UPDATE AND TRENDS OF THREE IMPORTANT SEABIRD POPULATIONS IN THE WESTERN NORTH ATLANTIC USING A GEOGRAPHIC INFORMATION SYSTEM APPROACH

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SUMMARY

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The productive waters of Newfoundland, Canada, render this region host to nationally and globally important breeding seabird populations. This study updates estimates and trends of three major populations using a Geographic Information System (GIS) approach to estimate occupied areas of high-density breeding seabirds, correcting for slope. Our results show that the Common Murre *Uria aalge* breeding population on Funk Island remains the largest in the western North Atlantic at 472 259 SE 32 740 (CI 398 669–545 849) pairs and increased at a rate of +0.3% per year between 1972 and 2009. The Atlantic Puffin *Fratercula arctica* colony on Great Island, Witless Bay, increased between 1979 and 1994 and continues to host the largest population of this species in North America at 174 491 (CI 147 559–201 423) breeding pairs estimated in 2011; the population has stabilized and may be showing signs of decline. Finally, Leach's Storm-Petrel *Oceanodroma leucorhoa* breeding on Great Island, previously the second largest population in the western North Atlantic, has declined by 55% since 1979; it was estimated at 134 139 (CI 76,818–191,459) pairs in 2011, and is the lowest to date. Our GIS approach incorporated a 3D model to correct for slope of nesting areas; compared with traditional non-GIS techniques, this approach increased the estimated occupied area by 5%–10% for flat surfaces occupied by murres, by 16%–36% for moderate slopes occupied by storm-petrels, and by 40%–46% for steep slopes occupied by puffins. The application of newer tools such as high resolution satellite imagery and digital elevation models, coupled with GIS, are becoming more common and continue to improve the efficiency and accuracy of assessing occupied areas of high-density breeding seabirds.

Key words: geographic information system, monitoring, Newfoundland, population estimate, population trend, seabirds

INTRODUCTION

The productive waters and rugged coastline of Newfoundland, Canada, render this region a host of nationally and globally important breeding seabird colonies (e.g. Sklepkovych & Montevecchi 1989, Chardine *et al*. 2003, Robertson *et al.* 2006, Chardine *et al.* 2013). Although some threats that seabirds face in the marine environment, such as drowning in gillnets and oil pollution, appear to have declined off the coast of Newfoundland (e.g. Wilhelm *et al.* 2009, Regular *et al.* 2013, Robertson *et al.* 2014), other concerns are on the rise, such as light attraction to coastal urban areas (Wilhelm *et al*. 2013) and interactions with oil and gas platforms (Ronconi *et al.* 2015). Furthermore, changes in the ocean's climate are yielding a more unpredictable environment for seabirds to successfully rear their young, causing ecosystem shifts and affecting predator-prey interactions (e.g. Massaro *et al.* 2000, Montevecchi *et al.* 2013). Monitoring the status and trends of breeding seabirds is an important tool to help assess the cumulative effects of these threats and develop conservation actions to minimize human-related activities.

By far the most abundant breeding seabird species in Newfoundland are Leach's Storm-Petrel *Oceonodroma leucorhoa*, Common Murre *Uria aalge* and Atlantic Puffin *Fratercula arctica* (Cairns *et al.* 1989, Lock *et al.* 1994), with a significant proportion of the breeding population protected within the boundaries of six Seabird Ecological Reserves; access to these reserves is managed by Newfoundland and Labrador's Department of Environment and Conservation (http://www.env.gov.nl.ca/env/parks/wer/find.html; accessed 22 May 2015). The Funk Island Ecological Reserve hosts the largest Common Murre colony in the western North Atlantic (Montevecchi & Tuck 1987), while the Witless Bay Ecological Reserve supports the largest Atlantic Puffin population in North America (Chardine 1999) and the second largest Leach's Storm-Petrel population in the western North Atlantic (Robertson *et al.* 2006).

Despite the regional importance of these colonies, the population size of these and other significant colonies of species with similar breeding habits are estimated only at irregular intervals, because of the challenges associated with obtaining reliable population estimates for species that breed in very high densities (e.g. Birkhead & Nettleship 1980, Gaston & Nettleship 1981, Guinet *et al.* 1995, Falk & Kampp 1997). The preferred method to estimate abundance in large, dense colonies is to multiply the density of breeding birds by the estimated occupied breeding area (e.g. Nettleship 1976, Birkhead & Nettleship 1980, Guinet *et al.* 1995, Egevang *et al.* 2003). Estimating populations of Atlantic Puffins and Leach's Storm-Petrels provides additional constraints, because the birds nest in burrows and rock crevices that are difficult to access (e.g. Rodway *et al.* 2003, Ambagis 2004).

This study updates the population size estimates of Common Murres breeding on Funk Island and Atlantic Puffins and Leach's Storm-Petrels breeding on Great Island (part of the Witless Bay Seabird Ecological Reserve) by applying a Geographic Information System (GIS) approach to calculate occupied areas of high density breeding seabirds at these sites and correcting for slope of the terrain. Prior estimates of occupied breeding areas of these colonies used a planimeter on hand-sketched maps or photographs; areas occupied by seabirds nesting on sloping surfaces were then corrected by incorporating slope information (e.g. Stenhouse *et al*. 2000, Chardine *et al.* 2003, Rodway *et al.* 2003). Because of the differences between these techniques, we contrast results of GIS and non-GIS (planimeter) methods, revise past breeding pair estimates based on revised occupied areas, and present updated population trends of these three important seabird colonies.

STUDY AREA AND METHODS

Species and study area

Funk Island (49°45′N, 53°11′W) is a small and relatively flat low-lying (approximately 14.2 m at its highest point) granite island located 60 km offshore from the northeast coast of insular Newfoundland (Fig. 1; Nettleship 1980). The Common Murre colony, which is characterized as a "flat-top colony" (Birkhead & Nettleship 1980), has been monitored since 1936, with the most recent population estimate, for 2006, being 434 702 breeding pairs (J.W.C., unpubl. data).

Great Island (47°11'N, 52°46'W) is one of four islands that form the Witless Bay Ecological Reserve (Fig. 1) and is characterized by a rocky, convoluted coastline, forming deep coves, with steep cliffs reaching heights of 75 m along its north side (Cairns & Verspoor 1980). The rugged coastline gives way to puffin habitat, characterized as steep grassy slopes (peaking at 90 m) and open peat. The interior edge of the puffin habitat is bounded by more gently sloping or level *Rubus* meadows that lead to a dense forest in the centre of the island, predominantly composed of Balsam Fir *Abies balsamea* and Black Spruce *Picea mariana*. Leach's Storm-Petrels are found throughout the *Rubus* meadow and forest, rarely encroaching on puffin habitat, although puffins are expanding their breeding area into the edge of the forest (Rodway *et al*. 2003). The puffin colony on Great Island has been monitored since 1950, with the most recent population estimate being 123 066 pairs, dating back to 1993/94 (Rodway *et al*. 2003). Two previous population estimates exist for the storm-petrel colony on Great Island, with the most recent having been conducted in 1997 (269 765 pairs; Stenhouse *et al*. 2000).

