IBIS
international journal of avian science

Ibis (2025) doi: 10.1111/ibi.13387

Using model-based distance sampling to estimate decadal population change in Northern Gannets (*Morus bassanus*) across periods spanned by different at-sea survey methods

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Seabirds are important sentinels of climate and ecosystem change, but many breeding populations are difficult to monitor because of the remoteness and inaccessibility of their colonies, and the sometimes cryptic nature of their nests and burrows. Large-scale monitoring of seabird populations at sea can also be used to estimate population trends and inform conservation efforts. However, although modern survey techniques can be used to estimate absolute abundance, many older survey methodologies have recorded only relative, and possibly biased, abundance. These approaches are exemplified in the western North Atlantic, where seabirds have been surveyed at sea using modern methods (Eastern Canada Seabirds at Sea, or ECSAS) since 2006, but under the simpler PIROP (*Programme intégré de recherches sur les oiseaux pélagiques*) protocol from 1965 to 1992. Methodological differences between these survey types limit our understanding of long-term trends in seabird populations, both in the western North Atlantic and elsewhere. Hence, we conducted simultaneous surveys using both methods from 2014 to 2021 and used advances in model-based distance sampling to allow comparison across these longer-term datasets. We validated our methodology by comparing population trends of Northern Gannets *Morus bassanus* using the at-sea data and breeding colony surveys. The trend in abundance at sea (2.69% increase annually) was similar to that at breeding colonies (2.91% increase annually), suggesting that our combined approach can be used to estimate seabird population changes robustly across the period spanned by the two survey programmes. We envision that analyses using similar combined survey methods could reveal decadal population trends and changes in conservation status of many seabird species that currently lack such information because of the absence of colony counts.

Keywords: abundance estimation, at-sea surveys, distance sampling, population trends, seabirds.

Seabirds are conspicuous and important sentinels of climate and ecosystem change as they are long-lived, feed on a wide range of trophic levels in diverse marine habitats, and exhibit sensitive

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responses to environmental change (Cairns 1988, Piatt *et al.* 2007, Durant *et al.* 2009, Einoder 2009, Velarde *et al.* 2019). To monitor seabirds as sentinels, and to assess the state and trajectory of the ecosystems on which they rely, long-term, large-scale monitoring programmes are essential (Sydeman *et al.* 2021). However, relatively few of the world's seabird populations are regularly monitored (Paleczny *et al.* 2015), making it difficult to adequately assess population status and changes. There are components of seabird breeding ecology and life history that make monitoring challenging in many circumstances. Seabirds can breed in dispersed locations, or more often in colonies, nesting on cliffs or in burrows that are inaccessible, and on remote islands or coastlines (Croxall *et al.* 2012). As a result, there is a persistent lack of knowledge about population status and trends for many seabird species (Paleczny *et al.* 2015).

As an alternative, attempts have been made to estimate population trends of some seabird species from at-sea surveys (van der Meer & Leopold 1995, Clarke *et al.* 2003, Ballance 2007), but such surveys can be impractical because many seabirds range for thousands to tens of thousands of kilometres in search of food (Mott & Clarke 2018). In addition, efforts to survey species at sea are hampered by many methodological issues (Tasker *et al.* 1984, Gaston *et al.* 1987, van der Meer & Camphuysen 1996, Clarke *et al.* 2003), including non-random sampling and uneven coverage from survey vessels, clustering of seabirds at sea, and difficulty in detection based on unmodelled observer bias and sea conditions. All of these can cause large biases and variation in density estimates (Matthiopoulos *et al.* 2022). Field-based and statistical methods have been developed to account for some of these issues when estimating population trends using at-sea surveys (Clarke *et al.* 2003, MacLean *et al.* 2013, Mercker *et al.* 2021). However, updates in at-sea survey methodology to account for past survey biases have rendered many datasets using older, non-random survey methods unusable for estimating long-term population trends of seabirds, such as those collected in the Pacific Ocean (1963–66) and in South Africa and France in the early 1980s (see examples in table 1 of Tasker *et al.* 1984).

In addition to breeding colony-based counts (Gaston *et al.* 2009), the Canadian Wildlife Service has used geo-referenced vessel-based surveys to monitor breeding and migratory seabirds in Atlantic Canada for the past six decades (Brown *et al.* 1975, Gjerdrum *et al.* 2012, 2024). The *Programme intégré de recherches sur les oiseaux pélagiques* (PIROP) was established in the 1960s (Brown *et al.* 1975, Brown 1977, 1986). Survey data were collected aboard ships-of-opportunity from 1965 to 1992 to summarize the seasonal abundance of seabirds in the western North Atlantic and to examine oceanographic drivers of seabird distributions (Brown *et al.* 1975, Lock *et al.* 1994, Huettmann & Diamond 2001). PIROP surveys originally consisted of unlimited-width transects, and did not use distance sampling or account for bias due to the movement of flying birds relative to the survey vessel (Brown *et al.* 1975). After 1983, PIROP surveys adopted a fixed-width strip transect method (Tasker *et al.* 1984). However, most (94.7%) survey effort preceded this change and the PIROP programme in eastern Canada ended in 1992. In 2006, the Canadian Wildlife Service developed the Eastern Canada Seabirds at Sea (ECSAS) standardized method for surveying seabirds from ships in the western North Atlantic based on methods used in the eastern Atlantic Ocean (Tasker *et al.* 1984, Webb & Durinck 1992, Camphuysen *et al.* 2004), which uses a fixed-width line transect survey with binned distances (Buckland *et al.* 2001) for all birds sighted, and 'snapshots' for birds in flight (see Methods) (Tasker *et al.* 1984, Gjerdrum *et al.* 2012). Due to the methodological differences between PIROP and ECSAS, it is difficult to compare and/or combine data from the two programmes, thereby limiting an understanding of long-term trends of seabirds in the western North Atlantic.

