Status of the Largest Breeding Concentration of Atlantic Puffins, *Fratercula arctica,* in North America

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Suspected declines due to oil pollution, accidental entrapment in fishing gear, expanding gull populations, and the Capelin (*Mallotus villosus*) fishery have generated concern for the Atlantic Puffin (*Fratercula arctica*) population in the western Atlantic. The majority of that population breeds on three islands within the Witless Bay Seabird Ecological Reserve off the southeast coast of Newfoundland. We conducted a census of the numbers of puffins breeding on the largest colony there on Great Island in 1993-1994. The product of three component measurements, colony area of 15.2 ha, average burrow density of 0.92 ± 0.04 burrows/m^2, and average burrow occupancy rate of 87.9 ± 3.1%, gave a breeding population estimate of 123 000 ± 7 000 pairs. Most of the difference between our estimate and a previous estimate of 52 000 pairs from 1979 was attributed to the fact that burrow occupancy in 1979 was determined during the late chick stage after many eggs and chicks would have failed, thus giving a lower estimate of the number of pairs initiating breeding. Similar burrow density in 1979 and 1994, and expansion of colony area from 12.9 to 15.2 ha, mainly due to colonization of interior habitat, provided evidence that the breeding population of Atlantic Puffins on Great Island has expanded in recent years.

Key Words: Atlantic Puffin, *Fratercula arctica*, Great Island, census, populations, survey methods, Newfoundland.

Breeding colonies of Atlantic Puffins (*Fratercula arctica*) in the northwest Atlantic were severely reduced or eliminated by hunting, egg collecting, habitat destruction, and the introduction of domestic animals throughout the 18th and 19th centuries (Drury 1973-1974; Nettleship and Evans 1985). Most colonies were eliminated in the Gulf of Maine and Bay of Fundy, and numbers were greatly reduced in Newfoundland, Labrador, and along the north shore of the Gulf of St. Lawrence (Bent 1919). Reduction of human exploitation allowed puffin populations to recover partially during the early and mid-20th century. However, factors such as mortality from oil pollution, accidental entrapment in fishing nets, fisheries impacts on Capelin (*Mallotus villosus*)—the puffins' primary summer prey (Rodway and Montevecchi 1996)—and increasing numbers of kleptoparasitic and predatory Herring (*Larus argentatus*) and Great Black-backed (*L. marinus*) gulls, have renewed concern for Atlantic Puffin populations since the 1970s (Nettleship and Evans 1985; Nettleship 1996).

Since at least the mid-1960s, a significant proportion of the North American Atlantic Puffin population has bred on three islands (Gull, Green, and Great) within the Witless Bay Seabird Ecological Reserve off the southeast coast of Newfoundland (Nettleship and Evans 1985). Observations of puffins nesting in Witless Bay date from the mid-19th century, but quantitative estimates were not attempted until 1967 when D. N. Nettleship and L. M. Tuck made preliminary estimates of 75 000 pairs on Gull, 20 000 pairs on Green, and 100 000 pairs on Great islands (Nettleship and Evans 1985). More detailed surveys gave estimates of 60 000, 17 000, and 148 000 pairs in 1973 (Nettleship and Evans 1985), and 30 000, 9300, and 52 000 pairs in 1979 (Cairns et al. 1989) for Gull, Green, and Great islands, respectively.

Different methods used in 1973 and 1979 made comparisons difficult and prevented conclusions that breeding numbers had really declined during that period (Cairns and Verspoor 1980*; Nettleship, unpublished data). However, other evidence suggests that puffin numbers have declined in the past on Great Island. Small sections of the colony showed reductions of 22-25% in the number of burrows recorded between 1973 and 1979 (Cairns and Verspoor 1980*; Nettleship, unpublished data), and counts of adults in attendance early in the season at one study plot declined 76% between 1974 and 1981 (Nettleship et al. 1989*).

