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Population dynamics of Northern Gannets in North America, 1984–2009

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ABSTRACT. Northern Gannet (*Morus bassanus*) colonies ($N = 6$) in North America have been regularly censused since the late-1960s. Monitoring populations of a top-predator like gannets provides insight into possible changes in the marine environment and contributes to an understanding of their demography. We report the results of aerial censuses of gannet colonies conducted from 1984 to 2009. Standard methods were used and involved making high-quality photographs of colonies from a fixed-wing aircraft, and subsequently counting apparently occupied sites (AOS) in the photographs. As of 2009, the breeding population of gannets in North America was estimated to be 116 825 pairs, or ~27% of the world population. From 1984 to 2009, the population grew at an average rate of 4.4% per annum and this growth was likely the result of continued population recovery after acute persecution in the past. Growth rates began to slow during the latter part of our study, likely due to density-dependent effects and reductions in food availability. Despite the growth of the North American gannet population, gannets have not established new colonies, possibly because populations had been so depressed that growth could be accommodated within existing colonies.

RESUMEN. **Dinámica poblacional de *Morus bassanus* en Norte América entre 1984–2009** Las colonias de *Morus bassanus* en Norte América ($N = 6$), han sido censadas desde tarde en los 1960. El monitorear las poblaciones de un depredador de punta, como esta ave, provee detalles ante posibles cambios en el ambiente marino y contribuye a entender su demografía. Informamos los resultados de censos aéreos de colonias de estas aves llevados a cabo de 1984 al 2009. Se utilizaron métodos estándares, lo que conlleva tomar fotografías de alta calidad desde un aeroplano y contar, subsiguientemente, los sitios ocupados por las aves en las fotografías. En el 2009, el numero de estas aves en Norte América fue estimado en 116 825 parejas, o aproximadamente el 27% de las aves en el mundo. De 1984 al 2009 la población creció a una tasa de 4.4% anual y este crecimiento parece ser el resultado de la recuperación poblacional de esta especie a la persecución en el pasado. La tasa de crecimiento comenzó a reducirse durante la parte final del estudio debido a factores asociados a la densidad, como la reducción en la disponibilidad de alimentos. Pese al crecimiento poblacional en Norte América, no se han establecido otras colonias de estos pájaros, posiblemente debido a que el crecimiento poblacional del ave aun puede ser acomodado en las colonias existentes.

Key words: census, growth rate, Gulf of St. Lawrence, *Morus bassanus*, Newfoundland, seabird

Northern Gannets (*Morus bassanus*; hereafter gannets) breed at only six locations in North America (NA), all in eastern Canada. Three colonies are in the Gulf of St. Lawrence (Bird Rocks, Bonaventure Island, and Anticosti Island), and three are off the east and southeast coasts of insular Newfoundland (Funk Island, Baccalieu Island, and Cape St. Mary's; Mowbray 2002). Nettleship and Chapdelaine (1998) provided the most recent summary of population trends of gannets for NA and reported increasing trends for all NA colonies, with a per annum (pa) rate of increase of 1.7% from 1969 to 1984. Wanless and Harris (2004) reported an annual increase of 2.0% in British and Irish gannet colonies from 1969/70 to 1984/85, and an overall world population increase of 2% pa since 1900.

Monitoring populations of a top-predator like gannets contributes to an understanding of their demography, and provides valuable insight into possible changes in the marine environment (Chapdelaine et al. 1987, Montevecchi and Myers 1997, Montevecchi 2007). Seabird monitoring studies are essential in providing a baseline against which the effects of environmental

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damage from events such as oil spills can be assessed (e.g., Irons et al. 2000). In April 2010, an explosion at the Deepwater Horizon drilling rig caused the largest marine oil spill in history and affected a large area of the northern Gulf of Mexico (Camilli et al. 2010). Montevecchi et al. (2012) reported that 25% of satellite or geologger-tagged NA gannets migrated to the area affected by the Deepwater Horizon event. Beach surveys revealed that gannets were the third most abundant bird recovered on Gulf beaches after the oil release, and recovered birds were the most frequently oiled of all species encountered (63%; Montevecchi et al. 2012). The impacts of the Deepwater Horizon event on NA gannets are currently being assessed and part of this assessment will be a study of population trends at each colony, post-event. Therefore, to improve our understanding of gannet demography and provide baseline, pre-Deepwater Horizon population trends for NA gannets against which the future population trajectory can be compared, we report the results of five aerial censuses of NA gannet colonies spanning 25 years from 1984 to 2009; we include 1984 data reported by Nettleship and Chapdelaine (1988) for continuity.