Assuming that, at the macro-scale, at-sea distributions of seabird populations are relatively stable within a season, population trends at sea during the breeding season should reflect those across regional breeding colonies. Hence, data from colony monitoring can be used to validate methods of inferring trends from at-sea survey data (e.g. PIROP and ECSAS). One species in the western North Atlantic for which we have reliable and consistent breeding population censuses since the 1960s is the Northern Gannet *Morus bassanus* (hereafter 'Gannet'). Gannets are a large, conspicuous, colonially breeding seabird endemic to the North Atlantic. During the breeding season, adults range extensively (>120 km) within the waters of the western North Atlantic and throughout the

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Gulf of St Lawrence (Mowbray 2020) in areas where we have appropriate survey coverage. Immature Gannets spend several years at sea before establishing a nest-site at around 5 or 6 years of age (Nelson 2005). The world population includes approximately 416 000 breeding pairs in the eastern North Atlantic (Murray *et al.* 2015, Barrett *et al.* 2017, Jeglinski *et al.* 2023) and approximately 114 000 breeding pairs in the western North Atlantic (Chardine *et al.* 2013, this study), with little population interchange between the eastern and western populations (Nelson 2005). Global Gannet populations have grown ~3% per year since the early to mid-1900s (Mowbray 2020). The reasons for this are unclear but probably include improved breeding and foraging habitat, reductions in egg removal and killing of adults for meat and feathers, and bans on dichlorodiphenyltrichloroethane (DDT) and other chemicals (Nelson 2005, Mowbray 2020). Since the 1970s, breeding Gannets in North America have increased by 2–4% per year (Chardine *et al.* 2013, Environment and Climate Change Canada & Birds Canada 2024). Here, we used recent advances in distance sampling analyses to estimate the western North American Gannet population trend using more than 50 years of data from the PIROP and ECSAS at-sea survey programmes (1969–2021), and compared this trend with the population trend obtained from breeding colonies in eastern Canada. First, we conducted at-sea surveys for 8 years employing both the PIROP and ECSAS methods simultaneously in order to develop a correction factor and adjust density estimates between the programmes. Second, we used line-transect distance sampling (Buckland *et al.* 2001) to account for imperfect detection separately for Gannets in flight and on the water. Lastly, to validate our methods, we compared population growth based on our analysis of at-sea survey data with that derived from surveys of six breeding colonies in the western North Atlantic.

METHODS

Survey methods

To estimate the long-term population trend in Gannet abundance, we used two at-sea survey datasets that were collected by the Canadian Wildlife Service from ships engaged in a variety of scientific, transport and supply activities (also known as ships-of-opportunity) – PIROP (1965–92) and ECSAS (2006–21). These surveys were geographically representative of the at-sea foraging range of breeding Gannets in the western North Atlantic and occurred throughout the time in which Gannets are present at breeding sites (Fifield *et al.* 2014; see Analyses below). During PIROP surveys from 1965 to 1983, all birds sighted on either side of the vessel (Fig. 1, Table 1) were recorded (Brown *et al.* 1975, Brown 1977, 1986). After 1983, sightings were truncated to a 300-m strip on one side of the vessel's track. Surveys consisted of 10-min observation periods (hereafter 'segments') with ship parameters (i.e. position, speed, heading, etc.), and survey conditions (i.e. weather, wind speed, visibility, etc.) recorded at the beginning of each segment and thereby associated with each observation within the segment. Distance of the sighting from the observer was not estimated. PIROP observations from 1984 to 1992 were excluded because of low survey effort and poor spatial coverage. No Canadian Wildlife Service pelagic seabird surveys were conducted from 1992 to 2005.

During ECSAS surveys from 2006 to 2021, observers were assigned to either the port or starboard side of the vessel by the ship's bridge crew based on the navigational requirements of the ship. Transect width was truncated to a 300-m-wide transect on one side of the vessel and we recorded all birds detected on the water within the transect (Gjerdrum *et al.* 2012) (Fig. 1, Table 1). For birds initially detected in flight, we used the 'snapshot' method to correct for the effect of random directional bird movement relative to the movement of the survey vessel (Tasker *et al.* 1984, Spear *et al.* 1992, Gjerdrum *et al.* 2012). Snapshots were timed based on the speed of the ship, so they occurred approximately every 300 m along the survey track. At each snapshot, any flying birds within a 300 × 300-m box at the time of the snapshot were recorded as 'in transect' (Fig. 1). We recorded perpendicular distances from the trackline for all birds, including group size, and whether they were on the water or in flight in one of four distance bins (with limits 50, 100, 200 and 300 m) (Gjerdrum *et al.* 2012). Binned distance sampling is a common technique in distance sampling (Buckland *et al.* 2001) and the 300-m transect width is common for at-sea surveys of seabirds (Camphuysen *et al.* 2004, Camphuysen &