Colony mapping and occupied area analysis using a GIS approach

Funk Island

Vertical aerial photographs of the Common Murre colony on Funk Island were taken between 11h00 and 13h00 on 15 July 2000, 8 July 2006 and 13 July 2009 through a manhole located on the underside of a single-engine Beaver aircraft, flying at an altitude of 304.8 m (1 000 feet). The camera used in 2000 was a Pentax 645 equipped with Kodak TMAX 100 black and white film (Chardine *et al*. 2003), while the 2006 and 2009 aerial photographs were taken with Canon digital SLR cameras at a resolution of 1 pixel = 10 cm. In 2009, the three subsections of the colony (Southwest, Central and Indian Gulch, Fig. 2) were photographed with one image each, allowing overlap between photographs so that the entire colony could be reconstructed into a photomosaic in ArcGIS 10.0 ESRI Inc. The three images were georeferenced based on a total of 18 distinct landmarks visible on the photographs. Coordinates for these locations were collected on the ground using a handheld Geographic Positioning System (GPS) in July 2010.

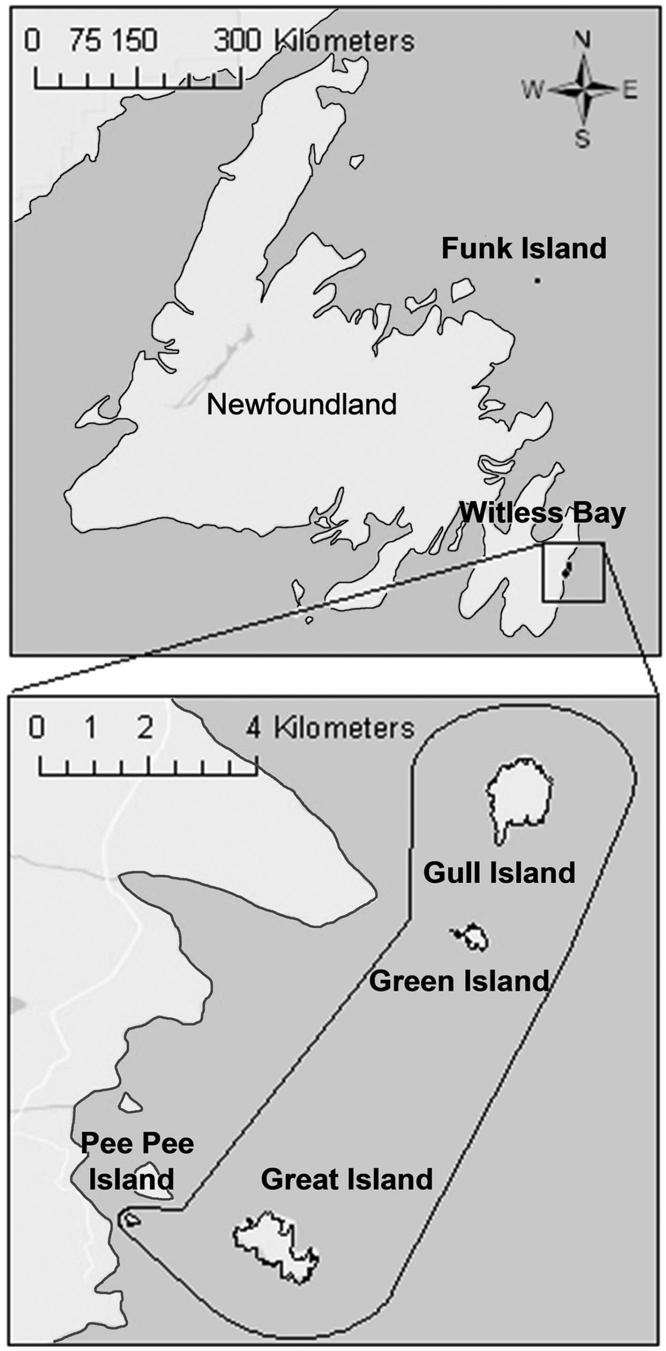

Fig. 1. Location of Funk Island and Great Island (part of the Witless Bay Seabird Ecological Reserve) in eastern Newfoundland, Canada.

To assess the area occupied by murres in 2009, each sub-colony, as well as isolated groups of murres bordering the sub-colonies, were delineated as separate polygons in ArcGIS at a scale of 1:150. The perimeter of the colony is easily determined, as the densely packed breeding murres appear as a uniform dark blanket on the images (Chardine *et al*. 2003). Pools of water within each sub-colony were also delineated and excluded from the total occupied area. Population estimates for 2000 and 2006 were based on occupied area derived by tracing the perimeter of the colony on a printed photograph (12 × 16 inches) at a mean scale of 1:575 (Chardine *et al*. 2003). For this study, we used the same outlined perimeters as those determined for previous population estimates by scanning the original tracings on printed images and georeferencing the boundaries in ArcGIS as outlined above; the extent of the murre colony, or occupied area, was subsequently re-calculated for each year in ArcGIS.

Great Island

We digitized a habitat map that outlined the areas occupied by puffins and storm-petrels on Great Island in 1979 (Cairns & Verspoor 1980) and georeferenced this map in ArcGIS by using 10 distinct landmarks around the periphery of the island (e.g. sharp rock tips at mouth of coves) obtained from Google Earth 5.1. Three points were ground-truthed using a handheld GPS unit in the field, and these revealed that the locations obtained from Google Earth were accurate within 5–10 m of those obtained from the handheld GPS, which in turn are accurate within 3 m.

Rodway *et al*. (1996, 2003) generated maps delineating the boundaries of the puffin and vegetation types on Great Island in 1994; areas identified as *Rubus* meadow and forest were inferred as areas occupied by storm-petrels in 1994 (Stenhouse *et al*. 2000).

