EVALUATING SURVEY DURATION WITH COMMUNITY ATTRIBUTES OF MARINE BIRDS IN THE SOUTH ATLANTIC BIGHT

J. CHRISTOPHER HANEY[1] & DAVID S. LEE[2†]

[1]*Defenders of Wildlife, 1130 17th Street, NW, Washington, DC 20036 (chaney@defenders.org)*
[2]*Tortoise Reserve, P.O. Box 7082, White Lake, NC 28337*
†Deceased

SUMMARY

HANEY, J.C. & LEE, D.S. 2015. Evaluating survey duration with community attributes of marine birds in the South Atlantic Bight. *Marine Ornithology* 43: 53–64.

The expense of conducting dedicated marine bird surveys creates incentives to optimize sampling effort. We appraised spatiotemporal effort in two shipboard surveys off the southeastern coast of the United States using analyses of seabird community structure. By applying randomization routines from both data-analytic (curve-fitting) and sampling-theoretic methods (bootstrap, jackknife, coverage), we assessed sampling adequacy for estimating numerical and biomass dominance, species accumulation rates and species richness. Maximum-likelihood estimators indicated that each survey had been carried out long enough for cumulative species richness (S_{obs}) to reach an apparent asymptote. Data stratification by season did not reduce the asymptotic-based estimates of minimum survey effort overall. Three estimators of total species richness ($\hat{S}_{max}$) were equal to or less than values actually observed (S_{obs} = 53 species in each survey). Five other estimators of $\hat{S}_{max}$ exceeded S_{obs} by 5%–18%, suggesting few species remained undetected by the time our surveys ended. Indeed, after >600 additional observation days, only six more offshore species were detected (all extralimitally rare), a tally that fell within error terms for estimators noted above. The two avifaunal surveys examined here were two to six times longer than required (36–65 days) to detect community dominants (species comprising ≥95% of numerical abundance and biomass). We conclude that sampling effort as appraised by community attributes was minimally adequate in both surveys. Measures of saturation in community structure can be applied while inventories are in progress to complement analyses of sample size based on statistical power, and may help minimize costs associated with over-sampling in dedicated surveys for marine birds.

Key words: survey adequacy, sampling effort, South Atlantic Bight, western Atlantic Ocean, seabird community structure, species accumulation rate, species richness

INTRODUCTION

Beginning in the 1970s, seabird management in the context of hydrocarbon exploitation (Ainley *et al.* 2012) prompted numerous inventories along the continental shelf margins of North America, Europe and elsewhere (e.g. Brown *et al.* 1975, Briggs *et al.* 1981, 1985, Gould *et al.* 1982, Powers 1983, Tasker *et al.* 1984, Abrams 1985). Some survey programs were motivated by the sensitivity of seabirds to marine pollution, including floating plastics (Azzarello & Van Fleet 1987) and oil (Barrett 1979, Boersma 1986, Lee 1999). Competition with and mortality from commercial fisheries were the impetus behind others (Ainley *et al.* 1981, Furness 1982, Burger & Cooper 1984).

Regardless of purpose, the challenging logistics require critical evaluation of the methodology used in marine bird surveys (Briggs *et al.* 1985). Substantial time, personnel and costs are devoted to these survey programs, some of which span decades (Ainley *et al.* 1996, Veit *et al.* 1996, Ribic *et al.* 1997). Fees levied for dedicated ship use can exceed $5 000–$15 000 per day (Dufour 2012). Given the high financial costs, surveys are often done from ships of opportunity, which risks compromising the sample representation. Considerations of survey design thus beg scrutiny: How much survey effort is adequate? What is the minimum temporal and/or spatial coverage necessary to achieve optimal efficiency in offshore surveys? What consequences arise from using different appraisal methods for evaluating this adequacy?

Answers to these questions depend on the intent of the surveys and the nature of the particular research issue addressed (Ainley *et al.* 2012). Seabird responses to temporal or spatial changes in their environment might be evaluated at the focal individual (Votier *et al.* 2010), population (Oedekoven *et al.* 2001) or multi-species level (Ballance *et al.* 1997). Therefore, different response variables may be required to address spatial pattern (Fritz *et al.* 2003, Johnston *et al.* 2014), numerical abundance (Maclean *et al.* 2013) or community structure (Wiens *et al.* 1996).

In preliminary stages, survey programs for marine birds are often exploratory, intended to describe community composition for estimating feeding requirements (Schneider & Hunt 1982) or to assess species' vulnerability to oil spills (Seip *et al.* 1991, Begg *et al.* 1997). Species richness and other community-level metrics may also be used as the primary response variable in some environmental impact assessments (Wiens *et al.* 1996). Confidence that most species have been detected in a survey is a fundamental prerequisite to any community-level analysis (Cam *et al.* 2002).

Here we use attributes of seabird community structure to retroactively examine minimal survey adequacy for two shipboard

studies in the South Atlantic Bight off the southeastern United States. These attributes include community dominance, total species richness and the rate at which new species were added as a function of continued survey effort. We distinguish this approach for evaluating survey adequacy from individual- or population-based methods, including analysis of spatial changes (Fritz *et al.* 2003) or numerical trends (Kinlan *et al.* 2012, Maclean *et al.* 2013). Finally, and after re-evaluating our findings in the context of additional, later observations carried out in the same region, we offer recommendations for making objective decisions about whether marine bird survey effort can be deemed minimally adequate at a particular stage using measures of community composition.

STUDY AREA AND METHODS

Marine bird surveys were conducted in the South Atlantic Bight off the southeastern United States (Fig. 1). The survey in the northern portion of the bight off North Carolina was carried out mostly in an area of steep, converging bathymetric contours adjacent to the Outer Banks (OB). The survey in the south-central portion of the bight was conducted over the broad and shallow continental shelf in the large indentation of the coastline termed the Georgia Embayment (GE).

Regional oceanography throughout this region is dominated by the Gulf Stream, which flows over the Blake Plateau just seaward of and adjacent to the continental shelf break (Olson *et al.* 1983). Along-shore current fluctuations promote episodically high but localized productivity in the offshore (Yoder *et al.* 1981, Atkinson & Targett 1983). Other distinguishing features of the South Atlantic Bight include high, turbid river discharges in the Georgia Embayment (Blanton & Atkinson 1983), greater temporal changes in offshore than in coastal winds (Weisberg & Pietrafesa 1983), and strong seasonal influence of atmospheric cooling on continental shelf water masses (Atkinson *et al.* 1983). These and other factors lead to substantial patchiness, i.e. high local variation in seabird distributions across the region (e.g. Lee 1995, Haney 1986, Hass 1997). Spatial dispersion of both surveys examined here was sufficient to represent most (if not all) of this environmental variation, from middle shelf marine regions proceeding seaward (see Results).

Survey techniques

Standardized counts for seabirds were available from 223 days of dedicated shipboard surveys using continuous counts off the Outer Banks (Moser & Lee 2012), and 143 days of opportunistic shipboard surveys at intervals using 300 m strip transects in the Georgia Embayment (Haney 1986). Data analyzed here were collected entirely in the open ocean (≤200 km from shore), outside sounds, bays, and inlets. OB surveys were carried out from 1975 to 1989 and GE surveys from 1982 to 1985. Surveys were conducted during all months of the year, but effort was not allocated proportionately across seasons (Table 1).

OB surveys recorded seabird locations throughout the day, and these were summed as daily totals within plotted transects of varying lengths and periods. GE surveys originally recorded bird count data within 15 min periods (Haney 1986). Seabird numbers from the GE survey were therefore re-binned into daily totals to achieve grain-size compatibility (Hortal *et al.* 2006) between the two surveys. Non-quantitative information on species composition was also gathered during each survey. Although this extra information was not compatible with most of the numerical analyses examined here, we report the additional species detected in the joint total of all species observed in both surveys (these totals are distinguished within and between surveys in Appendix 1, available on the website).
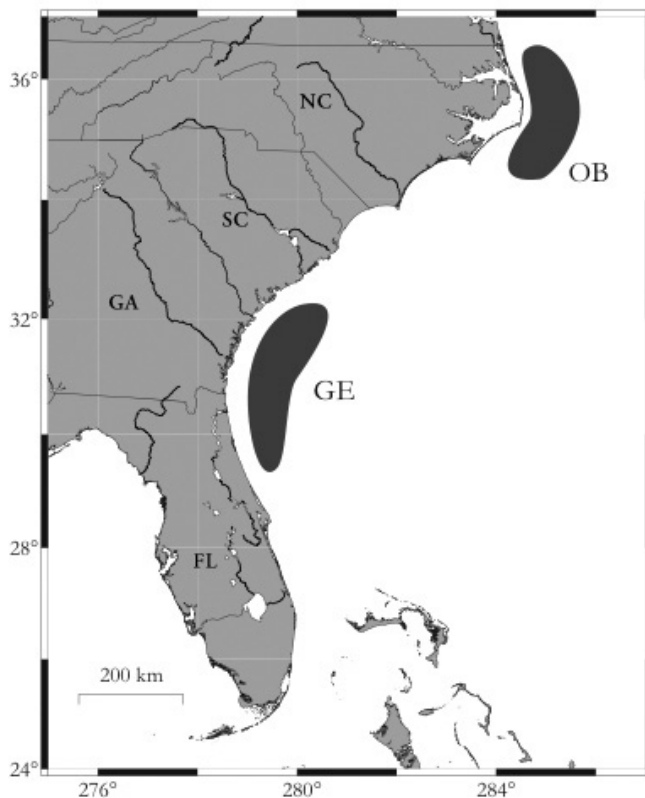

Fig. 1. Study areas for two marine bird surveys off the coast of the southeastern United States (general locations only). Most sampling off the Outer Banks (OB) and Georgia Embayment (GE) occurred on or near the middle and outer continental shelf (50–500 m depths).