We estimated the numbers of Atlantic Puffins breeding on Great Island in 1993-1994, using methods that could be easily replicated for future comparisons. We also mapped the distribution of different vegetation types that may be related to the activities of nesting birds (Harris 1984). We confined our efforts to Great Island because it is the largest colony in the northwest Atlantic, most previous data indicating population declines pertained to that colony, and limited resources allowed a thorough survey of only

*See Documents Cited section

one major colony. We compare our results to previous studies, and extrapolate conclusions about the status of the Great Island breeding population to the Witless Bay population as a whole.

Methods

Great Island (47° 11′ N, 52° 46′ W) is part of the Witless Bay Seabird Ecological Reserve and lies approximately 2.4 km offshore of southeast insular Newfoundland (Figure 1). The island has been described in detail by Nettleship (1972).

Three component measurements were used in the calculation of a breeding population estimate for puffins on Great Island: burrow density, the proportion of burrows that were occupied by nesting birds (occupancy rate), and colony area (Nettleship 1976; Evans 1980; Bibby et al. 1992). Burrow occupancy was determined on 17-28 June 1993 as part of a larger study on puffins in 1992-1993 (Rodway et al. 1998). Burrow density was determined and colony area mapped 22 July to 8 August 1994 (more details are given in Rodway et al. 1996*).

Burrow density was estimated by calculating the average density of burrows in 237 sample quadrats. Quadrats were distributed using a stratified, centred start, systematic sampling scheme (Madow 1953) to ensure adequate representation of different parts of the colony. Ten permanently marked parallel transects, 100 m apart, were run east and west across the island from a centre line measured down the long axis of the island (Figure 2). Quadrats 2 × 2 metres in size were established at 5 m intervals throughout the puffin colony along each transect. Numbers of burrows were counted and angle of slope was measured to the nearest degree in each quadrat. An entrance was called a burrow if its tunnel extended more than 50 cm and did not connect with another entrance within 100 cm. In rare cases, tunnels less than 50 cm were called burrows if they contained obvious nest cups, eggs, or chicks.

Occupancy rate was determined by a single check of a sample of burrows during the mid-incubation period. This provided a conservative estimate of burrow occupancy because some eggs may have been lost before or laid after burrows were checked. Occupancy was determined in 140 burrows (28 plots of five burrows each). Sample plots were stratified by habitat and location to minimise possible biases due to position in the colony (see Nettleship 1972; Rodway et al. 1998). A burrow was considered