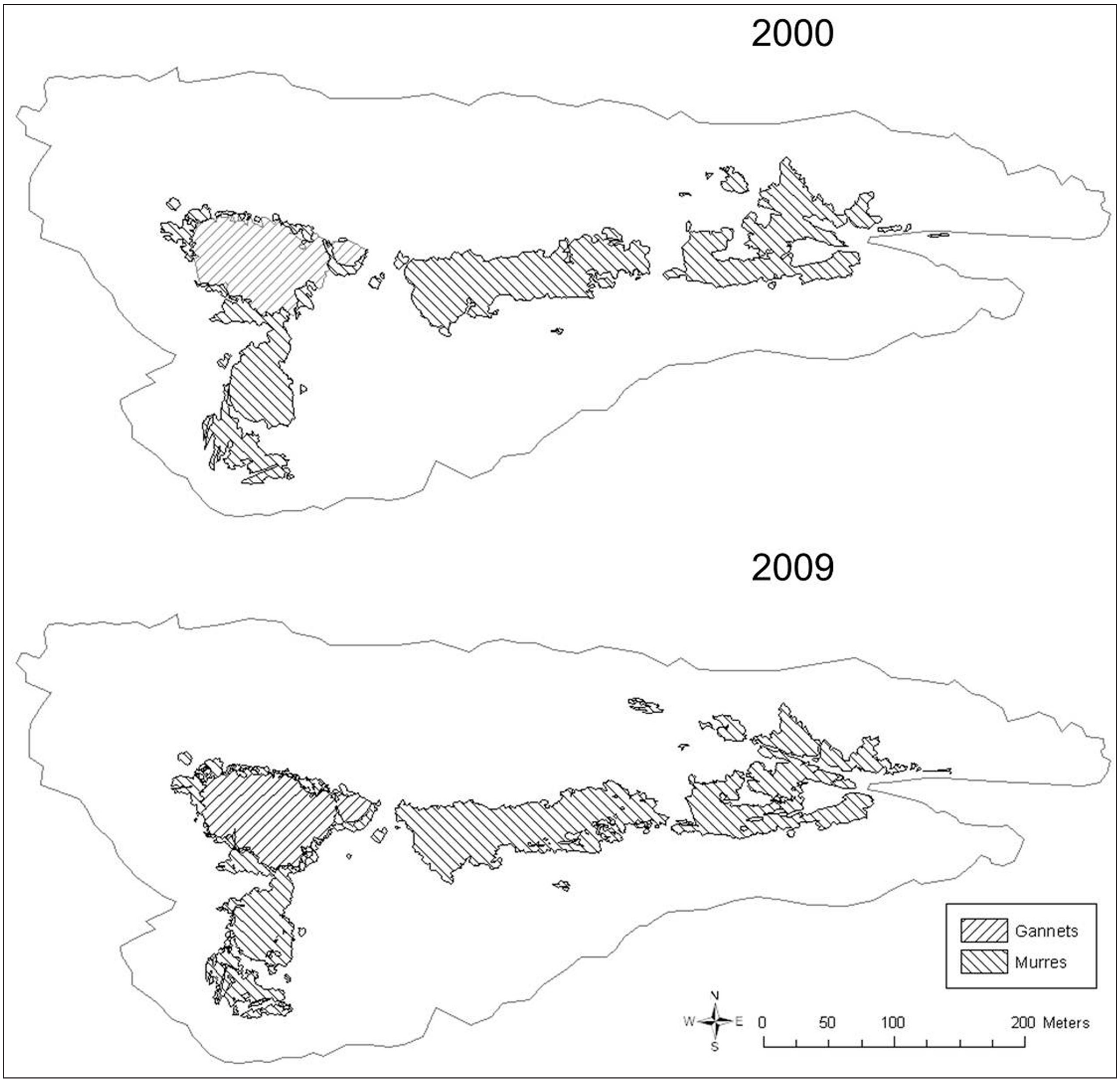

Fig. 2. Maps of Funk Island showing area occupied by Common Murres and Northern Gannets in 2000 and 2009.

Both images were digitized and georeferenced using ArcGIS, and the areas occupied by both species were digitized following the procedures outlined above.

To update the puffin and storm-petrel colony map, a vertical high-resolution digital aerial photograph of Great Island, taken during the summer of 2008, was obtained from Surveys and Mapping Division, Department of Environment and Conservation, Government of Newfoundland and Labrador. This image was georeferenced in ArcGIS in the same manner as described above. This photograph served as the basis to delineate the three prominent types of habitat on Great Island (bare rock, low-lying vegetation and forest) as separate polygons in ArcGIS, at a scale of 1:800. The low-lying vegetation was further sub-divided into the puffin-occupied grass and storm-petrel-occupied *Rubus* meadow as follows. In August 2011, two of the authors (S.I.W. and J.M.) walked along the border of the two habitat types while holding a handheld GPS set to acquire location coordinates at 10 m intervals; this track was subsequently imported into ArcGIS and served as the boundary between grass and *Rubus* meadow. This habitat delineation was further refined during field activities related to assessing burrow density and occupancy (see below).

A topographic map of Great Island at a scale of 1:943 with 3.048 m (10′) contour intervals was digitized into polyline format in ArcGIS (Fig. 3). A three-dimensional (3D) island was subsequently extruded in ArcGIS to produce a 3D island based on elevation. The aerial photo and the digitized boundaries of the puffin and storm-petrel colonies for 1994 and 2011 were draped over the 3D island and formed the basis of the 2D and 3D occupied areas calculated in ArcGIS.

Breeding bird density

Common Murre

Mean densities of breeding Common Murres on Funk Island have been previously estimated at 22.9 pairs/m^2, but no variance was reported (Birkhead & Nettleship 1980). Obtaining updated information on Common Murre densities on Funk Island is not possible, because researchers no longer visit this colony during the incubation period. However, Common Murre breeding densities were collected on South Cabot Island (49°10′N, 53°21.5′W), a smaller but structurally similar colony located approximately 65 km south of Funk Island. During late incubation in 2005, twelve 1 m × 1 m plots were established at random within the colony, and all eggs were counted in each plot, revealing a mean density of 23.0 SE 1.6 pairs/m^2, with a range of 18–37 pairs/m^2. The Cabot Island colony, although not as large (~10 000 breeding pairs, S.I. Wilhelm, unpubl. data) as the one on Funk Island, has similar characteristics. It is located on a flat bedrock island and also meets the criteria for a high density flat-top colony (Birkhead & Nettleship 1980). Because the density of Common Murres breeding on Cabot Island was no different than those observed on Funk Island, we used the results from Cabot Island, which has an associated variance around the mean, to calculate the number of breeding pairs on Funk Island in 2009.

Atlantic Puffin

In ArcGIS, we overlaid an island-wide 50 m × 50 m grid over the georeferenced aerial photograph of the 2008 image and retrieved the coordinates for all intersections that fell within low-lying vegetation (i.e. not bare rock or forest; Renner *et al*. 2006, Reynolds & Renner 2014). Between 23 and 29 June 2011, coinciding with late incubation/early chick rearing, each of these intersections were visited and a 3 m × 3 m plot was established in grass or exposed peat habitat, using rope anchored by pegs at each corner, to assess burrow density and occupancy rates. Within each plot (n = 65), observers inserted their arms down each hole and tunnel to assess its contents and assigned each hole to one of the following categories: (1) extra entrance to a burrow, (2) too short to be a burrow (tunnel <30 cm in length), or (3) burrow (tunnel ≥30 cm long) and status of burrow (i.e. empty, adult, adult and egg, egg only, adult and chick, chick only, or could not be determined). If the observer's arm did not reach the end of the burrow, a wooden spoon was used to help extend the observer's reach and "feel" for an adult, chick, or egg. During this time, observers also recorded the angle of the slope (to the nearest degree) using a Suunto clinometer and the vegetation type associated with each puffin plot (grass or exposed peat) to ground-truth and modify the habitat map accordingly.