TABLE 1
Seasonal allocation of effort (in days) during two multi-year shipboard surveys conducted in the northern (Outer Banks) and southern (Georgia Embayment) portions of the South Atlantic Bight, United States

Season[a]	Outer Banks		Georgia Embayment	
	Number of days	Percent of total	Number of days	Percent of total
Winter (Nov–Mar)	43	19.3	37	25.9
Transitional (Apr–May, Sep–Oct)	72	32.3	65	45.4
Summer (Jun–Aug)	108	48.4	41	28.7
Total	223	100.0	143	100.0

[a] Seasons are differentiated on the basis of regional marine climate (Atkinson *et al.* 1983).

Data treatment

Survey data were organized into two large matrices (one for each region) consisting of individual dates, species and number of individuals per species. Each matrix was initially configured with the survey dates in chronological order. Matrix manipulations were the bases for three types of analyses, most of which used various randomization routines to evaluate simultaneously the number of species and either species' abundances or presence/absence. Because statistical estimation of the number of species is notoriously resistant to a single solution (Foggo *et al*. 2003, Hortal *et al*. 2006, Reichert *et al*. 2010), we screened both data-analytic and sampling-theoretic approaches (Bunge & Fitzpatrick 1993). Performance among estimators was evaluated by conducting a regression analysis of the observed with the predicted accumulation curve, then comparing the amount of variance explained among the different model types. Standard notation is used throughout the text for species richness estimators (Chazdon *et al*. 1998).

Data-analytic methods. Data-analytic methods included both descriptive and diagnostic techniques. A general property of counting species is that more new species are detected during the initial stages of surveys, so relationships between species number and effort were examined first as curvilinear functions (Tjørve 2003). To remove influence of sample order in shaping the actual curves, we used an iterative routine to calculate average species richness (S) over the entire curve. Curve smoothing was accomplished by random permutations of the one-day survey samples with a procedure set to n = 1 000 runs (PISCES 1.2; Henderson & Seaby 1997). Curves depicting number of species in actual survey order were depicted with n = 1 run.

Asymptotic functions can be suitable for some species accumulation curves (Miller & Wiegert 1989, Soberon & Llorente 1993, Keating *et al*. 1998). If an asymptote for total species ($\hat{S}_{max}$) can be estimated, the corresponding level of survey effort can be interpolated from the curve's horizontal axis. A parametric maximum-likelihood estimator (Raaijmakers 1987) was used to calculate whether an asymptote was evident. Sampling was assumed complete if the asymptotic estimate was equal to or less than the observed value of S (Colwell & Coddington 1994). This diagnostic routine was applied incrementally to larger combinations of randomly shuffled one-day survey samples (n = 1 000 runs each) until this "stopping rule" (*sensu* Scharff *et al*. 2003) indicated that sampling was adequate.

Accurate estimation of $\hat{S}_{max}$ may be compromised unless accumulation curves are derived from a homogeneous species pool (Hortal *et al*. 2006, Reichert *et al*. 2010). As a prelude to other estimations of $\hat{S}_{max}$ (see below), we compared mean randomized accumulation curves (n = 1 000 runs) to a hypothetical curve expected if all individual birds recorded over all survey samples had been assigned randomly to individual samples (Colwell & Coddington 1994). If the expected curve (using the function described by Coleman *et al*. 1982) lies above the observed species accumulation curve, the samples are of diverse origin (e.g. Flather 1996). If heterogeneity was detected, subsamples of species richness were re-binned and then analyzed separately by season to examine whether survey efficiency could be improved by this stratification. Improvement was indicated if asymptotes were identified for the separate accumulation curves, and if fewer cumulative survey-days (relative to the cumulative total) would have been required by this alternative allocation of survey days.

Sampling-theoretic methods. Sampling-theoretic methods included estimation of both maximum species richness as well as functions that predicted the curve (or rate) of species accumulation. Survey adequacy was also evaluated by comparing differences (if any) between the total species richness observed and the maximum species richness that was estimated ($\hat{S}_{max}$). Because no single model has been found to be universally suitable for species richness data (Bunge & Fitzpatrick 1993), a variety of non-parametric models were tested. Models included bootstrap, jackknife, and coverage (the latter were both incidence-based and abundance-based [ACE]; Chazdon *et al*. 1998).

Two different Chao estimators of $\hat{S}_{max}$ were used. An abundance-based estimator and variance for species richness (Chao 1984), respectively, are given by the following equations:

$$S_{Chao1} = S_{obs} + (F_1^2/2F_2), \text{ and var } (S_{Chao1}) = F_2(G^4/4 + G^3 + G^2/2),$$

S_{obs} is the total number of species observed in all samples pooled, F_i is the number of species that have exactly i individuals when all samples are pooled, and $G = F_1/F_2$. An incidence-based estimator and variance of species richness (Chao 1987), respectively, are given by the following equations:

$$S_{Chao2} = S_{obs} + (Q_1^2/2Q_2), \text{ and var } (S_{Chao2}) = F_2(G^4/4 + G^3 + G^2/2),$$

In this estimator, Q_1 is the number of species that occur in exactly one sample (uniques), and Q_2 is the number of species that occur in exactly two samples (duplicates).

Two additional coverage estimators were used for species richness based on abundance (Chao & Lee 1992). The general form of these ACE estimators is given by the following equation:

$$S_{ACE} = S_{abund} + \frac{S_{rare}}{C_{ACE}} + \frac{F_1}{C_{ACE}}\gamma_{ACE}^2,$$

where S_{abund} is the number of abundant species (each with more than 10 individuals) when all samples are pooled, S_{rare} is the number of rare species (each with 10 or fewer individuals) when all samples are pooled. Therefore:

$$C_{ACE} = 1 - (\frac{F_2}{N_{rare}}), N_{rare} = \sum_{i=1}^{10} iF_i, \text{ and } \gamma_{ACE}^2 = \max(\frac{S_{rare}}{C_{ACE}}\frac{\sum_{i=1}^{10} i(i-1)F_1}{(N_{rare})(N_{rare}-1)} - 1, 0),$$

as computed in Henderson & Seaby (1997).

The bootstrap estimator of $\hat{S}_{max}$ used here was that described by Smith & van Belle (1984). Jackknife estimators of species richness included both the first-order (Burnham & Overton 1978, Heltshe & Forrester 1983) and the second-order, robust-limiting forms (Burnham & Overton 1979, Palmer 1991). Non-parametric estimates of $\hat{S}_{max}$ were computed with n = 143–1 000 runs of randomly shuffled one-day samples from each survey. Computational routines for these and related estimators are available from Colwell (2014), Henderson & Seaby (1997), and Hines *et al*. (1999).

Community dominance. Products of mean body mass (Appendix 1, available on the website) and the number of individuals for each species recorded were used to calculate the total abundance and biomass of the seabird community pooled over all samples collected across the entire duration in each of the two surveys. This procedure

formed the basis of two retrospective analyses aimed at measuring saturation in community dominance.

In the first analysis, we computed the minimum number of survey days required to detect only those species that composed 95% of the total abundance and biomass. This approach involved ranking species by their importance values (numbers or contributions to total biomass) until the cumulative total came to 95%, then identifying the shortest duration that would have detected these same species, given the actual start date and sampling sequence used in each survey.

In the second analysis, Monte Carlo trials were employed with different start dates assigned randomly to hypothetical surveys. Using subsamples of species richness from the real surveys, hypothetical surveys were "conducted" for the same duration identified in the analysis described above. This resampling approach therefore simulated the extent to which alternative start dates (as surveys can only progress forward) might have influenced identification of the community dominants.