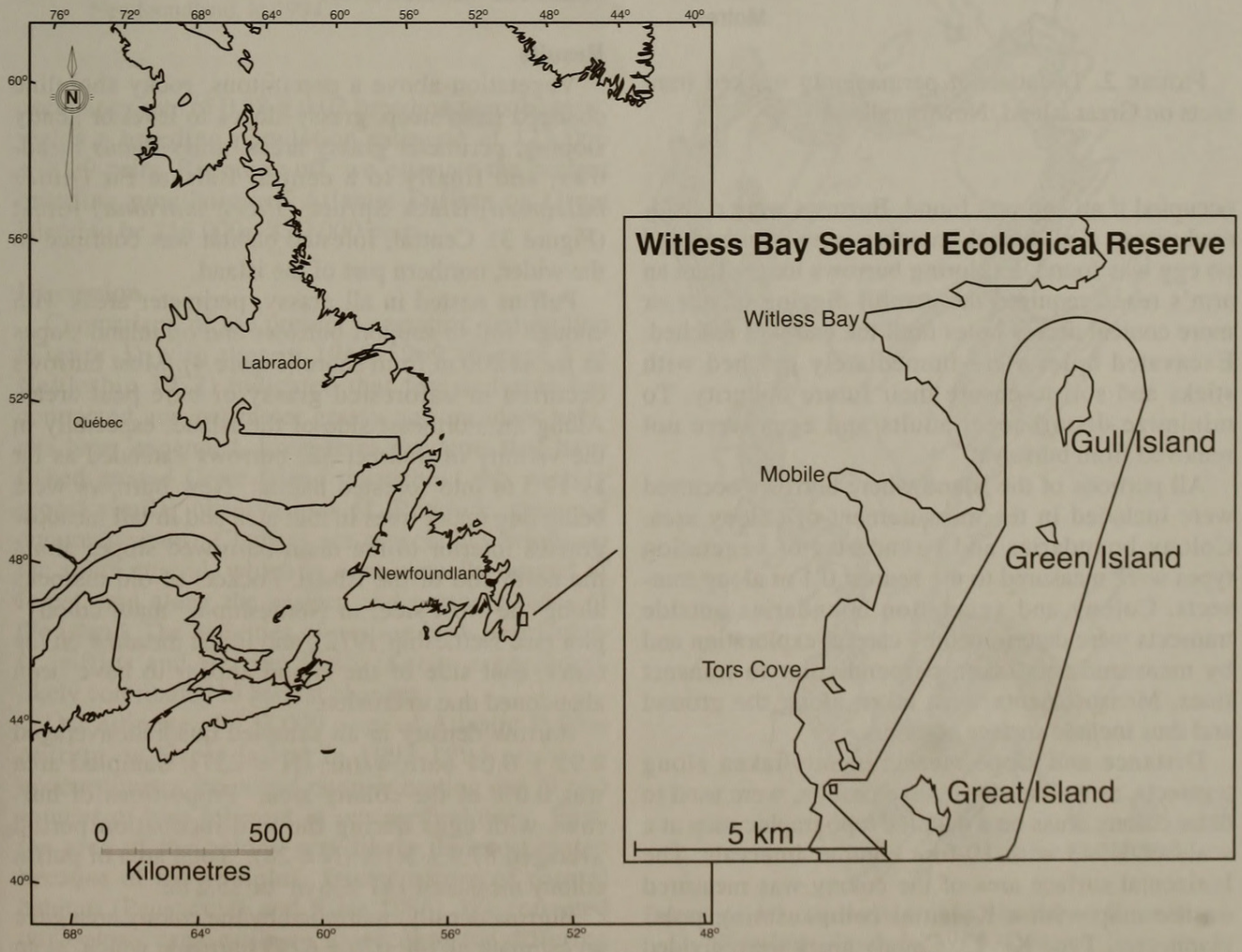

FIGURE 1. Location of Great Island and Witless Bay Seabird Ecological Reserve, Newfoundland.