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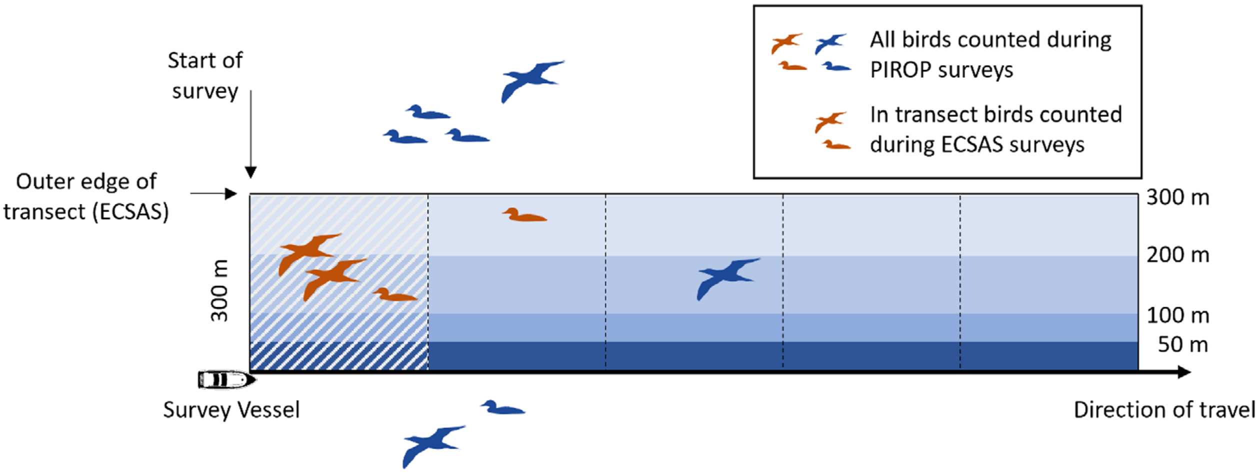

Figure 1. Representation of a seabird survey where an observer is located on the survey vessel detecting birds to one side of the vessel (modified from Tasker *et al.* 1984, Gjerdrum *et al.* 2012). In this representation, the vessel is positioned at the beginning of a survey segment and the birds depicted on water and in flight are those that the observer can see at this initial position (i.e. the configuration of birds will change as the ship continues its path along the segment). PIROP survey methods (1965–83) count all birds sighted both on the water and in flight regardless of their distance from the observer (i.e. both the blue and orange birds are recorded). ECSAS survey methods (2006–21) count all birds sighted on the water within a 300-m distance perpendicular to the trackline (black arrow; including those on the water within the segment up ahead of the observer) and those in flight at 300-m intervals (dashed vertical lines). The stippled area depicts the area within which the flying birds are counted during one of the ECSAS instantaneous counts (also known as snapshots). Orange birds depict those that would be counted using ECSAS methods (the blue flying bird shown within the 300-m transect is outside the count area for flying birds (stippled area) and is therefore not counted during ECSAS surveys. It may, however, be counted in a subsequent snapshot as the vessel moves forward into the next count area). The perpendicular distances of all sightings from the trackline are recorded during ECSAS surveys in one of four distance bins (50, 100, 200, 300 m; blue shading). Silhouettes of Gannets were provided by Mmo iwdg (https://creativecommons.org/licenses/by-sa/3.0/).

Garthe 2004). Further, analysis of a subset of ECSAS data showed that a 1000-m cut-off is inferior to a 300-m cut-off because of the low detection probability of birds between 300 and 1000 m (Bolduc & Fifield 2017). Similar to PIROP, surveys consisted of consecutive 5-min segments (except for 10-min segments in 2006–08) with ship and weather information collected at the start of each segment. For both PIROP and ECSAS surveys, consecutive segments that all shared the same date, observer, vessel and direction were grouped into transects, which were the sample units for

Table 1. Differences in survey methods between PIROP and ECSAS.

Dataset	Birds recorded on water	Birds recorded in flight	Number of observations
PIROP (1969–83)	No strip width – recorded all birds seen on water on both sides of vessel	All flying birds recorded on both sides of vessel	2193 observations (5266 transects; total = 42 175 km)
ECSAS (2006–21)	300-m strip width – only recorded those birds on water within 300-m perpendicular distance to observer on one side of vessel	Snapshot used – counted only those birds in flight within strip width every 300 m on one side of vessel	4181 observations (11 158 transects; total = 110 899 km)
Combined (2014–21)	Recorded all birds seen on water; also recorded whether birds were seen in or out of 300-m transect on one side of vessel	Recorded all birds in flight; also recorded whether birds were seen in or out of the snapshot on one side of vessel	3749 observations (4608 transects; total = 36 273 km)

See Figure 1 for more detail on surveys. The observations in the ECSAS row that were conducted from 2014 to 2021 ($n = 1622$) are included in the Combined row. In addition, analyses with ECSAS data used distance sampling methods to account for detection probabilities, while PIROP surveys did not (see Analyses).

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analysis. Transect effort was calculated as the sum of the segment lengths (km) making up each transect.