Post-survey evaluation of effort and cost

To appraise whether our surveys were carried out long enough using compositional criteria, we compared the species richness totals we observed (and their statistical estimators) to the cumulative species totals detected later as the consequence of two decades of

additional offshore marine bird observations conducted in the same region. Between 1988 and the present, one of us (D.S.L.), as well as commercial operators, ran various one-day excursions in the South Atlantic Bight. The longest-running excursions have been those off North Carolina by Brian Patteson (http://seabirding.com/), most of which were conducted off the Outer Banks coastline (Fig. 1).

We assessed the species composition recorded in these additional observations (n = 619 survey days from 1988 to 2013) for any offshore species that had not been recorded during our earlier surveys. We interpolated the number of additional survey days that were required to detect each additional species. Then we derived a range of equivalent costs for dedicated ship time for this added survey effort based on the average 2012 daily charge rates for coastal- ($5000–$10000) and regional-capable vessels ($10000–$15000) that are suitable for outer continental shelf surveying, and operated expressly for such purposes under the Atlantic fleet of the University National Oceanographic Laboratory System (Dufour 2012).

Fig. 2. Mean randomized species accumulation compared with the species richness tallied in actual chronological order for each of two surveys off the southeastern United States. The smoothed curve for average species richness was computed with n = 1 000 iterations of randomly shuffled, one-day survey samples.

TABLE 2
Actual and mean estimated species richness of the seabird communities detected by shipboard surveys in the northern (Outer Banks) and southern (Georgia Embayment) portions of the South Atlantic Bight, United States

Technique	Outer Banks		Georgia Embayment	
	Species richness, $\hat{S}_{max} \pm SE$	Model fit (r^2)[a]	Species richness, $\hat{S}_{max} \pm SE$	Model fit (r^2)[a]
Actual survey	53.0	–	53.0	–
Maximum-likelihood	51.1	0.787	52.8	0.632
Coverage 1 (Chao & Lee 1992)	53.0	0.998	53.0	0.998
Coverage 2 (Chao & Lee 1992)	53.0	0.998	53.0	0.998
Chao$_1$ (1984: abundance-based)	59.3 ± 0.4	0.996	59.1 ± 0.4	0.976
Chao$_2$ (1987: incidence-based)	56.0 ± 0.1	0.906	63.0 ± 0.5	0.865
First-order jackknife	59.0 ± 0.2	0.990	62.9 ± 0.3	0.988
Second-order jackknife	58.0 ± 3.1	–	60.0 ± 3.7	–
Bootstrap	56.2	0.984	57.5	0.988

[a] Values for model fit for each estimation technique are based on least-squares regressions of the observed on the estimated species accumulation curves, as generated from selected sampling-theoretic techniques.
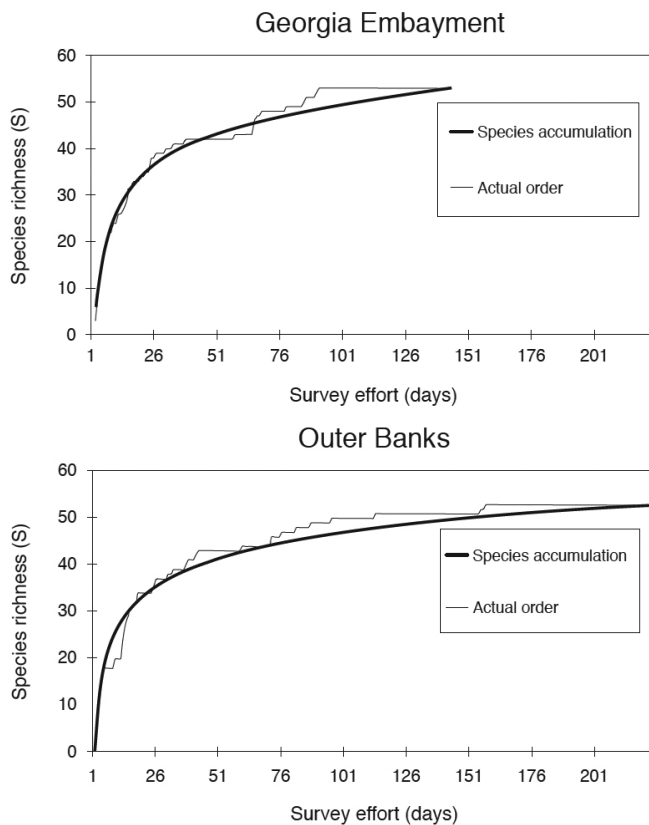
RESULTS

Species richness

Both surveys recorded a total of 53 seabird species, but this number was achieved in 80 fewer sampling days in the GE (Fig. 2). Maximum-likelihood estimators identified asymptotes for each of the two survey's seasonally combined daily samples. The asymptote for the OB survey corresponded to 46 species and 88 days of surveys. The asymptote for the GE survey corresponded to 52 species and 135 days of surveys. Distinct curve shapes of each asymptote, however, indicated that the underlying statistical functions for the maximum-likelihood estimators were different (Fig. 3). Of estimators examined, the maximum-likelihood estimator provided the poorest fit to the entire observed accumulation curves (Table 2), tending to greatly overshoot S during the earliest stages of these surveys (Fig. 3).

Although species accumulation curves were asymptotic for each survey, additional diagnostic tests indicated that the daily samples collected during each survey were heterogeneous (Fig. 4). Differences between the observed and homogeneous community curves ranged from about 5 to 17 species, and 5 to 18 species, during the first 20 days of the OB and GE surveys, respectively.

Despite this heterogeneity, stratifying samples by season did not materially reduce the asymptote-based estimates of minimum survey effort. Except for the OB during summer, no asymptotes were identified for any of the other single-season species accumulation curves (Table 3). Even so, values for $\hat{S}_{max}$ were within a single species of the observed richness for the two remaining seasons in the OB area. Observed and estimated values of $\hat{S}_{max}$ in the GE were closest in summer (<2 species), despite relatively few days of sampling during that season (Table 1). Asymptotic estimators for $\hat{S}_{max}$ during winter and transitional seasons in the GE were at least 3 species greater, however, than the values of species richness observed.

Three of eight estimators for species richness were equal to or less than the species richness actually observed in the surveys (Table 2). Coverage estimators gave highly accurate point estimates for $\hat{S}_{max}$ in each survey, and explained more than 99% of the variance in species richness along the entire accumulation curves. The bootstrapped estimator for $\hat{S}_{max}$ gave the next most accurate estimate of total species richness in each survey. The bootstrap also explained high variance (>98%) in species richness along the entire accumulation curve. In general, non-parametric estimates of species richness in the GE were slightly higher than comparable values from the OB, but low precision in these estimators casts doubt on attaching particular biological significance to the differences (Table 2).

Species dominance

As few as 18 species contributed ≥95% of all individual seabirds ultimately recorded during the GE survey (Table 4). Based on the
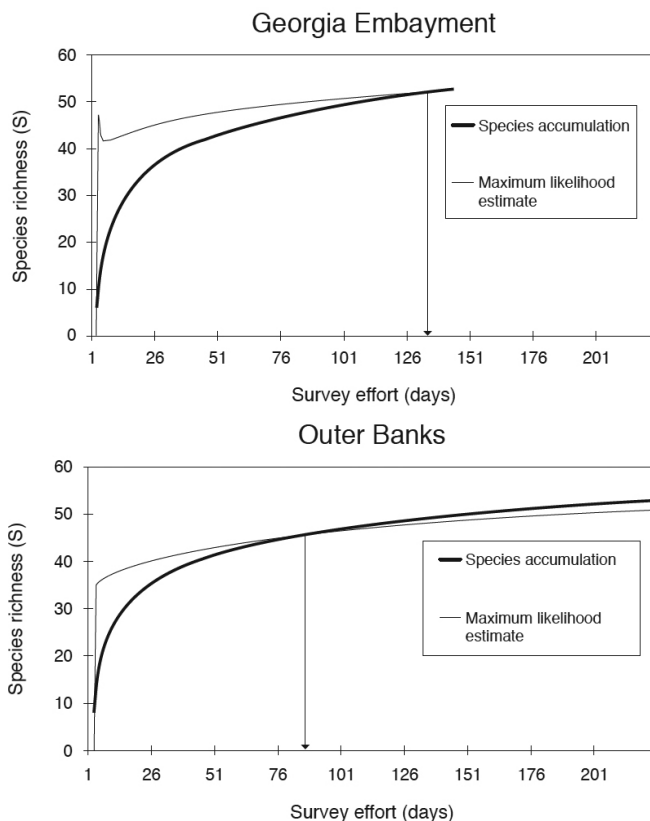