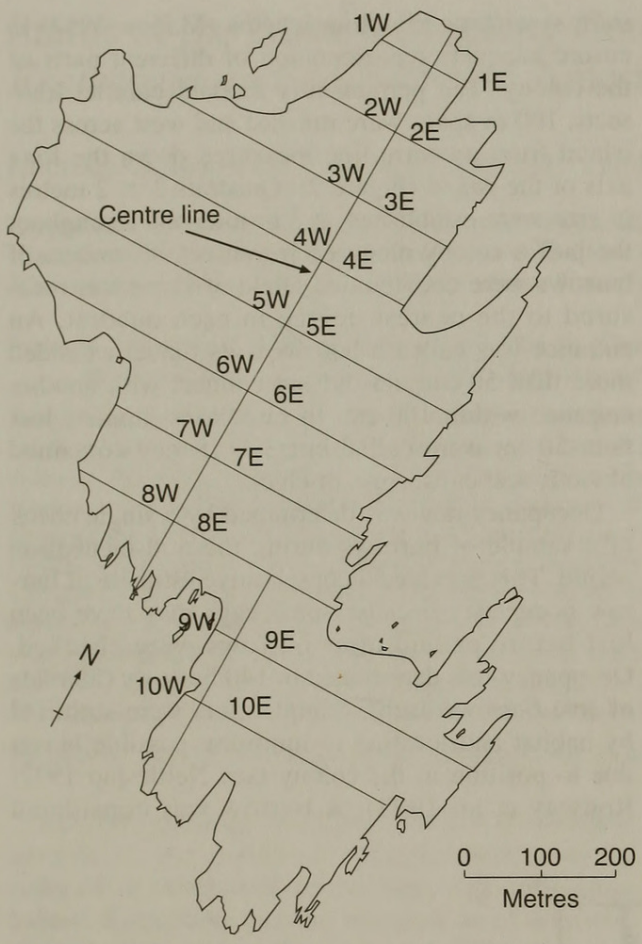

FIGURE 2. Location of permanently marked transects on Great Island, Newfoundland.

occupied if an egg was found. Burrows were considered empty if all tunnel branches were explored and no egg was found. Exploring burrows longer than an arm's reach required the careful digging of one or more conical access holes until the end was reached. Excavated holes were immediately patched with sticks and soil to ensure their future integrity. To minimize disturbance, adults and eggs were not removed from burrows.

All portions of the island where burrows occurred were included in the measurement of colony area. Colony boundaries and boundaries of vegetation types were measured to the nearest 0.1 m along transects. Colony and vegetation boundaries outside transects were determined by careful exploration and by measurements taken perpendicular to transect lines. Measurements were taken along the ground and thus include surface contours.

Distance and slope measurements taken along transects, as well as during exploration, were used to draw colony areas on a detailed topographic map at a scale of 1:943 with 10-foot contour intervals. The horizontal surface area of the colony was measured on the map with a Koizumi compensating polar planimeter, Type KP-23. Colony areas were divided into sections with similar slopes. Adjusting for slope, the area of individual sections was given by:

$$C_s = A_h T^2 (\cos Q)^{-1},$$

where C_s is the colony surface area, A_h is the area on the map, T is the scale of the map, and Q is the mean slope along the transects or, if measured areas did not fall along transects, the average slope calculated from the spacing of the 10′ contour lines. To improve accuracy, each small section delimited on the map was measured three times with the planimeter, and the mean of those three measures was used to calculate the area. Colony area calculations took into account the average uphill slope, but not the undulations between quadrats or between transects. Therefore our calculations give a conservative estimate of the total surface area available to birds for nesting.

The total number of burrows in the colony (B) is the product of the overall average density of burrows, as determined in the quadrats, and the total area of the colony. B multiplied by the occupancy rate (R) gives an estimate of total nesting pairs (P). The standard error (SE) of P is calculated as follows:

$$SE(P) = (B^2 \text{ Variance}(R) + R^2 \text{ Variance}(B) - \text{Variance}(B) \text{ Variance}(R))^{1/2}$$

(Rodway et al. 1996*. Means are quoted plus or minus one standard error.

Results

Vegetation above a precipitous, rocky shoreline changed from steep, grassy slopes to level or gently sloping, perimeter grassy areas, grass-*Rubus* meadows, and finally to a central Balsam Fir (*Abies balsamea*)/Black Spruce (*Picea mariana*) forest (Figure 3). Central, forested habitat was confined to the wider, northern part of the island.

Puffins nested in all grassy, perimeter areas with enough soil to support burrows and on inland slopes as far as 200 m from shore (Figure 4). Most burrows occurred in unforested grassy or bare peat areas. Along the northeast side of the island, especially in the vicinity of transect 3E, burrows extended as far as 17.5 m into forested habitat. New burrows were being dug under trees in that area and in tall meadow grasses interior to the main burrowed slopes along the north end of the island. Pockets of old tussocks along the west side, in Nettleship's "main colony" plot (see Nettleship 1972), and in the meadow on the outer, east side of the island appear to have been abandoned due to erosion.

Burrow density in all sampled quadrats averaged 0.92 ± 0.04 burrows/m^2 (N = 237). Sampled area was 0.6% of the colony area. Proportions of burrows with eggs during the mid-incubation period averaged 87.9 ± 3.1% (N = 28). Total area of puffin colony measured 151 936 m^2 or 15.2 ha.