In order to develop a correction factor to adjust density estimates between the two survey programmes, we conducted both PIROP and ECSAS methods simultaneously during ship-based surveys from March 2014 to October 2021 (hereafter 'combined surveys'; Table 1). Many of the ECSAS survey routes were repeated annually, so the combined surveys were spatially representative similar to ECSAS surveys shown in Figure 2a. We recorded birds on water and in flight, indicating when each sighting was 'in or out of transect' (ECSAS methods), thereby distinguishing those sightings that followed PIROP methodology. We assumed that because PIROP counted all sighted birds, including those on the water outside the transect or in flight between snapshots, that we could adjust PIROP to ECSAS density estimates using a calculated correction factor to make density results from the two programmes comparable. Note that original PIROP surveys counted birds on both sides of the vessel, whereas the PIROP method within combined surveys counted only on one side. This is accounted for in the analysis – see Figure S1 for a description of the datasets and procedures for calculating the correction factor. Combined surveys were carried out for 8 years, which is ~50% of the 15-year PIROP and 16-year ECSAS datasets.

Analyses

Data preparation and filtering

As the PIROP and ECSAS data were collected aboard ships-of-opportunity, some observations were recorded outside the typical at-sea breeding range of Gannets (e.g. >55°N; Mowbray 2020). Therefore, we filtered PIROP and ECSAS records of Gannets spatially by calculating the 95% minimum convex polygon generated from spatial observations using the R package adehabitatHR (Calenge 2006), and removing the 5% of outlier observations located outside that polygon that were not representative of Gannet at-sea range (Fig. 2a). We also verified spatially and temporally (Fig. 2; Fig. S2) that there was an appreciable overlap between the monitoring programmes to ensure a robust comparison between the PIROP and ECSAS datasets. As the result of changes in the core distribution of Gannets at sea throughout

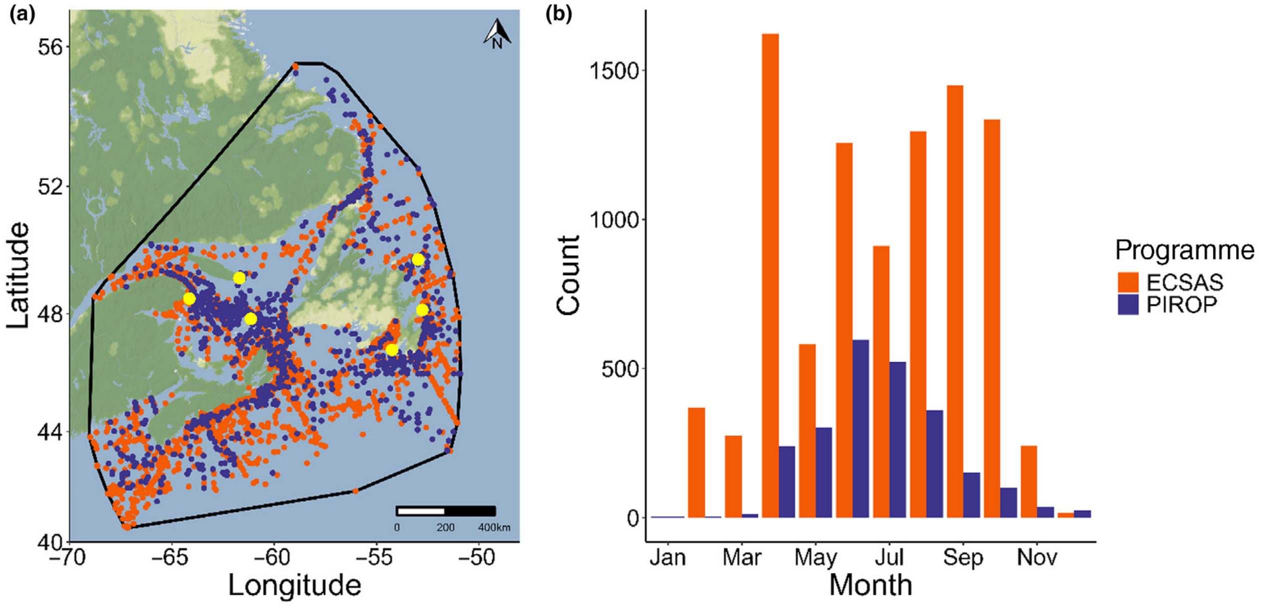

Figure 2. (a) Spatial overlap of Northern Gannet *Morus bassanus* observations in the western North Atlantic between PIROP and ECSAS monitoring programmes, where the black polygon indicates the 95% minimum convex polygon calculated with survey data. Yellow dots indicate the locations of North American breeding colonies. (b) Bar chart showing temporal overlap of Northern Gannet observations between monitoring programmes by month.

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the year, as well as variation in Gannet migratory departure and colony arrival dates (Fifield *et al.* 2014), we used survey data from all months (Fig. 2b). However, we do note that Gannets are absent from much of the study area in January–February (Fifield *et al.* 2014), aligning with our decline in Gannet observations during this time.

Survey effort for the monitoring programmes is shown in Figure S2.

Modelling approach

Our modelling approach comprised the following: (1) estimating annual Gannet density from the original PIROP surveys (1969–83); (2) estimating annual Gannet density from the ECSAS surveys (2006–21); (3) modelling the difference in Gannet density estimates between PIROP and ECSAS methodologies during our combined surveys (2014–21) to create a correction factor; (4) adjusting PIROP (1969–83) density estimates from (1) using the correction factor in (3) to make them comparable to the ECSAS densities from (2), and using these to estimate the Gannet population trend (1969–2021); and (5) comparing this at-sea survey-based trend to the Gannet population trend computed from breeding colony counts. The following sections provide details of each step (see Fig. S1 for workflow diagram).