Fig. 3. Minimum survey effort interpolated from an asymptotic estimate of total species richness, $\hat{S}_{max}$, for each of two surveys of marine birds off the coast of the southeastern United States. Asymptotes were calculated with a maximum-likelihood estimator (Raaijmakers 1987).
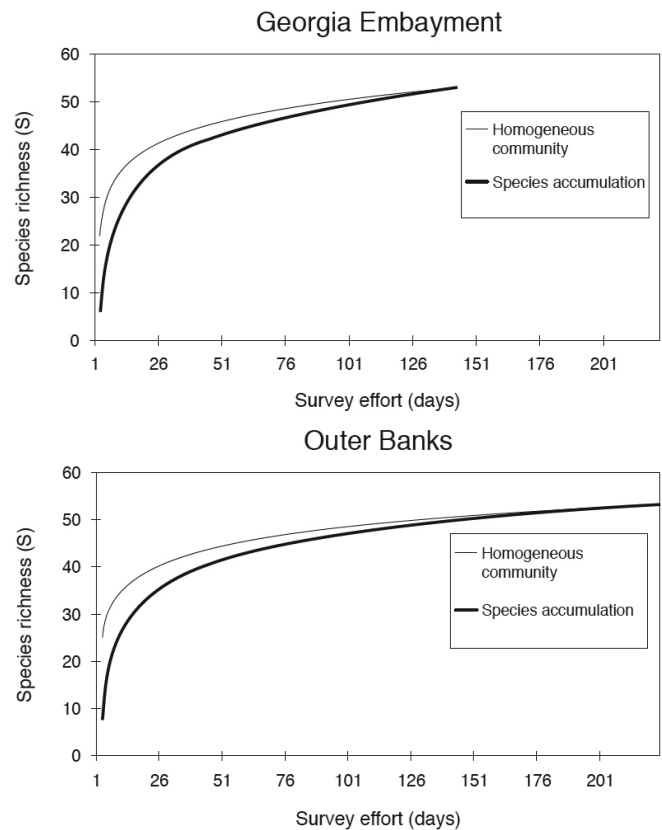
Fig. 4. Test for community heterogeneity in the species pool for two surveys of marine birds conducted off the coast of the southeastern United States. Curves for a homogeneous community are based on the method described by Coleman *et al.* (1982). The observed species accumulation curve was derived from n = 1 000 randomized iterations of one-day survey samples.

actual chronological sequence of the GE survey and the shortest possible detection time for these 18 dominants, a minimum of 66 consecutive survey days, or 46% of this survey program's total duration, would have been required to record dominant species. With a random start date, a hypothetical GE survey with duration 66 days had a 95% likelihood of recording all 18 dominants (n = 20 trials). As few as 16 species contributed ≥95% of all seabird biomass detected in the GE survey. Based on actual chronological sequence and the shortest possible detection time to observe these dominants, a minimum of 65 consecutive survey days, or 45% of this survey program's total duration, would have been required to detect these species. With random start dates, a hypothetical GE survey with duration 65 days had a 95% likelihood of recording these same 16 dominants (n = 20 trials).

As few as 14 species contributed ≥95% of all individual seabirds ultimately recorded during the OB survey (Table 4). Based on actual chronological sequence of the OB survey and the shortest possible detection time for these 14 dominants, a minimum of 43 consecutive survey days, or 19% of this survey program's total duration, would have been required to record these species. With a random start date, a hypothetical OB survey of duration 43 days had only a 45% likelihood of recording all 14 dominants (n = 20 trials). A hypothetical OB survey with a duration equivalent to that used in the GE analysis above (66 days), however, would have a 60% likelihood of recording these 14 dominants (n = 20 trials). As few as 11 species contributed ≥95% of all seabird biomass in the OB survey. Based on the actual chronological sequence of the OB survey and the shortest possible detection time for these 11 dominants, a minimum of 43 consecutive survey days, or 19% of this survey program's total duration, would have been required to detect these species. With a random start date, a hypothetical OB survey with duration 43 days had a 55% likelihood of recording these same 11 dominants (n = 20 trials).

Consequences of "missed" species

The joint total for both South Atlantic Bight surveys was 60 species, not including those species detected outside the quantitative portions of the surveys analyzed here (Appendix 1, available on the website). As of 2014, 60 species represents about 75% of a total pool (*sensu* Cam *et al.* 2000) consisting of all aquatic bird species known to occur from the region's marine waters (e.g. see http://www.

carolinabirdclub.org/brc/checklist_of_North_Carolina_birds.html). Most of the species we "missed" during our surveys were lacking either as a result of revised taxonomy (e.g. Patteson & Armistead 2004) or because particular taxa (e.g. certain sea ducks, grebes, larids) inhabit primarily neritic waters very near shore, habitats that we did not sample effectively from ships. However, one primarily offshore alcid known from the region was certainly missed during the quantitative phases of our surveys (Atlantic puffin *Fratercula arctica*), and five offshore procellariiforms ultimately recorded in the region went undocumented in our surveys (Table 5).

If added to our either of our survey totals, these six taxa (11% of each survey's S_{obs}) bring the total to 59 species, a value nearly identical to several point estimates for $\hat{S}_{max}$, or within the confidence limits of other estimators (Table 2). With the exception of *Fratercula arctica*, which is casual to rare in the region (Lowther *et al.* 2002), all other species detected after the mid-1980s are extralimital to the South Atlantic Bight. The second species added, Swinhoe's Storm-Petrel *Oceanodroma monorhis*, took 117 additional days to detect, a duration that hypothetically would cost $585 000–$1 755 000 using conventional research ships (Table 5). It took 579 additional days to detect the 59th species, Black-browed Albatross *Thalassarche melanophrys*, a survey duration equivalent to at least $2 895 000 in dedicated ship costs.

DISCUSSION

Survey duration in the South Atlantic Bight

As far as we are aware, ours is the first attempt to test various quantitative attributes of community structure to assess adequacy of survey duration for marine birds. Whether we gauged adequacy by species richness or community dominance, we conclude that total duration for each South Atlantic Bight marine bird survey was minimally adequate. Indeed, community-level measures indicate

TABLE 3
Total species richness (S_{obs}) and seasonal coverage for two seabird surveys conducted in the northern (Outer Banks) and southern (Georgia Embayment) portions of the South Atlantic Bight, United States

Season[a]	Outer Banks		Georgia Embayment	
	Observed	Estimate[b]	Observed	Estimate[b]
Winter (Nov–Mar)	33	34.1	33	36.2
Transitional (Apr–May, Sep–Oct)	42	42.7	41	44.0
Summer (Jun–Aug)	39	37.1	28	29.5

[a]　Seasonal periods are differentiated on the basis of regional marine climate (Atkinson *et al*. 1983).
[b]　Maximum-likelihood estimate for asymptote on the species accumulation curve (Raaijmakers 1987).

TABLE 4
Total species coverage compared with total duration for three different measures of community structure as measured from two seabird surveys conducted in the northern (Outer Banks) and southern (Georgia Embayment) portions of the South Atlantic Bight, United States

Measure	Number of species (%)		Number of equivalent survey days (%)	
	Outer Banks	Georgia Embayment	Outer Banks	Georgia Embayment
Asymptote of species richness[a]	46.0 (86.8)	52.4 (98.9)	88 (39.5)	135 (94.4)
Numerical dominance[b]	14.0 (26.4)	18.0 (34.0)	43 (19.3)	65 (45.5)
Biomass dominance[c]	11.0 (20.8)	16.0 (30.2)	36 (16.1)	65 (45.5)

[a]　Maximum-likelihood estimate for asymptote on the species accumulation curve (Raaijmakers 1987).
[b]　Number of seabird species composing ≥95% or all individuals recorded on all surveys.
[c]　Number of seabird species composing ≥95% or all biomass recorded on all surveys.

that our surveys had been conducted unnecessarily long in the context of our research goals. Setting aside extralimital species, detecting only community dominants could have been accomplished in as few as 36 to 65 total survey days (Table 4). This level of effort corresponds to an estimated nominal cost of $180 000 to about $1 000 000 in dedicated ship time. Judged by the same measures of community dominance, however, our surveys were conducted two to six times longer than necessary. Such supplemental effort in one survey alone could equate to overspending on dedicated ship use by as much as $2 800 000.

