Newfoundland experiences milder, wetter and windier conditions.

Information on ice conditions was obtained from the Canadian Ice Service (Available at: http://ice-glaces.ec.gc.ca/App/WsvPageDsp.cfm?ID=11391&QryRsrt=true&LnId=4&Lang=eng). The position of the ice front off Newfoundland and Labrador was measured as the latitude of the most southerly extent of ice between 50-55° W on 1 February each year during 1969-2005. That date was chosen as representing a point approximately midway through the hunting season for the two southernmost Newfoundland hunting zones (zone 3 and 4 - south of 49° N).

Independent of climate, the management of, and hunter participation in, the Newfoundland and Labrador guillemot hunt have changed since 1984. To reduce harvest levels thought to be unsustainable, regulations were introduced in 1993, limiting the hunting season to a maximum of 3.5 months (it was previously seven months long, 1 September - 31 March), and imposing a daily bag limit of 20 guillemots (Chardine et al. 2008). Migratory Game Bird Hunting Permit sales in Newfoundland and Labrador in 1984 to 2006 were extracted from Canadian Wildlife Service (CWS) files, and used as an index of annual potential harvest pressure. One adjustment to permit sales was necessary as guillemot hunters were only required to purchase a hunting permit starting in 2001, and permit sales noticeably increased in that year. To correct for the number of guillemot hunters that were not purchasing hunting permits prior to 2001, the increase in sales between 2000 and 2001 was assumed to indicate the proportion of hunters that hunted guillemots and did not purchase permits. Since there has been a decline in hunting permit sales since the 1980s, a further correction was made by determining the annual reduction in permit sales between 1996 and 2000 (a period of steady decline), which was determined to be 954 permits per year. Therefore, 954 permits were subtracted from the 2000 sales to estimate the number of permits that would have been sold in Newfoundland and Labrador in 2001 if the new regulation requiring guillemot hunters to purchase a hunting permit had not been introduced. The ratio between realized and expected sales in 2001 was 1.5297, and this ratio was used to adjust all permit sales numbers previous to 2001. Annual harvest estimates of guillemots taken were also extracted from CWS data files, and were based on special guillemot harvest surveys (similar to the National Harvest Survey, but specifically mailed to guillemot hunters) conducted sporadically between 1985 and 2006. There were harvest estimates available for ten years over this period. Relationships amongst the covariates and their trends over time were examined with simple Pearson correlations.

Results

Annual trends and relationships of ice, harvest and weather

During 1984-2006, the position of the ice front at the coast of Newfoundland and Labrador on 1 February varied from 47°00'N (1986 and 1994) to 52°00'N (2004, see Fig. 1). During 1969-2006, the median position was 48°50'N and between 1984 and 2006, it was 48°45'N. There was no secular trend in the position of the ice front on 1 February during 1969-2006 (the period for which comparable data are available; r = - 0.02, N = 38), but a northward retreat of the ice front took place between 1984 and 2006 (r = 0.79, N = 23, Fig. 2). Guillemot harvest (r = 0.925, N = 10) and hunting permit sales (r = - 0.965, N = 23) declined over the same period. As expected, guillemot harvest and hunting permit sales were related (r = - 0.877, N = 10). There was a strong relationship between southern extent of the ice and the harvest, with greater harvests when the ice front was further

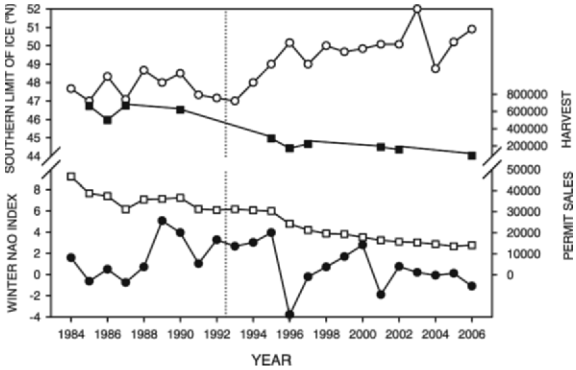

Figure 2. Trends in the winter NAO index (black circles), the southern extent of sea ice off Newfoundland on 1 February (white circles), total harvest of guillemots (black squares) and adjusted number of hunting permits sold in Newfoundland and Labrador (white squares) during 1984-2006.

south (r = - 0.936, N = 10). Although sample sizes were very small, when examining the periods before and after regulatory changes were introduced in 1993, the relationships between harvest and southern ice extent remained similar (pre-1993, r = 0.728, N = 4; 1993 onwards, r = 0.933, N = 6).