Density estimation

For the PIROP dataset (1969–83), the total area surveyed was unknown because of the unlimited-width transects used, precluding the computation of square densities as for ECSAS (see below). Our estimates for the PIROP surveys were therefore simply the number of animals observed divided by length of the survey transect (birds/km, hereafter linear density), and uncertainty arose only from sampling variability (Fewster *et al.* 2009). We included original PIROP data from 1969 to 1983, excluding data from 1965 to 1968 and from 1984 to 1992 because of low survey effort and poor spatial coverage, which if used would give unreliable density estimates for those years.

For the ECSAS dataset (2006–21), only birds recorded as ‘in transect’ were used to calculate density (i.e. all birds on water with the 300-m transect, and birds in flight within the 300-m transect recorded during snapshots). We used binned distance sampling (Buckland *et al.* 2001, 2015) to account for imperfect detectability, producing an estimate of absolute density (birds/km^2, hereafter square density). In distance sampling, the detection function (usually denoted $g(x)$) models the probability of detecting an animal given that it is at a distance (x, say) from the sampler. We fitted separate detection functions for Gannets observed in flight versus on the water using R version 4.2.3 (R Core Team 2023) and the R package Distance (Miller *et al.* 2019). We accounted for bias in the detection of Gannets due to large group sizes (mean group size 1.98 ± 12.64 standard deviation), because larger groups could be more easily observed than smaller groups further away. We followed Thomas *et al.* (2010) by estimating mean group size by using two linear regressions (for Gannets on water and in flight), in which log group size was regressed on the estimated probability of detection conditional on distance. We then used half-normal key functions with cosine adjustment terms (see Miller *et al.* (2019) for descriptions of key functions and adjustment terms for detection functions), accounted for differences in survey detectability according to observed group size and then combined these detection functions into a single distance sampling model (see detection function plots in Fig. S3). The number of cosine adjustment terms was chosen using the Akaike Information Criterion ($n = 1$ for on-water versus $n = 2$ for in-flight detection functions). We then calculated combined Gannet density (and its uncertainty) per year using a Horvitz–Thompson-like estimator, which are common in estimating mean density in distance sampling (Miller *et al.* 2019), having made the necessary adjustments outlined in Miller *et al.* (2021) to the dht2 function in the package to accommodate the multiple detection function set-up:

$$\widehat{D} = \frac{1}{a} \sum_{i=1}^{n} \frac{s_i}{p_i}, \qquad (1)$$

where a is the total area surveyed, i indexes the observations up to n, s_i is the size of the observed group of animals and p_i gives the probability of detection for that observation. We estimated the variance of $\widehat{D}$ via standard methods (Buckland *et al.* 2004). In our case the values of p_i come from two different detection functions. See Miller *et al.* (2019, 2021) for more mathematical details on distance sampling in R, using multiple detection functions in distance sampling models, and empirical examples on carrying out similar analyses.

Converting PIROP to ECSAS

We calculated both linear densities (PIROP methodology) and square densities (ECSAS

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methodology) from the combined survey data (2014–21). We adjusted the linear densities to account for the fact that the original PIROP surveys were double-sided whereas the combined survey was single-sided (Table 1), and therefore the former would, on average, detect twice as many Gannets as the latter. We created the factor to convert from PIROP linear densities to ECSAS square densities as the quotient of these two values for each year (correction factor = 2 × (birds/km)/(birds/km^2)), with units of km, and then we took the median of these yearly values. Finally, we divided the original PIROP linear densities by this correction factor to make them comparable to the modern ECSAS square densities (PIROP linear densities/correction factor = PIROP square densities) and combined the two to produce a time-series spanning 1969–2021. We explored the role of uncertainty in our correction factor affecting our density estimates using bootstrapping, and we did not find a significant difference in our results. We calculated the annual rate of increase from at-sea surveys by fitting a linear model using the lm function in R, assuming Gaussian errors and an identity link function, to this density time-series as a function of year. Lastly, we explored the importance of the length of the combined survey dataset (8 years) for the estimated rate of increase. To do so, we calculated the correction factor using randomized subsamples of the 8-year dataset from $n = 1$ year to $n = 8$ years, and then calculated the rate of increase to determine the number of years the combined survey needed to be carried out to have confidence in our correction factor.