Substantially less effort was required to detect community dominants than to achieve saturation in species richness (Tables 2, 4). Simulations indicated a high probability of detecting regularly occurring community dominants with less than half the survey effort actually expended in GE. Off the OB, however, simulations indicated only modest probability ($\leq 60\%$) of detecting dominants using similar survey durations. This disparity might be explained by differences between the two surveys with respect to spatial or temporal allocation of sampling across the continental shelf. Also, the OB survey devoted less effort in winter during its final stages, whereas simulations revealed a high likelihood of detecting only community dominants had the survey begun before day 100. If community metrics are contemplated as stopping rules (Scharff et al. 2003), we recommend that investigators: (1) survey evenly throughout each season to increase the likelihood of temporal representation, and (2) adopt quantitative criteria that yield a high probability (e.g. $\geq 95\%$) of detecting all dominants. Monte Carlo trials or other resampling methods can be used to test such dominance-based stopping rules (cf. Magnussen et al. 2010).

Although we detected substantial heterogeneity in our daily samples of species richness (Fig. 4), we nevertheless ultimately found asymptotes to $\hat{S}_{max}$ (Fig. 3). We attribute this somewhat unexpected finding to the peculiar variability that is common to marine bird survey data. Numerical variability in species richness can stem from several sources, including any differences in total time counting seabirds among survey days. Local seabirds are also patchily distributed due to behavioral (Haney et al. 1992), trophic

(Moser & Lee 2012) and oceanographic factors (Hass 1997), any of which may affect a species total by day. Weather can also alter survey date, duration and visibility of detection. Nevertheless, based on the observed saturation in species richness (e.g. Fig. 3; see also Table 5), we inferred that spatial coverage of our surveys was adequate (cf. Longino & Colwell 1997) to represent primary habitats in our study area (e.g. inner vs. outer shelf, Gulf Stream eddies, etc.).

Disparities between scales of data collection and environmental patchiness create noise from binning data into sampling frames of essentially arbitrary grain size (Haney & Solow 1992). Although this noise might increase differences in species richness observed among samples, it need not greatly influence the species accumulation curve. Indeed, several species richness estimators (e.g. ACE, Chao$_1$, jackknife, bootstrap) have been shown to be robust and precise despite variations in the grain size elected for the sampling frame (e.g. Hortal et al. 2006).

As in other species inventories (Longino & Colwell 1997), stratification did not reduce our asymptotic-based estimates for total survey effort (Table 3). This may be because seabird occurrence and species composition are partially independent of the seasons that we used for stratification; seabirds in the South Atlantic Bight originate from tropical, subtropical and temperate regions in both southern and northern hemispheres (Lee & Booth 1979, Lee 1995). Sub-adults of several species may reside at sea in this portion of the Atlantic for years before breeding. Some seabird communities may thus conform to those special cases in which a well-known or -studied taxon (Soberon & Llorente 1993) leads to well-behaved statistical properties in the underlying species richness data (e.g. Keating et al. 1998).

Choosing a community-based estimator for appraising survey duration

In this study, we used asymptotic estimates for species richness in two regional marine bird communities strictly as an informal, practical and descriptive guide to evaluate whether survey duration

TABLE 5

Duration and hypothetical costs associated with the extra effort required to find additional seabird species not detected during two prior, quantitative surveys in the South Atlantic Bight, United States

Species	Additional survey days[a]	Cost per species		Cumulative cost to survey	
		Minimum[b]	Maximum[c]	Minimum[b]	Maximum[c]
Atlantic Puffin *Fratercula arctica*	2	$10 000	$30 000	$10 000	$30 000
Swinhoe's Storm-Petrel *Oceanodroma monorhis*	117	$575 000	$1 725 000	585 000	$1 755 000
Atlantic Yellow-nosed Albatross *Thalassarche chlororhynchos*	155	$190 000	$570 000	$775 000	$2 325 000
Black-bellied Storm-Petrel *Fregetta tropica*	268	$565 000	$1 695 000	$1 340 000	$4 020 000
European Storm-Petrel *Hydrobates pelagicus*	409	$705 000	$2 115 000	$2 045 000	$6 135 000
Black-browed Albatross *Thalassarche melanophrys*	542	$665 000	$1 995 000	$2 710 000	$8 130 000

[a] Number of days required to detect species additional to those recorded during both the OB and GE surveys summarized here.
[b] Based on daily usage fees for a small-capacity vessel in the University National Oceanographic Laboratory System (UNOLS) fleet (Dufour 2012), capable of short-duration surveys (≤ 1 week) in coastal and shelf waters.
[c] Based on daily usage fees for a medium-capacity vessel in the UNOLS fleet (Dufour 2012), capable of medium-duration surveys (1–3 weeks) in shelf waters.

was minimally adequate. Before our two surveys, the seabird fauna in this portion of the western Atlantic Ocean were very poorly known. Community inventories carry an inherent risk that some species, typically the rarest, go undetected (Gotelli & Colwell 2001, Dorazio *et al.* 2006, Chao *et al.* 2009). Observations after our surveys ended confirmed that only species extralimital to the South Atlantic Bight had gone undetected (Table 5). For purposes of an environmental assessment, none of these species could be deemed at population risk within our study regions (and, in some cases globally, e.g. *Fregetta tropica*). Moreover, our survey durations were sufficient to detect the presence of arguably the most endangered seabird in the northwest Atlantic Ocean, the Bermuda Petrel *Pterodroma cahow* (see Appendix 1, available on the website).

In addition, we have shown that surveys carried out longer than necessary, at least from the standpoint of merely adding extralimital species, may carry exceedingly high costs. Using dedicated ships in the South Atlantic Bight to detect ever more species would have cost hundreds of thousands of dollars per species (Table 5). The cumulative costs to merely add more species to the community composition would have been even more expensive, exceeding millions of dollars. Thus, from a fiscal standpoint, there is great incentive to sample seabird communities with surveys that are both pragmatic and efficient.

More formally, the number of species detected in a survey (S_{obs}) is typically expected to be less than the number of species actually present ($\hat{S}_{max}$). Unless differences between S_{obs} and $\hat{S}_{max}$ are small, or biases that deflate S_{obs} remain constant, comparisons of relative species richness across space or time are problematic (Conroy & Noon 1996, Nichols *et al.* 1998). Ideally, detection probabilities for species in a community should be very close to 1 and should not vary greatly across sites or times (Boulinier *et al.* 1998). If detection biases are large (e.g. observability varies among species; Barbraud & Thiebot 2009), comparing species richness between surveys may be unwise. The probability of detecting all species in the South Atlantic Bight was likely close to 1, given that there are virtually no diving species in the offshore; that is, there is "no place to hide" for birds in open marine habitat. Because failures to detect bird species can be attributed to fundamental rarity instead of a truly low rate of detectability (Dorazio *et al.* 2006), we conclude that the differences between S_{obs} and $\hat{S}_{max}$ illustrated in our study arose largely from estimator performance.

Diverging performance (Table 2) in the various estimators for $\hat{S}_{max}$ was hardly unexpected. Because of unique properties of the individual data sets that underlie species richness, identifying a consistently accurate estimator has proven elusive (e.g. Esty 1986, O'Hara 2005). After considering bias, accuracy and precision (Hellman & Fowler 1999, Walther & Moore 2005), the performance of $\hat{S}_{max}$ depends on inherent attributes of community structure (Foggo *et al.* 2003), prevalence of rare species (Reichert *et al.* 2010) and extent to which the true number of species in the community is known (Ugland *et al.* 2003).

With the data generated from our study, more than one type of estimator gave fairly accurate predictions of the point estimate, $\hat{S}_{max}$, within and between the two surveys, some with confidence limits (Table 2) that encompassed addition even of exceedingly rare species observed well after our surveys ended (Table 5). Because our focus here was exploratory and practical, however, we are reluctant to endorse particular quantitative estimators for all

situations. Maximum likelihood was useful only for $\hat{S}_{max}$, not the entire accumulation curve (Table 2, Fig. 3). Coverage estimators are "better understood and…behaved" (Bunge & Fitzpatrick 1993), and they delivered accurate estimates for S_{obs} in our surveys (Table 2). The Chao$_1$ (1984) ACE and the first-order jackknife were almost exactly accurate for $\hat{S}_{max}$ (Table 2), once the additional species recorded after our surveys were included (Table 5). The non-parametric estimators are less biased and more precise than species accumulation curves (Brose *et al.* 2003). They have also performed well in other species inventories (Walther & Morand 1998, Foggo *et al.* 2003, Walther & Moore 2005), including surveys of bird communities (Walther & Martin 2001).

Survey duration in other contexts

We regard our approach for evaluating survey duration as representing the "floor" rather than "ceiling" for effort needed to characterize key species in a seabird community within a defined study area. Whereas minimum survey effort that fails to meet statistical criteria for community composition could be difficult to justify, additional considerations govern whether effort is sufficient for other purposes, including the frequency of sampling. For example, surveys spaced approximately three to five days apart have been found to be statistically independent, and surveys conducted over one to three years captured much of the inter-annual variance for marine habitats off the eastern United States (see Kinlan *et al.* 2012).