Burrow density was calculated for each plot by dividing the number of burrows present by the area sampled (9 m^2), including burrows for which the contents could not be determined but excluding holes categorized as an extra entrance or too short to be a burrow. A single burrow occupancy rate was derived for the entire colony by calculating the proportion of burrows occupied (i.e. burrows containing at least an adult and/or an egg/chick) in relation to all burrows where contents were assessed (i.e. occupied burrows and empty burrows but excluding entrances, burrows that were too short, or burrows where the contents could not be determined). In keeping with the approach used by Rodway *et al*. (2003), burrow occupancy rate was based on plots containing at least five burrows.

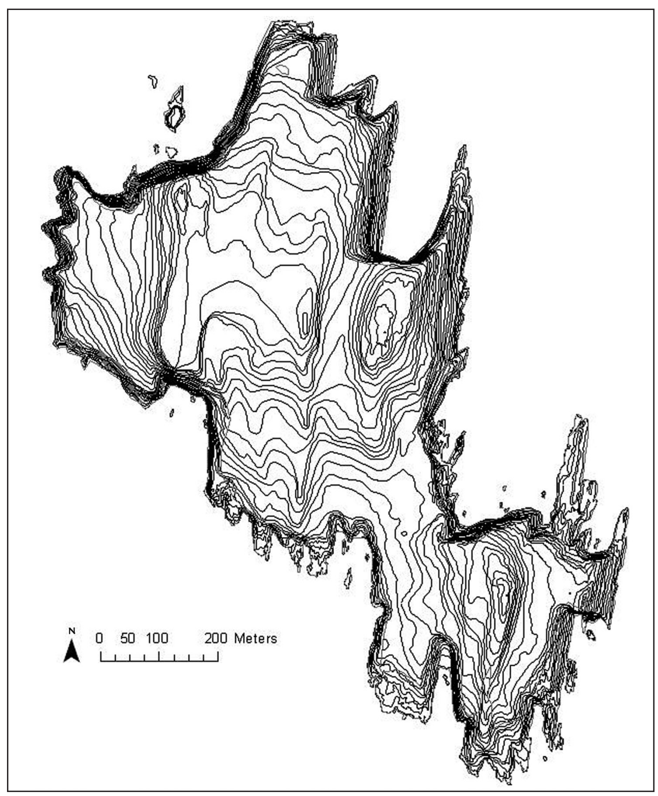

Fig. 3. Digitized topographic map of Great Island, Witless Bay, Newfoundland and Labrador. Contour lines are at 3.048 m (10 foot) intervals.

Because not all burrows within each plot could be determined for content, we further restricted our analyses to include plots for which at least 50% of the burrows could be assessed. A total of 46 plots met both criteria; the contents of 310 burrows within these plots were determined.

Leach's Storm-Petrel

In ArcGIS, the 50 × 50 m island-wide grid, described above, was used to randomly select sampling sites within the storm-petrel habitat to determine burrow density and occupancy rates. All grid intersections that fell within open storm-petrel habitat based on the colony mapping (i.e. low-lying vegetation not occupied by puffins) were visited on the ground. However, due to time constraints, only every other site along the east-west gridline was assessed in the forest habitat. A total of 48 plots (22 in open habitat, 26 in forest), each measuring 2.5 m × 2.5 m, were assessed between 23 and 29 June 2011, which coincided with late incubation/early chick-rearing. Three adjacent plots located in open habitat revealed no storm-petrels occupying these areas, but rather high concentrations of nesting Herring Gulls *Larus argentatus,* and were excluded from the study. Although other plots assigned as storm-petrel habitat also revealed no storm-petrels breeding within the plot (five in open habitat, three in forest), these were included in the burrow density analysis. Occupancy rates were assessed by an observer inserting an arm in each storm-petrel hole and assigning the outcome into one of the following categories: (1) extra entrance to a burrow, (2) too short to be a burrow (tunnel <30 cm long), or (3) burrow (tunnel ≥30 cm long); and status of burrow (i.e. empty, adult, adult and egg, egg only, adult and chick, chick only, or could not be determined). In addition, playback recordings were used on burrows for which contents could not be assessed, to elicit a response if an adult bird was in the burrow (Ambagis 2004); if no response was elicited, the status of these burrows remained unknown. All plots were thoroughly searched for holes by carefully combing through the vegetation; we assumed that all holes were detected. Observers also recorded the vegetation (*Rubus* meadow or forest) and slope associated for each plot. Contents were assessed for 34 burrows in open habitat and 128 burrows in forest habitat; occupancy rates were determined for each habitat type separately.

Data analyses

The number of Common Murre pairs breeding on Funk Island was calculated as the product of total occupied area and breeding bird density. The associated 95% confidence intervals (CI) were based on the standard error (SE) of breeding bird density. For all years, the estimated numbers of puffin and storm-petrel breeding pairs on Great Island were calculated as the product of burrow density, occupancy rate and total occupied area as determined using the 3D analysis. The SE of the breeding pair estimates was calculated following Rodway *et al*. (1996, 2003). The associated lower and upper confidence limits were calculated by multiplying the SE by the returned inverse of the *t*-distribution (df = number of plots) and either adding or subtracting this product to the breeding pair estimate. Regression analyses were used to determine whether the angles of the slope were related to burrow density of puffins (grass and exposed peat were pooled) and of storm-petrels breeding in open (*Rubus* meadow) and forest habitat. A Mann-Whitney rank sum test was applied to compare the burrow density of storm-petrels breeding in open and forest habitat. Burrow density and occupancy rates are presented as mean and SE, while population estimates are presented as the mean, SE and CI.