Gannet breeding population comparison

To compare at-sea surveys to breeding population surveys for Gannets, we calculated the annual rate of increase from population-wide colony count data from the six breeding colonies in the western North Atlantic: Bonaventure Island, Anticosti Island, Bird Rocks, Cape St Mary's, Baccalieu Island and Funk Island (Nettleship & Chapdelaine 1988, Chardine *et al.* 2013; Fig. 2a). Census methods for surveys followed those described in Chardine *et al.* (2013). Briefly, colonies were overflown during one day in mid- to late July (coinciding with the chick-rearing period) using fixed wing aircraft (Britten-Norman Islander, Partenavia P68 Observer and de Havilland Beaver), with digital photographs taken either through the window or an opening in the belly of the plane using digital cameras (Canon 10D, Canon 5D Mark II, Canon 50D). The exception was in 2018 for the three Newfoundland colonies (eastern-most in Fig. 2a), when surveys were flown using a Bell 206 Long Ranger helicopter, with photographs taken through a bubble window. Photographs were post-processed and counted using a combination of Adobe Photoshop (Adobe Inc. 2019) and ImageJ (Schneider *et al.* 2012) using marking and manual tallying methods. Photographs were marked using mouse point-and-click methods either by using the pencil tool onto each Apparently Occupied Site in Photoshop and analysed using the histogram function (Rail *et al.* 2013) or by using the Cell Counter plugin of ImageJ. An Apparently Occupied Site constituted one bird, or two birds close together, in a breeding area of the colony and represented one breeding pair of Gannets. To compare our data with the at-sea estimates, we restricted analyses to breeding population data collected from 1972 to 2018. We calculated per-colony annual rates of increase for breeding Gannets by fitting a linear model using the lm function in R, assuming Gaussian errors and an identity link function, to the population estimates as a function of year for each colony. We then computed the median overall annual rate of increase, adjusting for differences in colony size by weighting the per-colony rates of increase by colony size, as colony size is more representative of the population as a whole than per-colony annual rates of increase.

RESULTS

In total we collected: 2193 observations from 1969 to 1983 using the PIROP methodology (5266 transects); 4181 observations of Gannets from 2006 to 2021 using the ECSAS methodology (11 158 transects); and 3749 observations from 2014 to 2021 using our combined survey methodology (4608 transects) (Table 1). Under our combined survey methodology, 1622 observations (30.2% of the total) were recorded as 'in transect' (i.e. 300-m transect for birds on water, snapshot for birds in flight) (Table 1). The correction factor was estimated as 0.86 km (95% confidence interval (CI) 0.51–1.61 km) (Fig. 3). The rate of increase in Gannet density from 1969 to 2021 calculated using the at-sea PIROP and ECSAS survey data was 2.69% (95% CI 1.66–7.02%) per year (linear

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model $R^2 = 0.298$; $P = 0.001$) (Fig. 4a). We found that it took 3–4 years of combined surveys using both PIROP and ECSAS methodologies to approximate our estimated rate of increase with 8 years of surveys (~2–3%; Fig. S4). The rate of increase in Gannet population size calculated using the breeding population data was 2.77% (95% CI 1.00–4.15%) per year (linear model $R^2 = 0.917$; $P < 0.001$) (Fig. 4b). The weighted rate of increase was comparable at 2.91% (95% CI 2.26–4.16%).

DISCUSSION

The method described herein used two at-sea survey programmes with different count methods to quantify long-term changes in Gannet population size. Previous studies using at-sea survey data in the western North Atlantic to monitor large fluctuations in abundance have either used just one of these data sources (PIROP) (Huettmann & Dimaond 2000) or examined anomalies within the data without adjusting with a correction factor (Gjerdrum *et al.* 2018). Correction factors have been developed for PIROP in the past for certain species (Diamond *et al.* 1986) and for observational data in US waters (Powers 1982), but these were developed before ECSAS surveys began and did not account for differences in detection based on species in flight or on the water. The surveys that used both methods simultaneously, combined with our modelling approach, help to integrate these two datasets, representing an advance over past efforts to estimate spatial and temporal seabird population trends using long-term datasets collected at sea (Clarke *et al.* 2003, Renner *et al.* 2013) and effectively rescuing the extensive PIROP dataset from obsolescence.

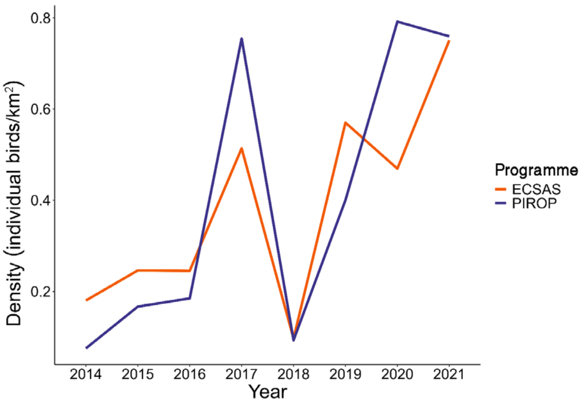

Figure 3. Density trends for Northern Gannets *Morus bassanus* in the western North Atlantic based on combined PIROP/ECSAS survey data (2014–21). Orange line shows density estimates based on ECSAS methodology (square densities; individual birds/km^2). Purple line shows density estimates based on PIROP methodology (linear densities; individual birds/km). PIROP linear densities were converted to ECSAS square densities by dividing PIROP density estimates by the correction factor computed from the combined PIROP/ECSAS survey data, 0.86 km (95% CI 0.51–1.61 km).