Choice of appropriate sample size is always a critical part of research planning (Morrison 1988, Dale *et al.* 1991). Our proposed cut-off criteria for survey duration (e.g. Fig. 3) are suitable only when community composition is the response variable (Wiens *et al.* 1996, Votier *et al.* 2004, Ainley *et al.* 2012). If population trends are the focus, statistical power analysis might guide decisions on whether enough samples were collected (e.g. Hatch 2003, Kinlan *et al.* 2012). Detecting offshore population changes may prove difficult if power gains cannot be achieved through extending duration, frequency and spatial extent of surveys. Maclean *et al.* (2013) report limited ability to circumvent this problem in one survey program. In such cases, other response variables, including changes to species composition (Wiens *et al.* 1996, Tittensor *et al.* 2010) or spatial pattern (Lapeña *et al.* 2010), may help inform impact assessments for marine birds in offshore marine environments. Algorithms based on bagged decision trees can also identify consistent aggregations or "hotspots" of seabird abundance (e.g. Nur *et al.* 2011, Santora *et al.* 2011).

Evaluating survey duration using community attributes could inform the selection of sampling lengths in preliminary or pilot settings elsewhere. One potential application is for identifying the minimum survey duration for impact assessments at offshore wind energy projects (Garthe & Hüppop 2004, Drewitt & Langston 2006, Watts 2010). Before siting of wind power installations, detecting bird species most susceptible to avoidance behavior (Desholm & Kahlert 2005), collision risk (Johnston *et al.* 2014) and habitat loss from turbines or other physical structures (Fox & Petersen 2006, Hüppop *et al.* 2006) is vital. Individual sites considered for offshore wind development are typically far smaller than our survey areas (Fig. 1), so we would not expect that minimum-length surveys would require as many as 65 days in order to detect community dominants over such local scales. To avoid any temporal bias in species detections, seasonal representation should be addressed explicitly.

Appraising survey duration using community-level criteria is also relevant to planning new large-scale, region-wide surveys. The Gulf of Mexico remains the least-studied offshore region for seabirds in the continental United States. Despite an immense infrastructure for offshore energy in the region (>4 000 offshore oil and gas production platforms; Dismukes 2010), long-term, baseline seabird surveys are still inexplicably lacking for the entire Gulf. Given parallels between the South Atlantic Bight and Gulf of Mexico's marine environments and seabird faunas, and given adequate spatial dispersion, we recommend that future Gulf surveys be conducted for at least 36–65 total days. Duration could be iteratively tested while such surveys were in progress using tools that rely upon any of several saturation criteria available (e.g. Table 2).

ACKNOWLEDGEMENTS

REFERENCES

ABRAMS, R.W. 1985. Environmental determinants of pelagic seabird distribution in the African sector of the Indian Ocean. *Journal of Biogeography* 12: 473–492.

AINLEY, D.G., DEGANGE, A.R., JONES, L.L. & BEACH, R.J. 1981. Mortality of seabirds in high-seas salmon gill nets. *Fisheries Bulletin* 79: 800–806.

AINLEY, D.G., SPEAR, L.B. & ALLEN, S.G. 1996. Variation in the diet of Cassin's Auklet reveals spatial, seasonal, and decadel occurrence patterns of euphausiids off California, USA. *Marine Ecology Progress Series* 137: 1–10.

AINLEY, D.G., RIBIC, C.A. & WOEHLER, E.J. 2012. Adding the ocean to the study of seabirds: a brief history of at-sea seabird research. *Marine Ecology Progress Series* 451: 231–243.

AMERICAN ORNITHOLOGISTS' UNION. 2014. AOU checklist of North and Middle American birds. [Available online at: http://checklist.aou.org/taxa/; accessed 8 April 2014]

ATKINSON, L.P. & TARGETT, T.E. 1983. Upwelling along the 60-m isobaths from Cape Canaveral to Cape Hatteras and its relationship to fish distribution. *Deep Sea Research* 30: 221–226.

ATKINSON, L.P., LEE, T.N., BLANTON, J.O. & CHANDLER, W.S. 1983. Climatology of the southeastern United States continental shelf waters. *Journal of Geophysical Research* 88: 4705–4718.

AZZARELLO, M.Y. & VAN FLEET, E.S. 1987. Marine birds and plastic pollution. *Marine Ecology Progress Series* 37: 295–303.

BALLANCE, L.T., PITMAN, R.L. & REILLY, S.B. 1997. Seabird community structure along a productivity gradient: importance of competition and energetic constraint. *Ecology* 78: 1502–1518.

BARBRAUD, C. & THIEBOT, J.-B. 2009. On the importance of estimating detection probabilities from at-sea surveys of flying seabirds. *Journal of Avian Biology* 40: 584–590.

BARRETT, R.T. 1979. Small oil spill kills 10–20 000 seabirds in North Norway. *Marine Pollution Bulletin* 10: 253–255.

BEGG, G.S., REID, J.B., TASKER, M.L. & WEBB, A. 1997. Assessing the vulnerability of seabirds to oil pollution: sensitivity to spatial scale. *Waterbirds* 20: 339–352.

BLANTON, J.O. & ATKINSON, L.P. 1983. Transport and fate of river discharge on the continental shelf of the southeastern United States. *Journal of Geophysical Research* 88: 4730–4738.

BOERSMA, P.D. 1986. Ingestion of petroleum by seabirds can serve as a monitor of water quality. *Science* 321: 373–376.

BOULINIER, T., NICHOLS, J.D., SAUER, J.R., HINES, J.E. & POLLOCK, K.H. 1998. Estimating species richness to make inferences in community ecology: the importance of heterogeneity in species detectability. *Ecology* 79: 1018–1028.

BRIGGS, K.T., CHU, E.W., LEWIS, D.B., TYLER, W.B., PITMAN, R.L. & HUNT, G.L., JR. 1981. Distribution, numbers, and seasonal status of seabirds of the southern California Bight. In: Summary report 1975–1978: marine mammal and seabird surveys of the southern California Bight area, volume III. Springfield, VA: US National Technical Information Service Publications. pp. 1–212.

BRIGGS, K.T., TYLER, W.B., LEWIS, D.B. & CARLSON, D.R. 1985. Comparison of ship and aerial surveys of birds at sea. *Journal of Wildlife Management* 49: 405–411.

BROSE, U., MARTINEZ, N.D. & WILLIAMS, R.J. 2003. Estimating species richness: sensitivity to sample coverage and insensitivity to spatial patterns. *Ecology* 84: 2364–2377.

BROWN, R.G.B., NETTLESHIP, D.N., GERMAIN, P., TULL, C.E. & DAVIS, T. 1975. Atlas of eastern Canadian seabirds. Ottawa, ON: Canadian Wildlife Service.

BUNGE, J. & FITZPATRICK, M. 1993. Estimating the number of species: a review. *Journal of the American Statistical Association* 88: 364–373.

BURGER, A.E. & COOPER, J. 1984. The effects of fisheries on seabirds in South Africa and Namibia. In: Nettleship, D.N., Sanger, G.A. & Springer, G.F. (Eds). Marine birds: their feeding ecology and commercial fisheries relationships. Canadian Wildlife Service Special Publication. Ottawa, ON: Canadian Wildlife Service. pp. 150–160.

BURNHAM, K.P. & OVERTON, W.S. 1978. Estimation of the size of a closed population when capture probabilities vary among animals. *Biometrika* 65: 623–633.

BURNHAM, K.P. & OVERTON, W.S. 1979. Robust estimation of population size when capture probabilities vary among animals. *Ecology* 60: 927–936.

CAM, E., NICHOLS, J.D., SAUER, J.R., HINES, J.E. & FLATHER, C.H. 2000. Relative species richness and community completeness: birds and urbanization in the mid-Atlantic states. *Ecological Applications* 10: 1196–1210.

CAM, E., NICHOLS, J.D., SAUER, J.R. & HINES, J.E. 2002. On the estimation of species richness based on the accumulation of previously unrecorded species. *Ecography* 25: 102–108.

CHAO, A. 1984. Non-parametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics* 11: 265–270.

CHAO, A. 1987. Estimating the population size for capture-recapture data with unequal catchability. *Biometrics* 43: 783–791.

CHAO, A. & LEE, S.-M. 1992. Estimating the number of classes via sample coverage. *Journal of the American Statistical Association* 87: 210–217.