METHODS

We followed census methods described by Nettleship and Chapdelaine (1988) with minor variations such as a switch to digital photography from film, and the adoption of more convenient methods of counting photographs. High-quality film or digital images of each colony (Bird Rocks, 47.83°N, 61.15°W, Bonaventure Island, 48.50°N, 64.15°W, Anticosti Island, 49.15°N, 61.70°W, Funk Island, 49.77°N, 53.18°W, Baccalieu Island, 48.12°N, 52.78°W, Cape St. Mary's, 46.83°N, 54.20°W; Fig. 1) were made through an open window or belly aperture of fixed-wing aircraft (Britten-Norman Islander and de Havilland Beaver). Colonies were overflown between 7 and 15 July in 1989, 1994, 1999, 2004, and 2009. This timing corresponded with a period of the breeding season when most birds would be attending a nest containing a chick or, rarely, an egg, but before chicks began to fledge (mid-September). At Cape St. Mary's, small areas of the colony were not visible from the air and were photographed during ground visits.

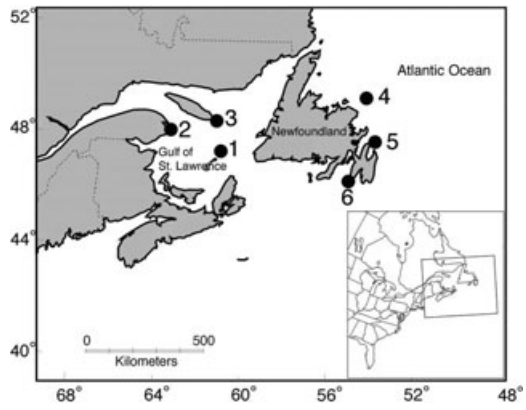

Fig. 1. Locations of the six North American Northern Gannet colonies. (1) Bird Rocks, (2) Bonaventure Island, and (3) Anticosti in the Gulf of St. Lawrence, and (4) Funk Island, (5) Baccalieu Island, and (6) Cape St. Mary's in Newfoundland.

Duplicate images made during flights allowed selection of the best for counting. Film was developed and printed large enough (20.3 cm × 25.4 cm) to clearly see individual gannets. Digital images were optimized (e.g., contrast adjustment and sharpening) and viewed on a computer display. Lines were drawn on overlapping images to eliminate double-counting on adjoining images. Lines were also drawn to separate breeding areas, where birds were spaced regularly and relatively tightly, from nonbreeding areas, where birds were more widely and randomly spaced. Any marks such as lines or dots were made on overlays (either acetate in the case of film or digital layers in the computer software) so the original image was not affected. The counting unit was an apparently occupied site (AOS) and constituted one bird, or two birds close together, in a breeding area of the colony. We assumed an AOS represented one breeding pair of gannets and population figures are reported as number of breeding pairs.

A pressure-sensitive pen connected to an electronic counter was used to enumerate gannets in the film images. A light pressure with the pen generated a "click" that simultaneously added one to the electronic counter and made a visible mark on the acetate sheet. We proceeded until all AOS's were marked on all enlargements. Digital images were counted in Adobe Photoshop (Adobe Systems Inc., San Jose, CA). A square dot of pixels (e.g., 3 × 3 or 5 × 5 pixels) of a

certain color (e.g., black or red) was placed over each AOS on a separate (counting) layer above the image using the pencil tool. The Histogram command in Photoshop could then be used to count the number of pixels in the counting layer which, when divided by the number of pixels per dot (usually $3 \times 3 = 9$ or $5 \times 5 = 25$), yielded the number of dots on the counting layer. Film or digital images were checked for errors of omission or commission before a final tally was made. Chardine (2000) checked the accuracy of the traditional and computer-aided counting method and found the error to be within that expected if traditionally counted images were re-counted (within 5%).

RESULTS

The total number of breeding pairs of gannets at all NA colonies combined was 116 825 in 2009, up from 40 102 in 1984 (Table 1). This represented a per annum average rate of increase of 4.4% (Table 2; see also Supplemental Tables 1 and 2 for information on colony sub-areas). Numbers increased between every census year. Per annum population growth rate peaked at 6.4% during the period from 1994 to 1999, then declined in both subsequent periods to a low of 2.8% pa from 2004 to 2009.