RESULTS

Funk Island

Occupied area

The total 2D area occupied by Common Murres on Funk Island varied between 19 820 and 20 533 m^2 between 2000 and 2009, with the overall area occupied by Common Murres having increased by 3% during that time period: Murres expanded their occupied areas in the Central and Indian Gulch sub-colonies by 8%, while the Southwest sub-colony retracted by 5% since 2000 (Table 1, Fig. 2). The occupied area of breeding Common Murres was previously assessed on Funk Island using a Koizumi Placom digital

TABLE 1
Estimated area occupied by breeding Common Murres on Funk Island, Newfoundland and Labrador, in 2000, 2006 and 2009, using a two-dimensional analysis in ArcGIS

Year	Occupied area, m^2 [a] (% difference compared with ArcGIS results)			
	Southwest	Central	Indian Gulch	Total
ArcGIS				
2000	6 570	6 917	6 365	19 852
2006	6 640	7 271	5 909	19 820
2009	6 224	7 439	6 870	20 533
Planimeter				
2000	6 023 (-8)	6 195 (-10)	5 713 (-10)	17 931 (-10)
2006	6 272 (-6)	6 909 (-5)	5 627 (-5)	18 807 (-5)

[a] Occupied areas previously assessed using a non-GIS approach (Koizumi Placom digital planimeter, as described in Chardine *et al*. 2003) are also presented for 2000 (Chardine *et al*. 2003) and 2006 (J.W. Chardine, unpubl. data) for comparison.

TABLE 2
Original and corrected estimated pairs of Common Murres breeding on Funk Island, Newfoundland and Labrador, Canada, from 1972 to 2009 and corresponding annual change

Year	Number (confidence interval)	
	Original estimates	Corrected estimates
1972	389 461 (372 857–405 337)[a]	426 104 (409 024–444 655)
2000	412 524 (373 427–451 621)[a]	452 227 (409 649–495 428)
2006	434 702 (380 440–488 965)[b]	456 949 (399 843–513 912)
2009	472 259 (398 669–545 849)[c]	472 259 (398 669–545 849)
Annual change 1972–2009	+0.6%	+0.3%

[a] Chardine *et al*. (2003)
[b] J.W. Chardine, unpubl. data
[c] This study

planimeter for the 2000 and 2006 surveys; compared with these two estimates, the GIS approach increased the estimated occupied area by 5%–10% (Table 1).

Breeding density, population status and trends

Densities of breeding murres appeared homogeneous across the three Funk Island sub-colonies, based on close visual examination of the high-resolution photographs taken in 2009. Applying the density factor of 23.0 SE 1.6 pairs/m^2 to the total estimated area occupied by murres on Funk Island yielded 472 259 SE 32 740 (CI 398 669–545 849) breeding pairs of Common Murres in 2009 (Table 2).

To assess changes in breeding pair estimates between 1972 and 2009, we revised the original 1972, 2000 and 2006 estimates by taking into account the proportion of the colony size underestimated by the non-GIS approach (Table 1). Because we did not have access to the 1972 photographs, we assumed that the occupied area was underestimated by at least the same proportion as that calculated for the 2000 survey, because similar techniques were used to assess occupied area between those two surveys (Chardine *et al*. 2003). The Common Murre breeding population on Funk Island has changed little over the past three decades, having increased at a rate of +0.3% per year between 1972 and 2009 based on corrected population estimates, and at a rate of +0.6% per year using original population estimates (Table 2).

Great Island

Occupied area

Using ArcGIS, the 3D approach estimated occupied area by puffins in 2011 at 265 289 m^2; this area was underestimated by 72% when the slope of the habitat was not accounted for (i.e. 2D approach; Table 3). Similarly, the estimated areas occupied by storm-petrels were underestimated by 24% in both open and forest habitats when analyzed using only a 2D approach. Previous puffin (1979 and 1994) and storm-petrel (1979) surveys corrected for slope by mapping the occupied areas for each species on the same topographic map used for the 2011 study and applying trigonometric corrections to the planimeter-estimated occupied area based on slope measurements (Cairns & Verspoor 1980, Rodway *et al*. 1996, 2003). This approach increased the 2D occupied area by 7%–8% for puffins and 6%–8% for storm-petrels, but continued to underestimate the 3D GIS area by 40%–46% and 16%, respectively (Table 3).

Since 1979, the area occupied by puffins on Great Island has increased by 11%, with notable expansions observed since 1994 along the southern portion of the island and to a lesser extent inland along the northern part of the colony (Fig. 4). In contrast, since 1979, area occupied by storm-petrels breeding in open habitat has decreased by 49% (Table 3), with habitat retraction apparent across the whole island since 1994 (Fig. 5a). While the overall occupied area has remained unchanged for storm-petrels breeding in forest habitat (Table 3), shifts in forest distribution have occurred, with the most southern forest patches having completely disappeared and new growth having occurred along the northern coast of the island (Fig. 5b).

Breeding density, population status and trends

In 2011, burrow density of Atlantic Puffins averaged 0.92 SE 0.05 burrows/m^2 (n = 65 plots), with an average occupancy rate of 0.72 SE 0.03 (n = 46 plots). Burrow density did not vary significantly with slope (r = 0.085, P = 0.503, n = 65). Based on the occupied burrow density and the 3D occupied area (Table 4), we estimate that 174 491 SE 13 380 (CI 147 559–201 423) pairs of puffins were breeding on Great Island in 2011. Previous population estimates were sporadic between the years 1973 and 1994 (Brown *et al*. 1975, Cairns & Verspoor 1980, Rodway *et al*. 1996, 2003, Robertson *et al*. 2004). The methodology used for the 1973 survey is not known; however, the surveys between 1979 and 1994 were based

TABLE 3
Estimated areas occupied by breeding Atlantic Puffins and Leach's Storm-Petrels (open and forest habitat) on Great Island, Witless Bay, Newfoundland and Labrador, in 1979, 1994 and 2011

	Area, m^2 [a] (% difference from ArcGIS results)								
	Atlantic Puffin			Leach's Storm-Petrel					
				Open			Forest		
Year	**2D**	**3D**	**% increase**	**2D**	**3D**	**% increase**	**2D**	**3D**	**% increase**
ArcGIS									
1979	120 606	238 306	97	109 538	140 645	24	159 563	199 791	25
1994	140 371	255 072	82	92 393	112 875	22	154 804	193 565	25
2011	154 190	265 289	72	58 001	71 758	24	161 902	200 835	24
Non-GIS slope-corrected approach									
1979		129 158 (-46)			117 780 (-16)			168 641 (-16)	
1994		151 936 (-40)			72 696[a] (-36)			128 460[a] (-34)	

[a] Occupied area was estimated by placing a 1 × 1 mm square grid over the habitat map provided in Rodway *et al*. (1996) and counting the number of squares falling into each habitat type (see Stenhouse *et al*. 2000), and using ArcGIS from which the delineated polygons were extruded as two-dimensional (2D) and three-dimensional (3D) surfaces. Percent increase in occupied areas using the 2D versus the 3D approach and change in occupied 3D occupied area from 1979 to 2011 are also presented. Occupied areas (m^2) previously assessed using a non-GIS approach are included for 1979 (Cairns & Verspoor 1980) and 1994 (Rodway *et al*. 1996, 2003; Stenhouse *et al*. 2000) for comparison.