Burrow density multiplied by the colony area gave an estimate of 140 070 ± 6245 burrows, which, at an

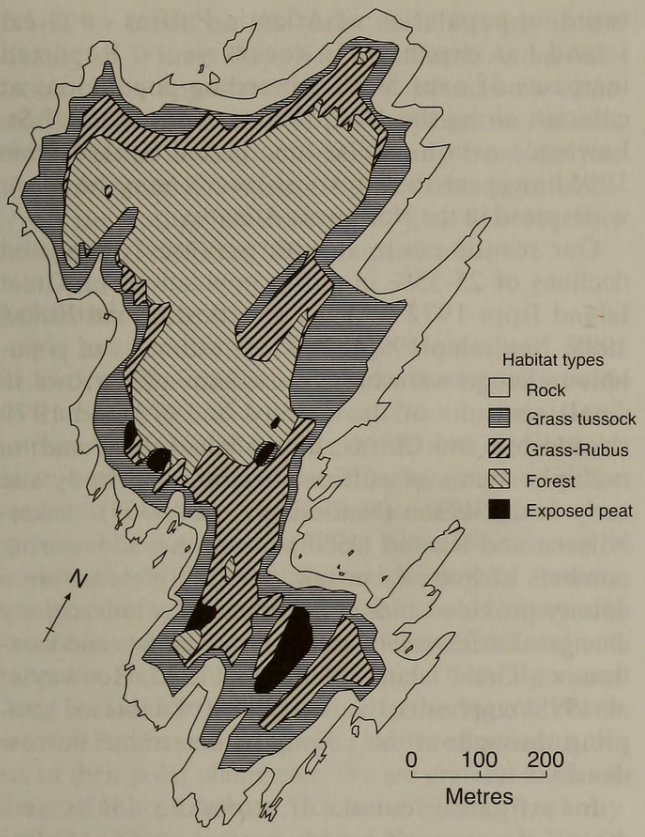

FIGURE 3. Distribution of vegetation types on Great Island, Newfoundland, in 1994.

occupancy rate of 0.88 ± 0.03 breeding pairs/burrow, yields a breeding population estimate of 123 066 ± 7029 pairs. Rounding off, we estimate the current breeding population of Atlantic Puffins on Great Island to be 116 000 – 130 000 pairs.

Discussion

Comparison of the present vegetation distribution (Figure 3) with that in 1968-1969 (Figure 2 in Nettleship 1972) indicated that forested area has contracted and perimeter grassy and meadow habitats have expanded. Long-term residents that have fished around Great Island throughout this century report similar observations (J. Reddick, personal communication). Changes are especially obvious on the southern end, which is now virtually devoid of forest, and along the eastern and northern sides of the island. The activities of nesting birds, particularly puffins and Herring Gulls (*Larus argentatus*), likely contributed to habitat changes.

Our estimate of 123 000 pairs of Atlantic Puffins nesting on Great Island in 1993-1994 probably underestimates the actual number nesting due to two sources of bias inherent in our methodology. First, the area of the colony was likely underestimated because of the complex, fractal nature of natural habitats (Pennycuick and Kline 1986). We corrected our colony area estimate to account for differing slopes in quadrats spaced 5 m apart along transects, which were spaced 100 m apart. However, smaller hills or valleys between quadrats or transects would not have been characterized at our scale of measurement. Second, occupancy rates may have been underestimated because any burrow in which an egg had been lost and not replaced before the single check during incubation would not be considered occupied. Although the present estimate is conservative, results from future surveys using the same methodology should be comparable.

Our 1993-1994 estimate was over double the latest previous estimate of 52 000 pairs obtained in 1979 (Cairns and Verspoor 1980*; Nettleship, unpublished data). The current estimate is closer to the earlier one of 148 000 pairs made in 1973 (Nettleship and Evans 1985). A detailed account of the methods used in the 1973 survey has not been published and so we were unable to compare our estimate with that one. Methods used in 1979 (Cairns and Verspoor 1980*) were in general similar to those used in this study, and some comparisons are possible.