From 1984 to 2009, the population growth rate of gannets in the Gulf of St. Lawrence (GSL; 4.8% pa) was 1.6% higher than in Newfoundland (NL; 3.2% pa). Population growth rates peaked at 7.4% pa in GSL colonies during the period from 1999 to 2004, and at 6.4% pa in the NL colonies from 1994 to 1999. In the NL region, growth rates were lower during the last two 5-year periods (0.7% and 2.0%, respectively) than during the previous two and growth rates were lowest in GSL during the last 5-year period (3.0%).

Numbers of gannets in all colonies increased during the study period and thus contributed to the overall population increase. Four of the six colonies reached their maximum size in 2009, and the other two in 2004. The two largest colonies, Bird Rocks and Bonaventure Island (both in GSL), contained 69–77% of total NA population depending on census year and, with their high per annum growth rates, contributed most to the overall increase in the NA population. Annual growth rates peaked at 11.3% pa at Bird Rocks during the period from 1994 to 1999 and, one 5-year period later, at 7.7% pa at Bonaventure Island. Annual growth rates also peaked during the period from 1994 to 1999 at the three NL colonies.

DISCUSSION

Our results indicate that the gannet population in North America has experienced healthy growth since 1984. The observed average annual growth rate of 4.4% for all colonies combined produces a population doubling time of about 16 years. The most recent population estimates for gannets breeding outside of North America are from the mid-1990s to the late 2000s (Wanless and Harris 2004, Wanless et al. 2005, Murray 2011). Based on those figures, the NA population in 2009 represented ~27% of the world population of 431 836 breeding pairs.

European gannet populations have also shown long-term increases (Wanless and Harris 2004). The British and Irish population increased by 2% pa from the late 1960s to the mid-1980s. From the late 1960s to 2009, the NA population grew at a somewhat higher rate of 3.2% pa (Nettleship and Chapdelaine 1988, this study). Nelson (1978) and Wanless and Harris (2004) considered these increases to be the result of recovery from long-term persecution. Reasons for the difference in growth rates of European and NA gannet populations are unclear. One possibility is that persecution in NA was particularly severe (see Gurney 1913) and likely diminished only sometime after the Migratory Bird Convention Act came into force in 1918 in most of Canada and in 1949 in Newfoundland. In the UK and Ireland, persecution continued up to the beginning of the 1900s (Wanless and Harris 2004). Thus, NA populations may have been reduced more relative to environmental carrying capacity than those in the UK and Ireland, and have had less time to recover.

We found that growth of the gannet population was relatively low in the first decade of our study (though still positive), rose to a peak in either the next 5-year period (1994–1999; four colonies) or the 5-year period after that (one colony), then slowed in the last 5-year period of our study. With the three-fold increase in NA gannet populations, density-dependent factors may have come into effect at the end of our study that reduced breeding success, survival rates, breeding propensity, or some combination

Table 1. The number breeding pairs of Northern Gannets at each colony in North America from 1984 to 2009.

		Number of breeding pairs Year					
Region	Colony	1984[a]	1989[b]	1994	1999	2004	2009
Gulf of St. Lawrence	Bird Rocks	6590	7640	9868	16 884	23 461	30 010
	Bonaventure Island	21 090	24 125	31 574	36 936	53 635	59 586
	Anticosti Island	155	–	208	210	221	200
	Gulf of St. Lawrence combined	27 835	–	41 650	54 030	77 317	89 796
Newfoundland	Funk Island	6075	–	7123	9837	10 047	9987
	Baccalieu Island	677	–	1041	1712	2050	2253
	Cape St. Mary's	5515	–	7179	12 156	12 432	14 789
	Newfoundland combined	12 267	–	15 343	23 705	24 529	27 029
All colonies combined		40 102	–	56 993	77 735	101 846	116 825

[a]1984 data from Nettleship and Chapdelaine (1988)
[b]Only Bonaventure Island and Bird Rocks colonies were censused in 1989.

Table 2. Population growth rates at each Northern Gannet colony in North America, 1984–2009.