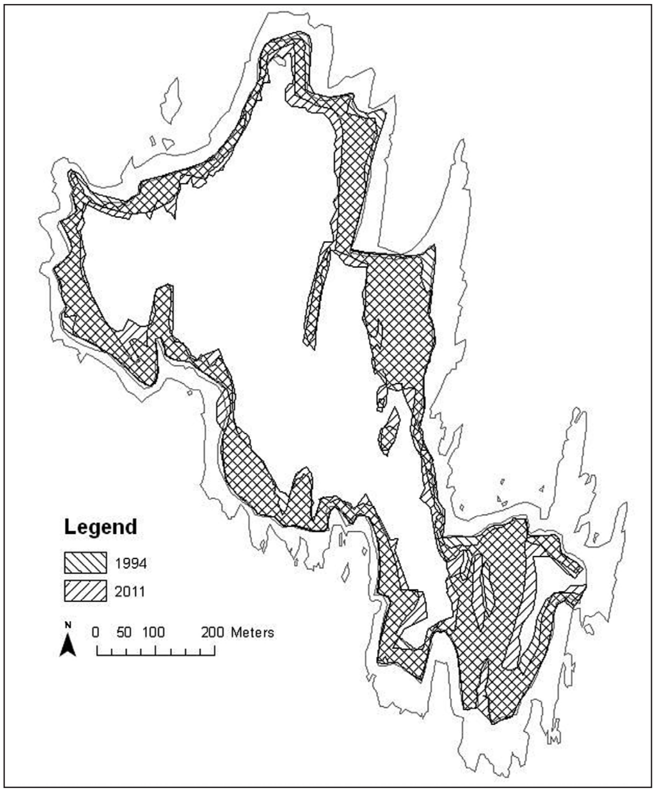

Fig. 4. Extent of the Atlantic Puffin colony on Great Island in 1994 and 2011. Boundaries for 1994 were digitized from Rodway *et al*. 1996.

on occupied burrow rate and occupied breeding area; to make these previous estimates comparable to the approach used for the 2011 estimate, we re-calculated the breeding populations by using the 3D occupied area of the GIS approach and occupied burrow densities previously reported. Based on previous population estimates, it would appear that the puffin colony on Great Island almost tripled in size, at a rate of +7.4% per year between 1979 and 2011; however, the population trend using corrected occupied area and breeding pair estimates showed a more modest increase of +1.5% per year (Table 4).

In 2011, storm-petrel burrow density in open habitat averaged 0.29 SE 0.08 burrows/m^2 (n = 19 plots) with an average occupancy rate of 0.64 SE 0.18 (n = 14 plots), while burrow densities in forest habitat averaged 0.69 SE 0.12 burrows/m^2 (n = 26 plots) with a mean occupancy rate of 0.88 SE 0.08 (n = 21 plots; Table 5). Storm-petrels bred in significantly higher densities in forest compared with open habitats (Mann-Whitney U = 137.5, $P = 0.001$). Burrow density did not vary significantly with slope for either open ($r = 0.442$, $P = 0.066$, n = 19) or forest habitats ($r = 0.246$, $P = 0.225$, n = 26). Based on the occupied burrow densities and the 3D occupied areas provided in Table 3, we estimate that 13 061 SE 3 065 (CI 6 603–19 518) pairs of storm-petrels were breeding in open habitat and 121 078 SE 21 510 (CI 70 215–171 941) pairs in forest habitat, for a total of 134 139 SE 24 575 (CI 76 818–191 459) pairs breeding on Great Island in 2011. We re-calculated the breeding populations by using the 3D occupied area of the GIS approach and occupied burrow densities previously reported. The corrected estimates increased the total number of pairs of storm-petrels breeding on Great Island by 18% for 1979 and by 29% for

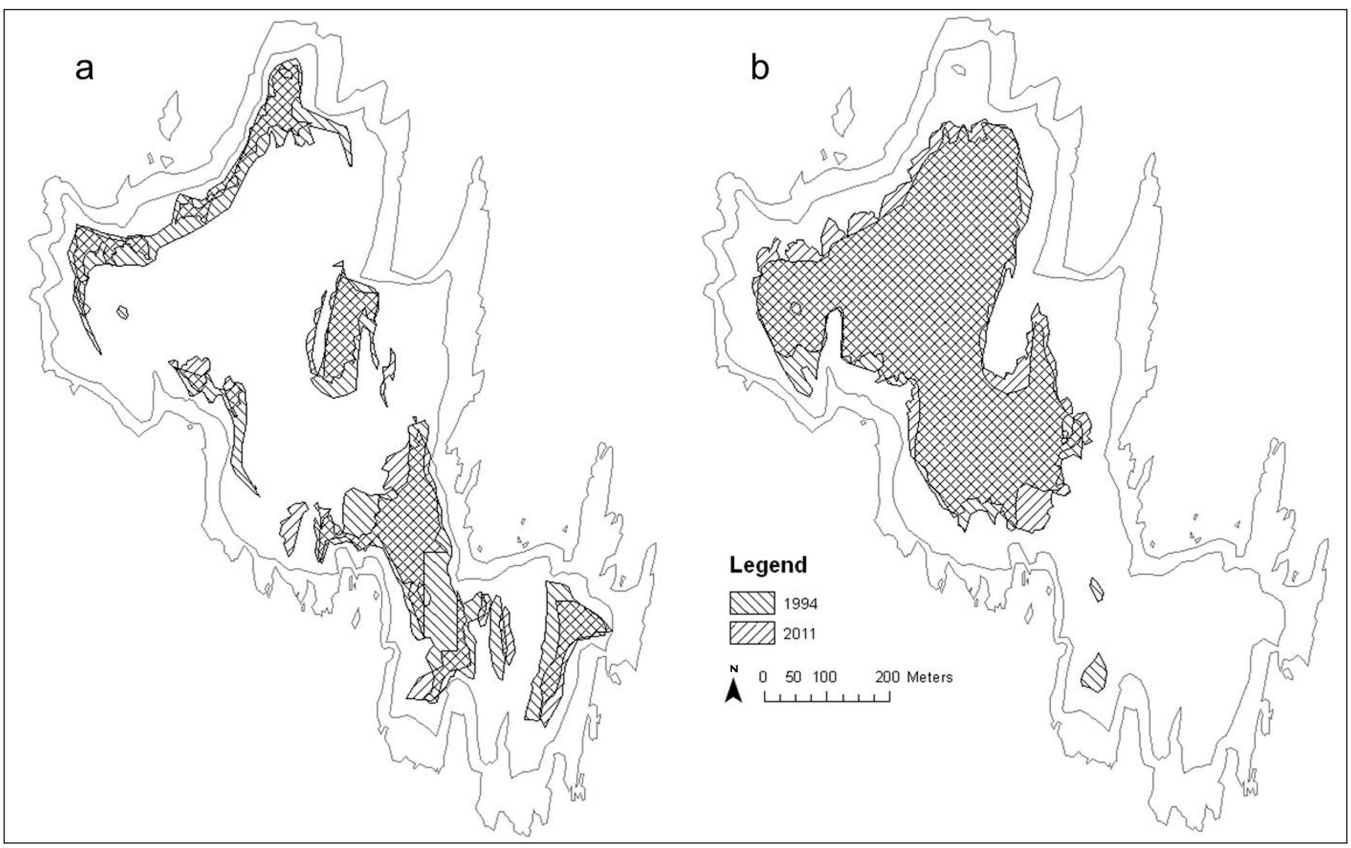

Fig. 5. Extent of the Leach's Storm-Petrel colony breeding in open (a) and forest habitat (b) on Great Island in 1994 and 2011. Boundaries for 1994 were digitized based on the habitat map illustrated in Rodway *et al*. (1996).