During 1969-2006, the NAO showed a negative correlation with the position of the ice front (r = - 0.40, N = 38) and a positive correlation with year (r = 0.35, N = 38). However, during 1984-2006, the NAO index was not obviously related to either ice extent (r = - 0.27, N = 23) or harvest (r = 0.32, N = 10).

Recoveries

Recoveries in the first winter varied from a minimum of 0 in 2002 to a maximum of 59 (2.6% of those ringed) in 1993 (years refer to years of ringing, not years of recovery). Corresponding numbers for birds in their second year were, minimum two (0.10-0.15%, 1994, 1995, 1997, 2001 and 2002 cohorts) and maximum 24 (1.65%, 1984). No three-year olds were recovered from the 1991, 1994 and 1999-2001 cohorts and the maximum was 16 (0.50%, 1988).

The proportion of guillemots recovered for all three age classes decreased over the study period, but no trend was apparent for adults (Table 1). Decreasing trends for second-year and third-year recoveries were approximately linear, but that for juveniles was modelled better by piecewise linear regression (two linear regressions with different slopes with a fitted breakpoint; $R^2 = 0.85$, breakpoint 1995). Up to 1997, > 0.5% of nestlings were recov-

Table 1. Relationships between southern extent of sea ice off Newfoundland (on 1 February), NAO (Hurrell 1995), adjusted hunting permit sales in Newfoundland and Labrador, guillemot harvest and years vs recovery rates of guillemots ringed on Coats Island, Nunavut and recovered in Newfoundland and Labrador. Relationships (slopes) are shown ± 1 SE with 95% confidence limits in parentheses below. Estimates were based on binomial generalized linear models for younger cohorts, while adults were modelled in Program MARK. Sea ice extent, NAO and hunting permit sales were modelled simultaneously (Type 3 analysis), and harvest and year were analysed separately due to strong colinearity among the variables.

Variable	Juveniles	Second-year	Third-year	Adults
Ice extent	-0.504 ± 0.057	-0.254 ± 0.093	-0.217 ± 0.144	-0.065 ± 0.164
	(- 0.616 - -0.392)	(- 0.436 - -0.072)	(-0.499 - 0.065)	(- 0.387 - 0.257)
NAO	-0.021 ± 0.026	-0.109 ± 0.038	-0.023 ± 0.068	-0.070 ± 0.080
	(- 0.072 - 0.029)	(- 0.183 - -0.035)	(- 0.155 - 0.109)	(- 0.228 - 0.088)
Hunting permit sales	0.258 ± 0.078	0.585 ± 0.149	0.598 ± 0.240	0.255 ± 0.173
	(0.105 - 0.411)	(0.293 - 0.878)	(0.129 - 1.068)	(- 0.086 - 0.596)
Harvest	0.266 ± 0.035	0.318 ± 0.057	0.397 ± 0.084	0.003 ± 0.012
	(0.198 - 0.334)	(0.207 - 0.430)	(0.232 - 0.562)	(- 0.027 - 0.021)
Year	-0.101 ± 0.009	-0.111 ± 0.015	-0.122 ± 0.025	-0.059 ± 0.041
	(- 0.118 - -0.085)	(- 0.140 - -0.082)	(- 0.170 - -0.074)	(- 0.140 - 0.023)

ered as juveniles in every year, whereas after 1997, this proportion was never achieved again (Fig. 3).

Recovery rates increased with increasing harvest levels in all young cohorts, while adult rates did not show any apparent trend with harvest (see Table 1). Given the tight correlation between harvest and ice extent, and the relationship between realized harvest and potential harvest (indexed by hunting permit sales), harvest was not considered further in the following models.