Data collected at sea since 1969 indicate Gannet populations in the western North Atlantic have increased at a rate similar to that estimated from data collected at breeding colonies (Fig. 4), and similar to rates of population growth in other parts of their range (Nelson 2005, Chardine *et al.* 2013, Mowbray 2020, Jeglinski *et al.* 2023). The global breeding Gannet population now totals ~1.05 million individuals, representing a consistent ~3% per year increase since the early 20th century (Nelson 1978, 2005). Estimates for most European breeding colonies are far below carrying capacity (Jeglinski *et al.* 2023), indicating a strong potential for consistent growth in the future. Estimating population trends over shorter periods of time with data collected at sea (e.g. within PIROP or ECSAS time periods of ~15 years) may not be possible because of the high variability in annual estimates and gaps in survey coverage (MacLean *et al.* 2013). However, at-sea surveys may represent a new avenue to understand how anthropogenic factors affect seabird population growth. For example, fluctuations in densities at sea during the early 2010s (Fig. 4a) coincided with increased nest abandonment, breeding failures and population declines in North American Gannet breeding colonies (Fig. 4b) due to a marine heatwave (Montevecchi *et al.* 2021). It remains to be seen whether the significant adult mortality caused by Highly Pathogenic Avian Influenza, observed at several major Gannet colonies in 2022 and causing population declines of up to 30% (Lane *et al.* 2024), will be detected in density estimates from more recent at-sea surveys.

Our approach of applying a correction factor, in combination with advances in distance sampling analyses, could be applied to other disparate surveys of seabirds and other marine animals (see Fig. S1 for a workflow of our approach), including those collected across jurisdictions. For example, seabird survey methods used in the US Atlantic (https://coast.noaa.gov/digitalcoast/data/atloffshoreseabird.html) differ from methods used in Atlantic

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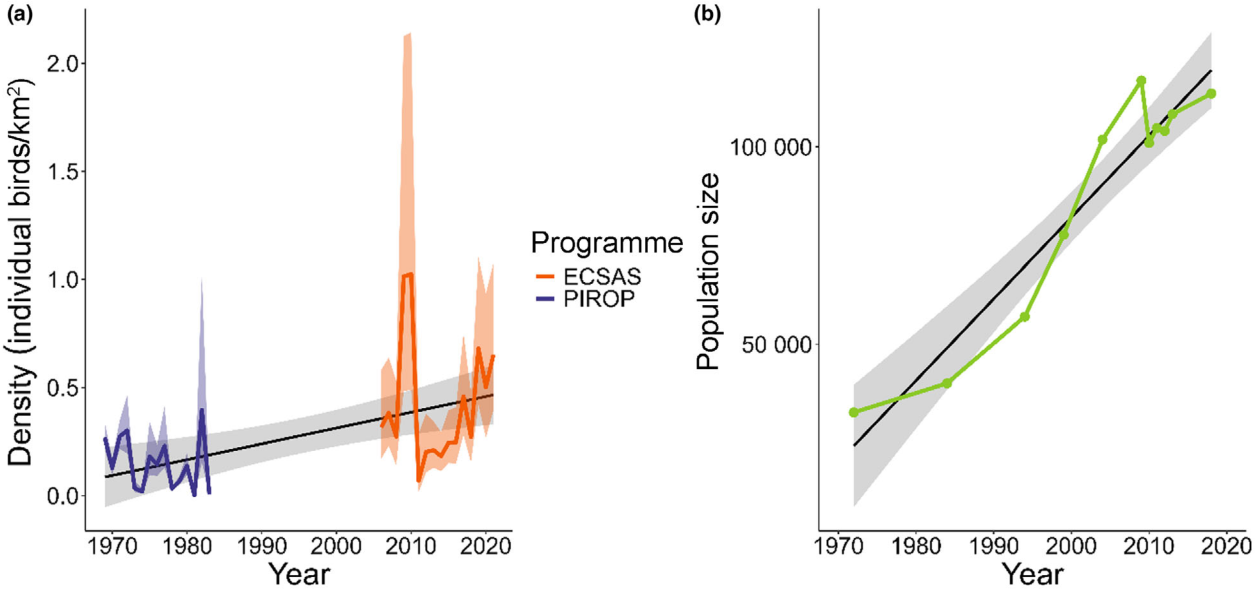

Figure 4. (a) Density (individual birds/km^2) trends for Northern Gannets *Morus bassanus* in the western North Atlantic based on at-sea survey data (PIROP, 1969–83; ECSAS, 2006–21). Density was not estimated between 1983 and 2006 because of low or no survey effort and poor spatial coverage. PIROP densities have been made comparable to ECSAS using our correction factor. Bold purple and orange lines show density estimates and ribbons represent 95% CI. Black line and ribbons show the linear model fit. The rate of increase from 1969 to 2021 was 2.69% (95% CI 1.66–7.02%) per year. (b) Breeding population trends (in number of breeding pairs) for Northern Gannets in the western North Atlantic. See Figure 2a for locations. Green dots and line show population size estimates. The rate of increase from 1972 to 2018 is 2.91% (95% CI 2.26–4.16%) per year.

Canada, although many seabird populations undergo large-scale movements during migration that cross these national boundaries, including the Gannet (Fifield *et al.* 2014). Combining datasets from across a species' range will strengthen species status assessments and help inform cross-jurisdictional protected area planning (Schuster *et al.* 2023). In addition, past analyses of historical datasets within both the North Pacific (Renner *et al.* 2013) and the Southern Ocean (Hunt *et al.* 1994) excluded seabird datasets collected at sea for missing transect widths (see table 1 in Tasker *et al.* 1984), limiting our understanding of modern-era population trends for many seabird species throughout the world.