CHAO, A., COLWELL, R.K., LIN, C.-W. & GOTELLI, N.J. 2009. Sufficient sampling for asymptotic minimum species richness estimators. *Ecology* 90: 1125–1133.

CHAZDON, R.L., COLWELL, R.K., DENSLOW, J.S. & GUARIGUATA, M.R. 1998. Statistical methods for estimating species richness of wood regeneration in primary and secondary rain forests of northeastern Costa Rica. In: Dallmeir, F. & Comiskey, J.A. (Eds). Forest diversity research, monitoring and modeling: conceptual background and Old World case studies. Paris: Parthenon Publishing. pp. 285–309.

COLEMAN, M.D., MARES, M.D., WILLIG, M.R. & HSIEH, Y.-H. 1982. Randomness, area, and species richness. *Ecology* 63: 1121–1133.

COLWELL, R.K. 2014. EstimateS: statistical estimation of species richness and shared species from samples. [Available online at: http://viceroy.eeb.uconn.edu/estimates/EstimateSPages/AboutEstimateS.htm; accessed 10 March 2013]

COLWELL, R.K. & CODDINGTON, J.A. 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society (B)* 345: 101–118.

CONROY, M.J. & NOON, B.R. 1996. Mapping of species richness for conservation of biological diversity: conceptual and methodological issues. *Ecological Applications* 6: 763–773.

DALE, V.H., FRANKLIN, R.L.A., POST, W.M. & GARDNER, R.H. 1991. Sampling ecological information: choice of sample size. *Ecological Modeling* 57: 1–10.

DESHOLM, M. & KAHLERT, J. 2005. Avian collision risk at an offshore wind farm. *Biology Letters* 1: 296–298.

DISMUKES, D.E. 2010. Fact book: offshore oil and gas industry support sectors. OCS Study BOEMRE 2010-042. New Orleans, LA: US Department of the Interior, Bureau of Ocean Energy Management, Regulation and Enforcement, Gulf of Mexico OCS Region..

DORAZIO, R.M., ROYLE, J.A., SÖDERSTRÖM, B. & GLIMSKÄR, A. 2006. Estimating species richness and accumulation by modeling species occurrence and detectability. *Ecology* 87: 842–854.

DREWITT, A.L. & LANGSTON, R.H.W. 2006. Assessing the impacts of wind farms on birds. *Ibis* 148: 29–42.

DUFOUR, R. 2012. NSF 2012 ship operation budget snapshot April AVOC meeting. [Available online from: http://www.unols.org/meetings/2012/201204rvo/As_Shown_RVOC2012_presentations/201204rvo_ap11.pdf; accessed 12 March 2014].

DUNNING, J.B. 1993. CRC handbook of avian body masses. Boca Raton, FL: CRC Press, Inc.

ESTY, W.W. 1986. Estimation of the size of a coinage: a survey and comparison of methods. *Numismatic Chronicle* 146: 185–215.

FLATHER, C.H. 1996. Fitting species-accumulation functions and assessing regional land use impacts on avian diversity. *Journal of Biogeography* 23: 155–168.

FOGGO, A., ATTRILL, M.J., FROST, M.T. & ROWDEN, A.A. 2003. Estimating marine species richness: an evaluation of six extrapolative techniques. *Marine Ecology Progress Series* 248: 15–26.

FOX, A.D. & PETERSON, I.K. 2006. Assessing the degree of habitat loss to marine birds from the development of offshore wind farms. In: Boere, G.C., Galbraith, C.A. & Stroud, D.A. (Eds). Waterbirds around the world. Edinburgh, UK: The Stationary Office. pp. 801–804.

FRITZ, H., SAID, S. & WEIMERSKIRCH, H. 2003. Scale-dependent hierarchical adjustments of movement patterns in a long-range foraging seabird. *Proceedings of the Royal Society B* 270: 1143–1148.

FURNESS, R.W. 1982. Competition between fisheries and seabird communities. *Advances in Marine Biology* 20: 225–307.

FURNESS, R.W. 1987. The skuas. Staffordshire, UK: T. and A.D. Poyser.

GARTHE, S. & HÜPPOP, O. 2004. Scaling possible adverse effects of marine wind farms on seabirds: developing and applying a vulnerability index. *Journal of Applied Ecology* 41: 724–734.

GOTELLI, N.J. & COLWELL, R.K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4: 379–391.

GOULD, P.J., FORSELL, D.J. & LENSINK, C.J. 1982. Pelagic distribution and abundance of seabirds in the Gulf of Alaska and eastern Bering Sea. US Fish and Wildlife Service Publication FWS/OBS-82/48. Anchorage, AK: US Fish and Wildlife Service.

HANEY, J.C. 1986. Seabird affinities for Gulf Stream frontal eddies: responses of mobile marine consumers to episodic upwelling. *Journal of Marine Research* 44: 361–384.

HANEY, J.C. & SOLOW, A.R. 1992. Analyzing quantitative relationships between seabirds and marine resource patches. In: Power, D.M. (Ed). Current ornithology, volume 9. New York: Plenum Press. pp. 105–162.

HANEY, J.C., FRISTRUP, K.M. & LEE, D.S. 1992. Geometry of visual recruitment by seabirds to ephemeral foraging flocks. *Ornis Scandinavica* 23: 49–62.

HANEY, J.C., FAANES, C.A. & BOURNE, W.R.P. 1983. An observation of Fea's Petrel *Pterodroma feae* (Procellariiformes: Procellaridae) off the southeastern United States. *Brimleyana* 18: 115–124.

HASS, T. 1997. Distribution of pelagic seabirds in relation to dynamic features of the Gulf Stream. Ph.D. dissertation. Chapel Hill, NC: University of North Carolina.

HATCH, S.A. Statistical power for detecting trends with applications to seabird monitoring. *Biological Conservation* 111: 317–329.

HELLMAN, J.J. & FOWLER, G.W. 1999. Bias, precision, and accuracy of four measures of species richness. *Ecological Applications* 9: 824–834.

HELTSHE, J. & FORRESTER, N.E. 1983. Estimating species richness using the jackknife procedure. *Biometrics* 39: 1–11.

HENDERSON, P.A. & SEABY, R.M.H. 1997. Species diversity and richness, version 1.2. Lymington, UK: PISCES Conservation Ltd..

HINES, J.E., BOULINIER, T., NICHOLS, J.D., SAUER, J.R. & POLLOCK, K.H. 1999. COMDYN: software to study the dynamics of animal communities using a capture-recapture approach. *Bird Study* 46(Suppl): S209–S217.

HORTAL, J., BORGES, P.A.V. & GASPAR, C. 2006. Evaluating the performance of species richness estimators: sensitivity to sample grain size. *Journal of Animal Ecology* 75: 274–287.

HÜPPOP, O., DIERSCHKE, J., EXO, K.-M., FREDRICH, E. & HILL, R. 2006. Bird migration studies and potential collision risk with offshore wind turbines. *Ibis* 148: 90–109.

JOHNSTON, A., COOK, A.S.C.P., WRIGHT, L.J., HUMPHREYS, E.M. & BURTON, N.H.K. 2014. Modelling flight heights of marine birds to more accurately assess collision risk with offshore wind turbines. *Journal of Applied Ecology* 51: 31–41.

KEATING, K.A., QUINN, J.F., IVIE, M.A. & IVIE, L.L. 1998. Estimating the effectiveness of further sampling in species inventories. *Ecological Applications* 8: 1239–1249.

KINLAN, B.P., ZIPKIN, E.F., O'CONNELL, A.F. & CALDOW, C. 2012. Statistical analyses to support guidelines for marine avian sampling: final report. OCS Study BOEM 2012-101. NOAA Technical Memorandum NOS NCCOS 158. Herndon, VA: US Department of the Interior, Bureau of Ocean Energy Management, Office of Renewable Energy Programs..

LAPEÑA, B.P., WIJNBERG, K.M., HULSCHER, S.J.M.H. & STEIN, A. 2010. Environmental impact assessment of offshore wind farms: a simulation-based approach. *Journal of Applied Ecology* 47: 1110–1118.

LEE, D.S. 1995. Marine birds off the coast of North Carolina. *Chat* 59: 113–171.

LEE, D.S. 1999. Pelagic seabirds and the proposed exploration for fossil fuels off North Carolina: a test for conservation efforts of a vulnerable international resource. *Journal of the Elisha Mitchell Scientific Society* 115: 294–315.

LEE, D.S & BOOTH, J., JR. 1979. Seasonal distribution of offshore and pelagic birds in North Carolina waters. *American Birds* 33: 715–721.

LONGINO, J.T. & COLWELL, R.K. 1997. Biodiversity assessment using structured inventory: capturing the ant fauna of a lowland tropical forest. *Ecological Applications* 7: 1263–1277.