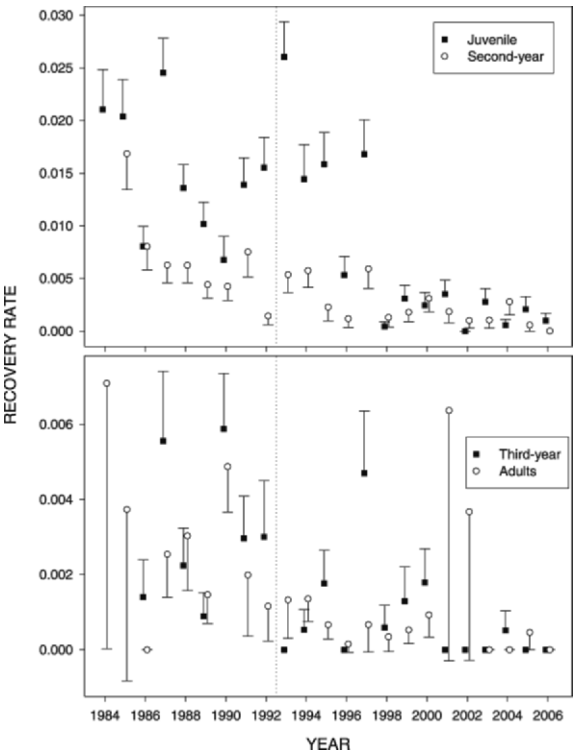

Figure 3. Recovery rates (± 1 SE) of Brünnich's guillemots ringed in Coats Island during 1984-2006, and recovered shot in Newfoundland and Labrador. The vertical dotted line represents when regulatory changes were made to the guillemot hunting season (shorter season and bag limits). Note the change in scale of the recovery rate axis between the two figures.

In models including ice extent, NAO and migratory game bird hunting permit sales, NAO was generally not related to recovery rates, except as a weak negative predictor of recovery rates in second-year birds (see Table 1). As expected, permit sales were positively related to recovery rates of all younger age classes, but not adults (see Table 1). Even controlling for harvest potential (i.e. permit sales), juvenile and second-year recovery rates were lower when ice remained further north each winter (no relationship for third-year and adult birds, see Table 1).

Further examination of the increases in juvenile recovery rates with sea ice extent shows they were similar before (β = - 0.575 ± 0.110, 95% CI: - 0.791 - - 0.359) and after (β = - 0.491 ± 0.073, 95% CI: - 0.634 - - 0.347) the regulatory changes in 1993, controlling for hunting permit sales (Fig. 4). A similar pattern was seen with second-year birds, although the relationships were weaker, and the relationship between southern ice extent and recovery rates was no longer significant after the regulatory changes (before: β = - 0.384 ± 0.163, 95% CI: - 0.703 - - 0.065; after: β = - 0.172 ± 0.141, 95% CI: - 0.448 - 0.105).

Discussion

The decline in recovery rates of Coats Island Brünnich's guillemots over the past two decades could be due to a decline in reporting rates. An effort to solicit

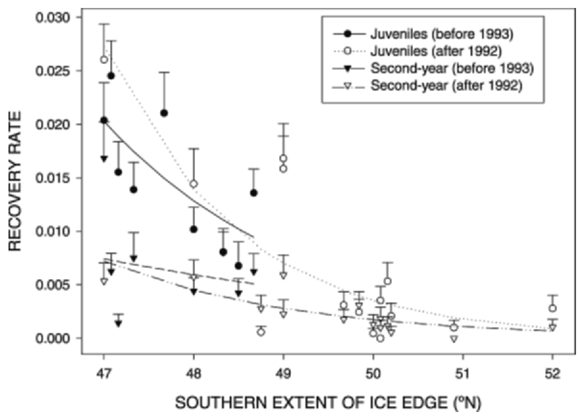

Figure 4. Recovery rates (± 1 SE) of juvenile and second-year Brünnich's guillemots ringed at Coats Island during 1984-2006, and shot in Newfoundland and Labrador, and southern edge of pack ice on 1 February. Separate lines are shown for before and after regulatory changes in 1993.

ring recoveries did occur in the mid-1980s. However, the observed reduction in the number of recoveries from Brünnich's guillemots ringed at Coats Island contrasts with data for common guillemots for which the proportion of direct recoveries of birds ringed as nestlings in Labrador and recovered by hunters has remained stable at 3-5% since the 1980s (G.J. Robertson, unpubl. data). In addition, the introduction of a toll-free phone number in 1996 to report ring recoveries led to notable increases in reporting rates of game birds in North America (Royle & Garrettson 2005). Hence, it seems unlikely that a change in the proportion of ringed guillemots being reported by hunters in Newfoundland and Labrador can be responsible for the notable decline in recovery rates.