1997; based on the corrected population estimates, the storm-petrel colony on Great Island has declined at an annual rate of -2.8% in open and -1.0% in forest habitats between 1979 and 2011 (Table 5).

DISCUSSION

Population status and trend

Common Murres breeding on Funk Island

The Common Murre colony on Funk Island is considered one of the oldest in the western North Atlantic (Tuck 1961). The colony was dramatically reduced by the late 1800s as a result of over-exploitation (Nettleship & Evans 1985, Montevecchi & Tuck 1987), but recovered to become the largest Common Murre colony in the western North Atlantic (Brown *et al*. 1975), which we currently estimate at 472 000 pairs. Based on occupied area and detailed mapping of the murre sub-colonies, the colony is expanding along the eastern side of the Central sub-colony and along both the northern and southern edges of the Indian Gulch sub-colony. The Southwest sub-colony has shown signs of retraction, with a 5% decline in occupied area since 2000. A decline was previously observed in this sub-colony between 1972 and 2000 and was attributed to the expanding Northern Gannet *Morus bassanus*

TABLE 4
Burrow density, burrow occupancy rate, original, and corrected estimated pairs of Atlantic Puffins breeding on Great Island, Witless Bay, Newfoundland, between 1979 and 2011

Year	Burrows/m^2 (SE)	Occupancy rate (SE)	Original estimate (CI)	Corrected estimate[e] (CI)
1979	0.91 (0.07)[a]	0.54[b]	51 653 (39 000–65 000)[a]	117 104 (108 096–126 112)
1984	0.76 (0.07)[c]	0.84 (0.02)[c]	86 692 (70 614–102 770)[c]	159 427 (129 877–188 977)
1985	0.70 (0.06)[c]	0.90 (0.01)[c]	82 076 (69 062–95 090)[c]	151 086 (127 017–174 917)
1993/94	0.92 (0.04)[d]	0.88 (0.03)[d]	123 066 (116 000–130 000)[d]	206 604 (182 687–230 520)
2011	0.92 (0.05)	0.72 (0.03)	174 491 (147 559–201 423)	174 491 (147 559–201 423)
Annual change 1979–2011			+7.4%	+1.5%

[a] Cairns & Verspoor (1980)
[b] Re-calculated based on Rodway *et al.* (1996)'s finding that burrow occupancy was under-estimated by 22% as a result of being assessed during late chick-rearing.
[c] Robertson *et al.* (2004)
[d] Rodway *et al.* (1996, 2003)
[e] Population estimates were corrected based on occupied area using the 3D GIS model from Table 3 for each corresponding year, with the exception of 1984 and 1985, which were based on the 3D occupied area of 1979 (Robertson *et al.* 2003).

TABLE 5
Burrow density, burrow occupancy rate, original, and corrected estimated pairs of Leach's Storm-Petrels breeding on Great Island, Witless Bay, Newfoundland, in 1979, 1997 and 2011

Year	Burrows/m^2 (SE)	Occupancy rate (SE)	Original estimate (CI)	Corrected estimate[e] (CI)
Open				
1979	1.26[a]	0.62[a]	104 000[a]	123 768 (93 832–153 704)[b]
1997	1.53[c]	0.56[c]	63 972 (48 315–79 629)[c]	99 330 (73 977–124 684)[d]
2011	0.29 (0.08)	0.64 (0.18)	13 061 (6 603–19 518)	13 061 (6 603–19 518)
Annual change 1979–2011			-2.7%	-2.8%
Forest				
1979	1.60[a]	0.67[a]	148 910[a]	175 816 (129 587–222 405)[b]
1997	2.21[c]	0.73[c]	205 793 (165 551–246 035)[c]	247 686 (184 445–390 127)[d]
2011	0.69 (0.12)	0.88 (0.08)	121 078 (70 215–171 941)	121 078 (70 215–171 941)
Annual change 1979–2011			-0.6%	-1.0%

[a] Cairns & Verspoor (1980)
[b] Based on occupied burrow rate of 0.88 SE 0.09 per m^2 as reported in Cairns & Verspoor (1980)
[c] Stenhouse *et al*. (2000)
[d] Based on occupied burrow rate of 0.88 SE 0.11 per m^2 as reported in Stenhouse *et al*. (2000)
[e] The 1979 population estimate was corrected based on occupied area using the 3D GIS model for that year while the 1997 corrected estimate is based on occupied area for 1994 (Table 3).

colony around which the murres breed and which has remained stable since 2000 (Chardine *et al*. 2013). The reason the occupied area for murres was lower in 2009 is probably a result of the ability to exclude more unoccupied breeding areas (e.g. pools of water of varying sizes) within the sub-colony using the GIS approach.

While it appears that the largest colony of Common Murres in the western North Atlantic is still showing signs of very modest growth, this colony is likely close to its maximum size and likely has been since the late 1950s (Tuck 1961). Although movement between and slight variations within sub-colonies will continue to be observed, this colony is unlikely to expand very much beyond its current boundaries, as most of the available unused areas around the periphery of this flat low-lying island are washed over by waves during storms and high seas (Chardine *et al*. 2003). In addition to habitat limitation, constraints associated with breeding in a colony inhabited by such a large biomass of pursuit-diving birds can quickly deplete local food supplies. Common Murres breeding on Funk Island have longer foraging trips, lower chick-feeding rates, and poorer-quality fledglings (Davoren & Montevecchi 2003) as a result of parents travelling long distances to find predictable food sources (Davoren *et al*. 2003). These breeding conditions may negatively affect reproductive success and adult survival and thereby limit recruitment and population growth.