To implement our methods, simultaneous surveys using both survey methods are necessary to calculate an appropriate correction factor, as we did from 2014 to 2021 (Fig. 1, Fig. S1). Secondly, advances in distance sampling analyses (Miller *et al.* 2019, 2021) that allow for multiple detection functions in one model can be used to estimate densities for one or both survey methods. We do note that in our case, distance sampling was only applied to ECSAS surveys and not PIROP surveys because of the lack of distance information on earlier PIROP surveys. Future analyses could leverage newer surveys using old methodology (i.e. the combined survey approach) to estimate missing distances in the earlier PIROP surveys. In addition, these analyses may require extensive at-sea data to spatially sample the species' at-sea breeding range (Fig. 2). Many of the seabird species in the PIROP and ECSAS surveys were sampled as much as or more extensively than Gannets. Other at-sea datasets may not have appropriate spatial coverage to use our methods. Lastly, once densities are adjusted using the correction factor, datasets can be combined to estimate long-term at-sea population trends.

One important future application of the correction factor approach and modelling advances made in this paper is to leverage at-sea observations to understand the population status and trends of seabirds for which breeding colony data are largely unavailable (Croxall *et al.* 2012, Paleczny *et al.* 2015). Unlike Gannets, few species have population counts from all (major) colonies whose breeders visit the western North Atlantic at some point during the year. For example, Dovekies *Alle*

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alle are well-documented by at-sea survey programmes (Gjerdrum *et al*. 2024) but breeding colony information is mostly unavailable (BirdLife International 2023). However, the use of at-sea observations in the absence of colony information for determining trends would need to acknowledge the contribution of non-breeding individuals to a population and the potential differences in their demography compared with breeders. Ignoring immature, non-breeding or 'floating' populations of seabirds can underestimate population size estimates by as much as 30% (Paleczny *et al*. 2015) and potentially hinder conservation and management actions by ignoring the source and role of potential immigrants to breeding colonies (Ainley *et al*. 2024). For Gannets, however, the population trend derived from at-sea surveys reflected that obtained from breeding adults at colonies, indicating that the non-breeding component of the population is tracking the breeding component. This may be because breeding colonies in the western North Atlantic are below carrying capacity with potential for future growth (Jeglinski *et al*. 2023). Conversely, seabirds at carrying capacity may have non-breeding populations that fluctuate while breeding populations stay stable because of limitations on colony growth (Ainley *et al*. 2024).

At-sea surveys could also help to supplement our understanding of the population status of seabird species that are inaccessible or dispersed (e.g. phalaropes, jaegers, Black Guillemots *Cepphus grylle*), a breeding strategy that makes it difficult to monitor population sizes and trends across the breeding range. For example, migratory Sooty Shearwaters *Ardenna grisea* are highly abundant but thought to be declining globally, as indicated by declines in their core breeding range in the South Pacific (Scott *et al*. 2008, Moller *et al*. 2009, Waugh *et al*. 2013). Yet populations in the Falkland Islands are increasing (Clark *et al*. 2019), and there are probably numerous colonies on the islands and fjord coastlines of Patagonia and Tierra del Fuego, where little is known about their population size or trend (Lawton *et al*. 2006, Reyes-Arriagada *et al*. 2007). At-sea population surveys in the Atlantic and other migratory regions could help to resolve these inconsistencies to better assess the global population trend and conservation status of Sooty Shearwaters. More generally, our approach can be used to combine disparate datasets to understand long-term trends in seabird populations, and cross-jurisdictional patterns of abundance, to help inform and guide conservation strategies.

We thank all the observers who participated in collecting the data over the years, with special thanks to those who conducted surveys using the two methods simultaneously: Sue Abbott, Holly Hogan, Rick Ludkin, Pierre Ryan, Brad Toms, Regina Wells and Jeannine Winkel. We also wish to thank the science staff, ships' officers and personnel for support at sea. We also thank anonymous editors and reviewers who helped to improve this manuscript.

AUTHOR CONTRIBUTIONS

T.J. Clark-Wolf: Conceptualization; writing – original draft; formal analysis. **David L. Miller:** Formal analysis; writing – review and editing. **Hannah Drake:** Writing – review and editing; investigation. **David A. Fifield:** Writing – review and editing; conceptualization; data curation; formal analysis. **Jean-François Rail:** Data curation; writing – review and editing. **Ewan D. Wakefield:** Conceptualization; writing – review and editing. **Sabina I. Wilhelm:** Data curation; writing – review and editing. **Sarah N.P. Wong:** Writing – review and editing; conceptualization; data curation. **Carina Gjerdrum:** Conceptualization; writing – review and editing; data curation.

FUNDING

Environment and Climate Change Canada.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

ETHICAL NOTE

None.

DATA AVAILABILITY STATEMENT

The code and data needed to reproduce this analysis is stored on GitHub and archived using Zenodo (https://doi.org/10.5281/zenodo.14563374). Seabird survey data can be found on the Government of Canada's Open Data Portal (https://search.open.canada.ca/opendata/).

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Received 6 August 2024;
Revision 3 December 2024;
revision accepted 8 December 2024.
Associate Editor: Lei Cao

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Workflow diagram describing the analysis of the combined, ECSAS and PIROP datasets.

Figure S2. Bar charts showing survey effort for Northern Gannets by month and by year.

Figure S3. Detection function plots for flying and swimming Northern Gannets.

Figure S4. Relationship between number of years used to calculate the correction factor and the rate of increase.

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