The population of Brünnich's guillemots breeding in the eastern Canadian Arctic is thought to have expanded somewhat since the 1970s (Gaston 2002b), potentially causing dilution of the ringed birds. Average annual rates of increase at two well-monitored colonies (Coats and Prince Leopold islands) have been about 1%, suggesting that the population expanded by about 23% since 1980. If a similar expansion has occurred at other colonies in the region, it could account for some of the reduction in the proportion of birds recovered, but only a small fraction of the observed change. However, at least one very large colony (Digges Island) probably increased $< 0.5\%$ annually (Gaston 2002a). In addition, numbers of Brünnich's guillemots breeding in West Greenland have declined (Kampp et al. 1994), and therefore, the total harvestable population seems unlikely to have changed much. Overall, the contribution of population change to changes in recovery rates probably is small.

What is more difficult to assess is the interpretation of the recovery rates of second- and third-year birds, which are confounded with annual survival rates. Common guillemot cohorts may show considerable variation in juvenile survival rates (Harris et al. 2007). Yet, for survival to explain the decline in recovery rates over time, juvenile and immature survival would have to be declining as well. As described above, populations of Brünnich's guillemots are stable or growing (Gaston 2002a, A.J. Gaston, unpubl. data), and there is no evidence that recruitment has suffered in recent years, at least at Coats Island (A.J. Gaston, unpubl. data). If there is no systematic trend in juvenile survival rates, then ignoring them when considering second- and third-year recovery rates merely adds noise to the data. Considering the positive relationship between guillemot harvest estimates and recovery rates for all younger age classes, the combined evidence suggests that recovery rates are tracking harvest pressure, and could serve as a reliable index of harvest.

Changes in regulations after 1993 are thought to have reduced the annual harvest. In addition, an overall decline in the number of hunters has occurred since before 1980. Harvest estimates from 2001 and 2002 suggested a total kill of about 173,000, about 28% of the annual kill in the 1970s (612,000, Chardine et al. 1999, Wiese et al. 2004). This ratio is similar to the change in the proportion of third-year birds recovered (1986-1988: mean = 0.25% and 1999-2002: mean = 0.08, i.e. a decline to 30%), but is higher than that seen for second-year birds (1985-1988: mean = 0.93% and 1999-2002: mean = 0.19%, i.e. a decline to 20%) and much greater than that seen for juveniles over the same period (1.85-0.23%, i.e. a decline to 12%). The magnitude in the reduction seems insufficient to account for the changes seen in juvenile recovery rates. Similarly, the number of hunting permits sold in the province has not declined that rapidly; in the 2000s, the number of permits sold was about 40% of numbers sold in the 1980s.

Patterns of raw recoveries for juveniles and second-year birds in relation to year and ice conditions were very similar. This observation suggests that the wintering behaviour of juveniles and second-year birds is similar, confirming the analysis of Donaldson et al. (1997) based on information from recoveries up to 1993. The close correlation between the position of the ice front on 1 February and the proportion of juvenile recoveries (Fig. 5) strongly suggests that ice distribution is important in determining the vulnerability to hunting of juvenile (and second-year) Coats Island Brünnich's guillemots. In years when the ice front remains north of 49° N, the population has a wide choice of feeding areas off the Newfoundland coast. This relationship was still apparent when potential harvest of guillemots by hunters, as indexed by the number of hunting permits sold, was included in the analysis. In years when ice clogs bays on the northeast shores of Newfoundland, birds are denied access to those areas and concentrate along the south coast of Newfoundland and off the Avalon Peninsula. This relationship between recovery rates and ice extent also held before and after the large regulatory changes in 1993 for juvenile guillemots, suggesting ice extent is a key determinant of overall harvest pressure, even under different harvest management regimes. No abrupt change in recovery rates was seen when the new regulations were introduced in 1993. However, for juveniles and to a lesser extent second-year birds, there was an abrupt step at 1997-1998. In contrast, weather patterns, as indexed by the NAO, did not appear to have much influence on the recovery rate of guillemots.