The difference in the population estimates from 1979 (Cairns and Verspoor 1980*) and 1993-1994 was due to a lower occupancy rate in 1979 (44.1 vs.

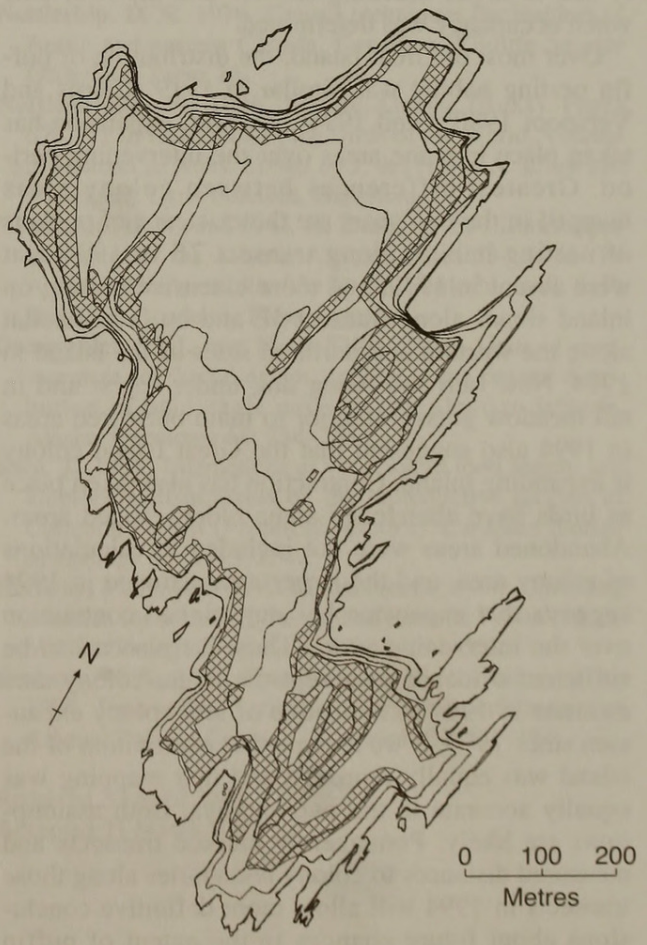

FIGURE 4. Atlantic Puffin colony (shaded) on Great Island, Newfoundland, in 1994. Contour lines are at 50-foot intervals.

87.9%), and larger colony area estimate in 1994 (15.2 vs. 12.9 ha). Differences in occupancy rates and area estimates accounted for 86% and 14%, respectively, of the difference in population estimates between the two years. Burrow densities in 1994 and 1979 were very similar (0.92 ± 0.04 vs. 0.91 ± 0.4 burrows/m^2, respectively).

The occupancy rate in 1979 was much lower than in 1993 because in 1979 burrow occupancy was determined during the late chick stage. In so doing, burrows in which an egg or chick was lost without replacement before the census were not considered occupied and, as a result, observed occupancy rates in 1979 were lower. Also, proportions of adult puffins that initiate breeding vary in response to environmental conditions, resulting in potentially large inter-annual changes in burrow occupancy rates (Ashcroft 1979; Harris and Murray 1981). Because occupancy rates depend to a large degree on breeding success up to the time of the survey, lower breeding success could also contribute to lower occupancy rates recorded in 1979. Breeding success indeed was lower on nearby Gull Island (Figure 1) in 1979 (Rice 1985) than on Great Island in 1993 (Rodway et al. 1998). Therefore, we conclude that the lower occupancy rate estimated in 1979 was likely due to lower breeding success and the later date when occupancy was determined.