LOWTHER, P.E., DIAMOND, A.W., KRESS, S.W., ROBERTSON, G.J. & RUSSELL, K. 2002. Atlantic Puffin (*Fratercula arctica*). In: Poole, A. (Ed). The Birds of North America Online. Ithaca, NY: Cornell Lab of Ornithology. [Available online from: http://bna.birds.cornell.edu/bna/species/709; accessed 17 March 2014]

MACLEAN, I.M.D., REHFISCH, M.M., SKOV, H. & THAXTER, C.B. 2013. Evaluating the statistical power of detecting changes in the abundance of seabirds at sea. *Ibis* 155: 113–126.

MAGNUSSEN, S., SMITH, B., KLEINN, C. & SUN, I.F. 2010. An urn model for species richness estimation in quadrat sampling from fixed-area populations. *Forestry* 83: 293–306.

MILLER, R.J. & WIEGERT, R.G. 1989. Documenting completeness, species-area relations, and the species-abundance distribution of a regional flora. *Ecology* 70: 16–22.

MORRISON, M.L. 1988. On sample sizes and reliable information. *Condor* 90: 275–278.

MOSER, M.L. & LEE, D.S. 2012. Foraging over *Sargassum* by western North Atlantic seabirds. *Wilson Journal of Ornithology* 124: 66–72.

NICHOLS, J.D., BOULINIER, T., HINES, J.E., POLLOCK, K.H. & SAUER, J.R. 1998. Inference methods for spatial variation in species richness and community composition when not all species are detected. *Conservation Biology* 12: 1390–1398.

NUR, N., JAHNCKE, J., HERZOG, M.P., HOWAR, J., HYRENBACH, K.D., ZAMON, J.E., AINLEY, D.G., WIENS, J.A., MORGAN, K., BALANCE, L.T. & STRALBERG, D. 2011. Where the wild things are: predicting hotspots of seabird aggregations in the California Current. *Ecological Applications* 21: 2242–2257.

OEDEKOVEN, C.S., AINLEY, D.G. & SPEAR, L.B. 2001. Variable responses of seabirds to change in marine climate: California Current, 1985–1995. *Marine Ecology Progress Series* 212: 265–281.

O'HARA, R.B. 2005. Species richness estimators: how many species can dance on the head of a pin? *Journal of Animal Ecology* 74: 375–386.

OLSON, D.B., BROWN, O.B. & EMMERSON, S.R. 1983. Gulf Stream frontal statistics from Florida Straits to Cape Hatteras derived from satellite and historical data. *Journal of Geophysical Research* 88: 4569–4577.

PALMER, M.W. 1991. Estimating species richness: the second-order jackknife reconsidered. *Ecology* 72: 1512–1513.

PATTESON, J. B. & ARMISTEAD, G.L. 2004. First record of Cape Verde Shearwater (*Calonectris edwardsii*) for North America. *American Birds* 58: 468–473.

PLATANIA, S.P., GRANT, G.S. & LEE, D.S. 1986. Core temperatures of non-nesting western Atlantic seabirds. *Brimleyana* 12: 13–18.

POWERS, K.D. 1983. Pelagic distributions of marine birds off the northeastern United States. National Oceanic and Atmospheric Administration Technical Memorandum NMFS-F/NEC-27. Woods Hole, MA: National Oceanic and Atmospheric Administration.

RAAIJMAKERS, J.G.W. 1987. Statistical analysis of the Michaelis-Menten equation. *Biometrics* 40: 119–129.

REICHERT, K., UGLAND, K.I., BARTSCH, I., HORTAL, J., BREMNER, J. & KRABERG, A. 2010. Species richness estimation: estimator performance and the influence of rare species. *Limnology and Oceanography Methods* 8: 294–303.

RIBIC, C.A., AINLEY, D.G. & SPEAR, L.B. 1997. Scale-related seabird-environmental relationships in Pacific equatorial waters, with reference to El Niño-Southern Oscillation events. *Marine Ecology Progress Series* 156: 183–203.

SANTORA, J.A., SYDEMAN, W.J., SCHROEDER, I.D., WELLS, B.K. & FIELD, J.C. 2011. Mesoscale structure and oceanographic determinants of krill hotspots in the California Current: Implications for trophic transfer and conservation. *Progress in Oceanography* 91: 397–409.

SCHARFF, N., CODDINGTON, J.A., GRISWOLD, C.E., HORMIGA, G. & BJØRN, P. 2003. When to quit? Estimating spider species richness in a northern European deciduous forest. *Journal of Arachnology* 31: 246–273.

SCHNEIDER, D.C. & HUNT, G.L., JR. 1982. Carbon flux to seabirds with different mixing regimes in the southeastern Bering Sea. *Marine Biology* 67: 337–344.

SEIP, K.L., SANDERSON, E., MEHLUM, F. & RYSSDEL, J. 1991. Damages to seabirds from oil spills: comparing simulation results and vulnerability indexes. *Ecological Modelling* 53: 39–59.

SMITH, E.P. & VAN BELLE, G. 1984. Non-parametric estimation of species richness. *Biometrics* 40: 119–129.

SOBERON, M.J. & LLORENTE, B.J. 1993. The use of species accumulation functions for the prediction of species richness. *Conservation Biology* 7: 480–488.

TASKER, M.L., JONES, P.H., DIXON, T. & BLAKE, B.F. 1984. Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standardized approach. *Auk* 101: 567–577.

TITTENSOR, D.P., MORA, C., JETZ, W., LOTZE, H.K., RICARD, D., BERGHE, E.V. & WORM, B. 2010. Global patterns and predictors of marine biodiversity across taxa. *Nature* 466: 1098–1101.

TJØRVE, E. 2003. Shapes and functions of species-area curves: a review of possible models. *Journal of Biogeography* 30: 827–835.

UGLAND, K.I., GRAY, J.S. & ELLINGSEN, K.E. 2003. The species accumulation curve and estimation of species richness. *Journal of Animal Ecology* 72: 888–897.

VEIT, R.R., PYLE, P. & McGOWAN, J.A. 1996. Ocean warming and long-term change in pelagic bird abundance within the California Current system. *Marine Ecology Progress Series* 139: 11–18.

VOTIER, S.C., FURNESS, R.W., BEARHOP, S., CRANE, J.E., CALDOW, R.W.G., CATRY, P., ENSOR, K., HAMER, D.C., HUDSON, A.V., KALMBACH, E., KLOMP, N.I., PFEIFFER, S., PHILLIPS, R.A., PRIETO, I. & THOMPSON, D.R. 2004. Changes in fisheries discard rates and seabird communities. *Nature* 427: 727–730.

VOTIER, S.C., BEARHOP, S., WITT, M.J., INGER, R., THOMPSON, D. & NEWTON, J. 2010. Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems. *Journal of Applied Ecology* 47: 487–497.

WALTHER, B.A. & MORAND, S. 1998. Comparative performance of species richness estimation methods. *Parasitology* 116: 395–405.

WALTHER, B.A. & MARTIN, J.-L. 2001. Species richness estimation of bird communities: how to control for sampling effort? *Ibis* 143: 413–419.

WALTHER, B.A. & MOORE, J.L. 2005. The concepts of bias, precision and accuracy, and their use in testing the performance of species richness estimators, with a literature review of estimator performance. *Ecography* 28: 815–829.

WATTS, B.D. 2010. Wind and waterbirds: establishing sustainable mortality limits within the Atlantic Flyway. Center for Conservation Biology Technical Report Series, CCBTR-05-10. Williamsburg, VA: College of William and Mary/Virginia Commonwealth University.

WEISBERG, R.H. & PIETRAFESA, L.J. 1983. Kinematics and correlation of the surface wind field in the South Atlantic Bight. *Journal of Geophysical Research* 88: 4593–4610.

WIENS, J.A., CRIST, T.O., DAY, R.H., MURPHY, S.M. & HAYWARD, G.D. 1996. Effects of the *Exxon Valdez* oil spill on marine bird communities in Prince William Sound, Alaska. *Ecological Applications* 6: 828–841.

YODER, J.A., ATKINSON, L.P., LEE, T.N., KIM, H.H. & McCLAIN, C.R. 1981. Role of Gulf Stream frontal eddies in forming phytoplankton patches on the outer southeastern shelf. *Limnology and Oceanography* 26: 1103–1110.

ZINO, F., BROWN, R. & BISCOITO, M. 2008. The separation of *Pterodroma madeira* (Zino's Petrel) from *Pterodroma feae* (Fea's Petrel) (Aves: Procellariidae). *Ibis* 150: 326–334.