Unlike the younger cohorts, recovery rates of adults were not related to ice extent or even harvest levels. Recovery rates of adults are very low to begin with, so there is little variation to explain. Given that adults are the most valuable segment of guillemot populations, in terms of their contribution to further population growth (Wiese et al. 2004), their apparent low vulnerability to the hunt makes regulating the hunt at sustainable levels more tractable. It is apparent that any changes in regulations or future shifts in ice distribution will likely effect harvest pressure primarily on the younger cohorts.

If the recovery rate for juvenile Coats Island guillemots has fallen faster than the rate of reduction in the harvest, then this could suggest that a greater proportion of birds from other colonies are being shot by Newfoundland hunters. Recent information from geologger devices deployed at colonies in the Eastern Canadian Arctic suggests that the majority of adult Coats Island guillemots winter to the north of Newfoundland, but that more northerly colonies winter further south (A.J. Gaston, P.A. Smith & L. Tranquilla, unpubl. data). If this is a general pattern, the changes that we describe here may lead to a shift in hunting pressure towards Brünnich's guillemots from more northerly colonies. As described previously, recovery rates of juvenile common guillemots from colonies to the south in Labrador have remained high, so it is possible that common guillemots now comprise a larger portion of the Newfoundland harvest than earlier. However, these ideas remain speculative at present, and will require future attention.

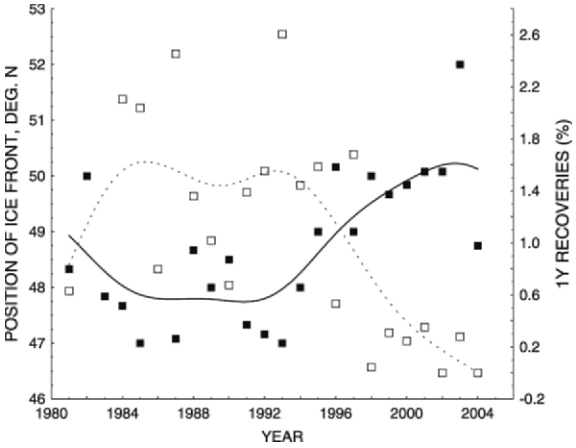

Figure 5. Proportion of juvenile Brünnich's guillemots recovered in Newfoundland and Labrador (white squares) and the southern limit of the pack ice front on 1 February (black squares), showing trends fitted by distance-weighted least squares method of Statistica version 7.1 (dotted line = juveniles recovered, solid line = pack ice limit).

Conclusions

Changes in the number of birds shot by hunters and, to a lesser extent, changes in the size of the total population, probably contributed to the steep decline in recovery rates for Coats Island Brünnich's guillemots in Newfoundland over the past two decades. However, there is no indication from our results that regulation changes in 1993 had any demonstrable effect on numbers recovered. The difference among age classes suggests that an additional factor was at work. For juvenile birds, heavy ice conditions in February were associated with higher recovery rates. Since 1997, the ice front in February has generally remained north of 48° N. This has been associated with very low recovery rates for juvenile birds, presumably because they were not limited to feeding in areas where they were especially vulnerable to hunters. Older birds (third-year birds and adults) seem to be less affected by ice conditions than juvenile birds. The behaviour of second-year birds may be intermediate between the two groups. Because all trends (ice conditions and recovery rates) are closely correlated with year, no definitive explanation can be identified. However, the data are most consistent with the idea that the proportion of juvenile recoveries is largely determined by ice conditions in late winter. Concerning the regulation changes adopted in 1993, the desired outcome of reducing the harvest of guillemots was achieved, but our study demonstrates that environmental factors, in this case sea ice conditions, may have a greater influence on the harvest than any regulatory changes.

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