		Population growth rate (% per annum) Period						
Region	Colony	1984–1989	1989–1994	1984–1994[a]	1994–1999	1999–2004	2004–2009	1984–2009
Gulf of St. Lawrence	Bird Rocks	3.0	5.3	4.1	11.3	6.8	5.0	6.3
	Bonaventure Island	2.7	5.5	4.1	3.2	7.7	2.1	4.2
	Anticosti Island	–	–	3.0	0.2	1.0	−2.0	1.0
	Gulf of St. Lawrence combined	–	–	4.1	5.3	7.4	3.0	4.8
Newfoundland	Funk Island	–	–	1.6	6.7	0.4	−0.1	2.0
	Baccalieu Island	–	–	4.4	10.5	3.7	1.9	4.9
	Cape St. Mary's	–	–	2.7	11.1	0.5	3.5	4.0
	Newfoundland combined	–	–	2.3	9.1	0.7	2.0	3.2
All colonies combined		–	–	3.6	6.4	5.6	2.8	4.4

[a]Only Bonaventure Island and Bird Rocks colonies censused in 1989, therefore population growth rate calculated for the decade 1984–1994 to provide a figure for the missed colonies at the beginning of this study.

of these factors. Fewer suitable nest-sites may now be available, and competition for food around colonies may be more severe (Birt et al. 1987, Cairns 1992, Lewis et al. 2001). The carrying capacity of the environment may also be declining due to reduced abundance of fish stocks either on the breeding grounds or in overwintering areas (e.g., Crawford et al. 2007), or to a mismatch in phenology of predator and prey (see Durant et al. 2007).

No new gannet colonies have been established in recent years in the western Atlantic, and one possible explanation for the lack of new colonies is that populations were so reduced in size through persecution and human disturbance (Gurney 1913, Nelson 1978) that even rapid growth could be accommodated within existing colonies. Abundant, currently unoccupied, and apparently suitable breeding habitat is available at Bonaventure Island, Cape St. Mary's (mainland), and Baccalieu Island, but less such habitat is available at Bird Rocks, Funk Island, and Anticosti Island. Thus, if population expansion continues in the western Atlantic, one or more new gannet colonies may be established in the near future.

Wanless et al. (2006) published age-related annual survival rate estimates for British and Irish gannets (1st year- 0.424, 2nd year- 0.829, 3rd year- 0.891, 4th year- 0.895, and adult- 0.919), so a simple population model with no density-dependence was constructed based on these data and the typical breeding success at Bonaventure Island from 1979 to 2005 (0.74 chicks per pair; J.-F. Rail, unpubl. data). The same breeding success was applied to all breeding age-classes (≥5 years old, Mowbray 2002). These demographic values produced a population growth rate of 1.0% pa, well below the 4.4% pa in our study. If we assume that the breeding success at Bonaventure Island was representative of all NA colonies, our population growth rate of 4.4% pa would necessitate an increase in the Wanless et al. (2006) survival rates of ~3% across age-classes. Thus, for example, our data suggest a survival rate of adult gannets in NA of 95% pa. However, the age-specific increment is likely not constant across age-classes and, for this reason, it is not possible to provide age-specific survival rate estimates for the NA population based on this analysis. Furthermore, a problem in reconciling vital rates and population growth rates is that the latter can be affected by the proportion of birds that breed (breeding propensity) and we do not have estimates of this demographic parameter for either side of the Atlantic. An increase in breeding propensity caused by recruitment from a pool of nonbreeding adults may have been partly responsible for the population increases reported in our study (Wanless et al. 2006, also see Porter and Coulson 1987, Morris and Chardine 1995). Sudden availability of nesting habitat, for example, when a lighthouse at Bird Rocks was abandoned, could mediate such a high increase in recruitment.

From April to July 2010, an unprecedented amount of crude oil was released into the northern part of the Gulf of Mexico following a blowout at the Deepwater Horizon drilling rig (Camilli et al. 2010). An estimated 25% of the NA population of gannets migrate to and winter in the zone of Deepwater Horizon pollution (Montevecchi et al. 2012). Although beach surveys revealed some gannet mortality in the weeks and months after the blowout (Montevecchi et al. 2012), the possible long-term impact of this event on populations of gannets and other species of birds remains to be determined. However, our results can be used as a baseline for comparison with future trends in the NA gannet population.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Supplemental Table S1. The number breeding pairs of Northern Gannets in recognizable sub-areas in the three largest colonies in North America, 1984–2009.

Supplemental Table S2. Population growth rates of Northern Gannets in recognizable sub-areas in the three largest colonies in North America, 1984–2009.