Atlantic Puffins breeding on Great Island

Puffins have been known to breed in Witless Bay since at least the 19th century, although reports of a colony on Great Island can only be traced back to the early 1940s (Montevecchi & Tuck 1987). The colony grew to become the largest Atlantic Puffin colony in North America (Chardine 1999) and continues to hold this status, with 175 000 breeding pairs estimated in 2011. Although this population has most certainly increased since 1979, it appears that it has stabilized or perhaps even declined since 1994, with fewer burrows being occupied by breeders. Visual representations of the occupied areas in the different years reveal that puffins are expanding inland, which encroaches on the more level storm-petrel habitat in both forested and low-lying vegetation, and away from the steeper sea-facing cliffs. Consistent with this, during field visits we observed that the grassy habitat along the outer edge of the coastal cliffs has eroded away, likely as a result of the puffins' excavating activity and exposure to harsh environmental conditions. Puffins may prefer the steeper coastal cliffs that allow quick access to their burrows when returning with a fish to avoid kleptoparasitism by gulls (Nettleship 1972, Harris & Wanless 2011).

The expansion of the puffin colony into forested areas and grassy meadows normally occupied by storm-petrels was already observed in 1993–1994, suggesting that puffins have saturated all suitable grass habitats on Great Island for some time (Rodway *et al*. 1996, 2003). Such expansion in Witless Bay corroborates the findings that breeding conditions were overall quite favourable up to the early 2000s, as inferred by high food availability, high chick growth rates (Rector *et al*. 2012) and high proportions of non-breeding birds observed on the breeding slopes (Calvert & Robertson 2002). However, since 2003, food availability has become more variable in Witless Bay, which is reflected in reduced growth rates of chicks (Rector *et al*. 2012). Furthermore, extreme cold and wet weather conditions in 2011 caused the death of thousands of puffin chicks across the Witless Bay Reserve during the late chick-rearing period (Wilhelm *et al*. 2013). Continued close monitoring of this internationally important colony is imperative in light of these concerns.

Leach's Storm-Petrels breeding on Great Island

Storm-petrels have been known to breed in Witless Bay since at least the 1940s (Montevecchi and Tuck 1987); however, previous population estimates for Great Island are only available for 1973 (170 000 pairs, Brown *et al*. 1975), 1979 (252 910 pairs, Cairns & Verspoor 1980) and 1997 (269 765 pairs, Stenhouse *et al*. 2000). The current population estimate of 134 000 pairs in 2011 is the lowest to date. The overall number of storm-petrels breeding on Great Island has declined by 55% since 1979, steeper than previously thought using non-GIS population estimates, with storm-petrels nesting in open habitat declining at three times the rate of forest-nesting birds. The decreasing number of storm-petrels breeding in the open habitat on Great Island was previously linked to high levels of Herring Gull predation on adult storm-petrels; in 1997, it was estimated that gulls consumed approximately 49 000 adult Leach's Storm-Petrels during a single breeding season (Stenhouse *et al*. 2000). It was predicted that such high levels of mortalities could not be sustained by this population; however, predicted declines were not observed between 1979 and 1997. There are several possible reasons that the predicted mortality did not occur: (1) storm-petrels shifted toward breeding in forest rather than open habitat; (2) some portion of the predated adults were likely non-breeders; or (3) the population was being sustained through recruitment from other colonies (Stenhouse *et al*. 2000).

Based on the current population trend, it appears that gull predation may finally be having an impact on the colony and that the population has likely been pressured for some time, based on the low numbers of burrows found in 2011. However, Herring Gull numbers have also been steadily declining in Witless Bay since the 1970s, with the largest colony on Gull Island having declined from 3 852 to 2 698 pairs between 1979 and 2000 (Robertson *et al*. 2001), and have continued to decline by 2011 to 1 881 pairs (Bond *et al*., *in press*). Great Island showed more dramatic declines, with Herring Gull populations decreasing from 2 771 to 1 640 pairs between 1979 and 2000 (Robertson *et al*. 2001), and totalled a mere 352 pairs in 2012 (Bond *et al*., *in press*). The high occupancy rates of burrows observed in 2011 may suggest that predation pressures are being reduced and that the population may be beginning to show signs of stability. Burrow occupancy rates tend to not vary considerably among colonies with stable populations, but have been shown to be low for declining colonies (Robertson *et al*. 2006). In addition to predation, habitat loss is also playing a role in the declining storm-petrel population on Great Island, as puffins are encroaching on their traditional breeding sites. Finally, elevated levels of mercury have also been reported for storm-petrels breeding in Atlantic Canada (Elliott *et al*. 1992, Bond & Diamond 2009), which can have a negative impact on adult survival and reproductive output, as observed in other species (Burgess & Meyer 2008, Heinz *et al*. 2009, Fort *et al*. 2015). Future research is required to better understand the causal relationship between all of these factors and their effects on storm-petrel populations.

Contrasting non-GIS and GIS approaches

Compared with conventional non-GIS techniques, the GIS approach incorporating a 3D model to correct for slope increased the estimated occupied area by 5%–10% for flat surfaces occupied by murres, by 16%–36% for moderate slopes occupied by storm-petrels, and by 40%–46% for steep slopes occupied by puffins. Generally, the GIS approach allows for a more accurate delineation of areas occupied by densely packed breeding seabirds, as the user can readily zoom into high-resolution digital images at a much finer scale than is possible using a hard copy of an image. Furthermore, we show that previous estimates using occupied area to extrapolate population size would have underestimated the occupied area by as much as half, as a result of the difficulties associated with incorporating slope into a model using a non-GIS approach. Previous studies acknowledged the limitations and conservative nature of the trigonometric approach, particularly the error associated with steep slopes (>35°) and the inferences made to calculate area between contour lines or plots for which slope information was available (Rodway *et al*. 1996, 2003). The 3D GIS approach has the advantage of creating a 3D model of the island by taking into account the irregular shape of each contour line and extrapolating a more realistic picture of the convoluted surface between the contour lines.

The development of newer tools such as high resolution satellite imagery and digital elevation models coupled with GIS are now more commonly used to assess the boundaries and size of occupied areas of seabird colonies (e.g. Guinet *et al*. 1995) and provide a means to more accurately monitor species that breed on surfaces with varying slopes and elevations (e.g. Rayner *et al*. 2007). Such technologies improve the quality of seabird population monitoring, as they increase the efficiency of conducting surveys, reduce the time required to process images, and increase the accuracy of the estimated occupied area at both the colony and landscape levels (e.g. Egevang *et al*. 2003, Rayner *et al*. 2007, Bricher *et al*. 2008, Southwell *et al*. 2009).

Furthermore, Light Detecting And Ranging (LiDAR) remote sensing technology is beginning to be more widely used to monitor a variety of avian species for which accurate information on elevation and habitat type play an important role (Bradbury *et al*. 2005, Lesak *et al*. 2011, Tattoni *et al*. 2012, Wickramagamage *et al*. 2012). The incorporation of LiDAR technology in future surveys will likely continue to improve the accuracy of the estimated occupied area of burrowing species breeding on sloped surfaces, such as puffins and storm-petrels.

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