Over most of Great Island, the distribution of puffin nesting habitat was similar in 1979 (Cairns and Verspoor 1980*) and 1994; however, expansion has taken place in some areas over the intervening period. Greatest differences between colony areas mapped in the two years are the existence of pockets of nesting habitat along transect 7E in 1994 that were absent in 1979, and more extensive nesting on inland slopes along transect 5E and on level habitat along the western and northern sides of the island in 1994. New burrows being dug under forest and in tall meadow grasses interior to main burrowed areas in 1994 also suggested that the Great Island colony is expanding inland. Contraction has also taken place as birds have abandoned some older, eroded areas. Abandoned areas were not included in calculations of colony area, and the larger area estimate in 1994 suggests that expansion has outweighed contraction over the intervening years. Thus, there seems to be sufficient evidence to accept the larger colony area estimate in 1994 as indicative of real colony expansion since 1979, if we assume that exploration of the island was equally thorough and that mapping was equally accurate in the two surveys. Both assumptions are likely. Permanently marked transects and measured distances to colony boundaries along those transects in 1994 will allow more definitive conclusions about future changes in the extent of puffin nesting habitat on Great Island.

Given that burrow density was similar in 1979 and 1994, the increase in colony area suggests that the breeding population of Atlantic Puffins on Great Island has expanded in recent years. Reported increases of over 50% in breeding populations at colonies along the North Shore of the Gulf of St. Lawrence over a similar time period (Chapdelaine 1995) suggest that upward trends may be more widespread in the Northwest Atlantic.

Our results contrast with previously reported declines of 25-35% in puffin populations on Great Island from 1972 to 1989 (Nettleship and Evans 1985; Nettleship 1996). Previous estimates of population change were based on counts of burrows in small sections of the colony in 1973 and 1979 (Nettleship and Cairns, unpublished data) and on multiple counts of puffins attending one study site early in the season (Nettleship et al. 1989*). Anker-Nilssen and Røstad (1993) found that monitoring numbers of burrows in few, selected plots within a colony provided biased estimates of whole-colony changes. Differences found among habitats and locations on Great Island (Nettleship 1972; Rodway et al. 1998) emphasize the importance of unbiased sampling throughout the colony to determine burrow density.

Investigating counts of attending adults as a means of censusing burrow-nesting puffins, Cairns (1979) reported error rates of 43% after 10 within-season replicate counts, and concluded that counts of attending puffins were of little use as indicators of population size. Thus, these methods are likely less reliable indicators of population change than the comparative colony-wide censuses conducted in 1979 and 1993-1994. Also, our exploration showed that the "Main colony" study area used by Nettleship to monitor attendance has been partially abandoned by the puffins. This may have contributed to apparent declines in attending adults.

For future surveys, we recommend that occupancy rates be determined early in the breeding season (i.e., during incubation) and that timing be standardized so that comparisons between years, habitats, or other factors are not confounded by differences in breeding success. Although burrow density estimates were almost identical in 1979 and 1993-1994, the use of more frequent, smaller quadrats in this study resulted in much narrower confidence limits than in 1979, and is recommended for future monitoring.

Population estimates for the puffin colonies on Gull and Green islands within the Witless Bay Seabird Ecological Reserve also were made in 1979 (Cairns and Verspoor 1980*; Nettleship, unpublished data). If we assume that the relative populations of the three Witless Bay islands have remained constant since 1979, our 1994 estimate for Great Island suggests a total population then of 200 000 – 230 000 pairs for the three colonies combined.

The total North American population of Atlantic Puffins is estimated to be in the region of 350 000 - 400 000 pairs (Chardine 1999*), of which over half

(54-62%) breed on the three main islands in the vicinity of Witless Bay, Newfoundland. As an indication of the importance of Great Island on a continental scale, about 30% of North American Atlantic Puffins breed at this location. Clearly then, the fate of North American Atlantic Puffins rests significantly on the future well-being of the Witless Bay colonies and on Great Island in particular.

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