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Spatially integrated assessment reveals widespread changes in penguin populations on the Antarctic Peninsula

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Abstract. As important marine mesopredators and sensitive indicators of Antarctic ecosystem change, penguins have been a major focus of long-term biological research in the Antarctic. However, the vast majority of such studies have been constrained by logistics and relate mostly to the temporal dynamics of individual breeding populations from which regional trends have been inferred, often without regard for the complex spatial heterogeneity of population processes and the underlying environmental conditions. Integrating diverse census data from 70 breeding sites across 31 years in a robust, hierarchical analysis, we find that trends from intensely studied populations may poorly reflect regional dynamics and confuse interpretation of environmental drivers. Results from integrated analyses confirm that *Pygoscelis adeliae* (Adélie Penguins) are decreasing at almost all locations on the Antarctic Peninsula. Results also resolve previously contradictory studies and unambiguously establish that *P. antarctica* (Chinstrap Penguins), thought to benefit from decreasing sea ice, are instead declining regionally. In contrast, another open-water species, *P. papua* (Gentoo Penguin), is increasing in abundance and expanding southward. These disparate population trends accord with recent mechanistic hypotheses of biological change in the Southern Ocean and highlight limitations of the influential but oversimplified "sea ice" hypothesis. Aggregating population data at the regional scale also allows us to quantify rates of regional population change in a way not previously possible.

Key words: Adélie Penguin; Antarctic Peninsula; Chinstrap Penguin; chlorophyll a; climate change; Gentoo Penguin; monitoring; population trend; Pygoscelis *spp.; regional scale; sea ice.*

Introduction

Time series data necessary for ascribing causes to population change often derive from a few long-term studies that yield detailed understanding of dynamics for particular local populations (e.g., Holmes et al. 1986, Coulson et al. 2001, Boersma 2008), but do not provide the spatial coverage required for regional-scale inference. The trade-off between demographic detail and spatial coverage plagues population biologists with limited resources (Marsh and Trenham 2008), and decisions about conservation and management often must be based on imperfect or incomplete information (Kareiva et al. 2000, Holmes 2001). This is particularly true in remote areas such as Antarctica, where logistical challenges limit most scientific research to permanent research stations.

As important mesopredators in the Antarctic marine ecosystem, penguins have long been hailed as indicators of environmental change, whether as a result of resource extraction (Ainley et al. 2006, 2007, Ainley and Blight 2009), human visitation (Cobley and Shears 1999, Carlini et al. 2007, Trathan et al. 2008, Lynch et al. 2010), or climate change (Fraser et al. 1992, Croxall et al. 2002, Forcada et al. 2006, Forcada and Trathan 2009, Trivelpiece et al. 2011). Hypotheses regarding the cause of penguin population change have been hotly debated as accepted dogma among penguin biologists has swung between various competing, but not incompatible, paradigms (Croxall 1992, Fraser et al. 1992, Croxall et al. 2002, Ainley et al. 2003, 2007, Nicol et al. 2007, Trivelpiece et al. 2011). Findings from detailed but spatially restricted demographic studies of local populations (Fraser et al. 1992, Forcada et al. 2006) frequently have been extrapolated to regional populations many orders of magnitude larger.

One of the challenges in understanding the environmental drivers of penguin population dynamics has been the almost exclusive reliance on detailed long-term studies of individual breeding populations. Although they provide invaluable information on diet (Volkman et al. 1980, Jablonski 1985, Lishman 1985, Lynnes et al. 2004, Rombolá et al. 2006, Miller and Trivelpiece 2007), breeding success (Cobley and Shears 1999, Lynnes et al. 2004, Rombolá et al. 2006, Hinke et al. 2007), recruitment (Trivelpiece et al. 2011), and foraging

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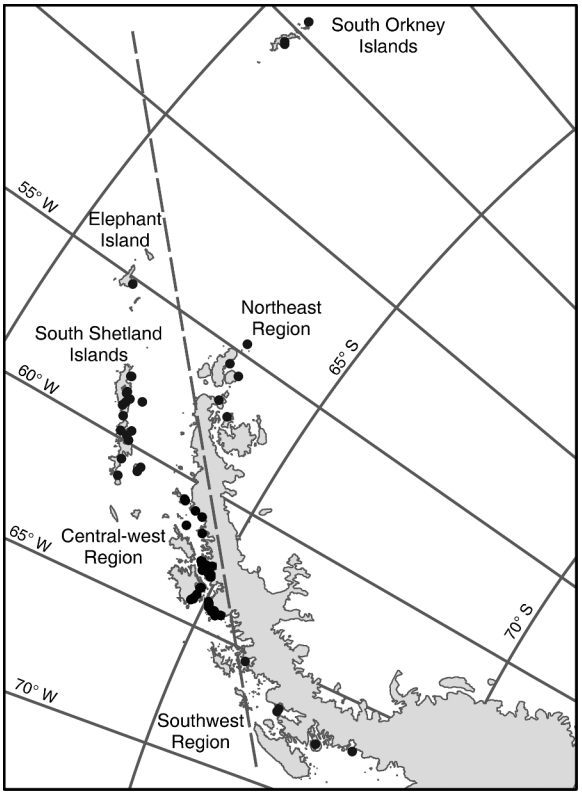

FIG. 1. Antarctic Peninsula and sites (solid circles) for which data for at least two years were available for trend analysis (see also Appendix: Table A1). The dashed line represents the first principal component of the geographic coordinates of these sites, which is used to order sites along a one-dimensional gradient reflecting the northeast–southwest alignment of breeding sites. Populations are grouped into six regions: the South Orkney Islands, Elephant Island, Northeast, South Shetland Islands, Central-west, and Southwest.

dynamics (Trivelpiece et al. 1987, Lynnes et al. 2002, Kokubun et al. 2010), such studies cannot address whether population changes at individual study sites reflect changes at other sites, nor can they be used to infer regional rates of population change. Although a few studies have attempted to draw inference from analyses at several sites, these studies are either confined to several neighboring populations (e.g., Fraser and Patterson 1997, Hinke et al. 2007) or focus on differences among very disparate populations experiencing wholly different environmental conditions (e.g., Croxall et al. 2002). Other than an analysis of trends at several long-term study sites in Woehler et al. (2001), we are aware of no synthetic analysis designed specifically to capture both local- and regional-scale spatial patterns of penguin population trend, as we have done in this analysis of the Antarctic Peninsula (AP) region.

Our goals for this analysis were threefold. First, we wanted to assemble the most complete, spatially explicit picture of population trends for the pygoscelid penguins (*Pygoscelis antarctica*, Chinstrap Penguin; *P. adeliae*, Adélie Penguin; *P. papua*, Gentoo Penguin) on the Antarctic Peninsula, focusing on the 31-year period (1979/1980–2009/2010) for which the vast majority of census data exist. Although previous publications, including several of our own (e.g., Naveen et al. 2000, Lynch et al. 2008, 2010), report census data in their raw form, and others discuss broadscale population changes, but in the absence of a detailed time series analysis (e.g., Trivelpiece et al. 2011), this is the first attempt to quantitatively synthesize all publically available penguin census data for the AP. Second, we wanted to use these spatially distributed time series data to estimate regional rates of population change, key conservation metrics that have heretofore been inaccessible. Finally, we wanted to determine whether spatial patterns in population trend were correlated with spatial patterns in key environmental variables and, in doing so, provide a complementary perspective to time series analyses of fixed study populations.

Our synthetic analysis draws heavily on data from an opportunistic vessel-based monitoring program called the Antarctic Site Inventory (ASI), which uses research vessels and commercial cruise ships as platforms for breeding bird surveys as described in Naveen et al. (2000) and Lynch et al. (2008). We have combined these data with additional published census data from 1979 through 2010 (including 11 breeding sites not included in the ASI) to create the most complete database of pygoscelid penguin census data currently available for the Antarctic Peninsula region (Fig. 1; Appendix: Table A1). This regional perspective allows us to model spatial variation in population trend as a function of environmental gradients, highlighting species-specific responses to the Antarctic Peninsula's changing climate. Additionally, our data and modeling approach allow us to produce the most accurate estimates to date of the magnitude of regional-scale penguin population change on the Antarctic Peninsula and, as importantly, their associated uncertainties.

Although opportunistic sampling, such as that provided by the Antarctic Site Inventory, follows none of the classic survey protocols (e.g., revisit every site every year, rotating panel; see Urquhart and Kincaid 1999), the distribution of visits can be approximately described as an augmented random revisit design whereby sites are surveyed at random among the finite population of penguin breeding sites and augmented with a (smaller) set of sites surveyed every year. Because regional estimates of population change require simultaneous estimates of abundance (or population status) and trend, an optimal survey design must balance the acquisition of data at new sites against repeated sampling at previously surveyed sites (Urquhart et al. 1998). Although only a full power analysis incorporating all of the variance components would allow for the development of an ideal sampling strategy (Urquhart and Kincaid 1999), regular surveys at more than a select few populations is currently infeasible due to the logistical challenges of

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Antarctic research. In light of these limitations, we consider opportunistic sampling supplemented with regular sampling at long-term study sites to provide the best currently available approach for genuine regional-scale inference.

Methods

Description of census data

Our unit for assessing population trends was the breeding "site," which (with few exceptions) we define as being all those penguins accessible by foot from a single landing point. Historically this has been defined as a penguin "rookery" (Penney 1968, Ainley et al. 1983). These sites and their names follow in the tradition of previous penguin monitoring and census data aggregation efforts on the Antarctic Peninsula (Croxall and Kirkwood 1979, Poncet and Poncet 1987, Woehler 1993, Woehler and Croxall 1997), and include several cases in which a chain of small islands or several small adjacent rookeries have been aggregated into a single site (e.g., the Fish Islands, the Yalour Islands, Beneden Head).

The traditional and widely adopted scheme for assessing penguin census precision involves a five-point scale (Croxall and Kirkwood 1979, Woehler 1993): N(C)1, nests (chicks) individually counted, accurate to better than ±5%; N(C)2, nests (chicks) counted in known area, then extrapolated over total colony area, accurate to ±5–10%; N(C)3, accurate estimate of nests (chicks), to ±10–15%; N(C)4, rough estimate of nests (chicks), accurate to ±25–50%; N(C)5, estimate of nests (chicks) to nearest order of magnitude.

There were 70 sites between 60°36′ S and 68°18′ S with two or more penguin abundance counts between 1979/1980 and 2009/2010 (Fig. 1), representing ~4%, 8%, and 41% of the Chinstrap, Adélie, and Gentoo Penguin populations in the region, respectively (H. J. Lynch, *unpublished data*). A complete description of all sites considered for analysis, along with data availability and data sources, is included in the Appendix: Table A1.

Analytical approach

Our analysis required the integration of census data of different types (i.e., both nests and chicks) drawn from multiple sources and of variable quality. Although 80% of all the census data were nest counts and the majority (86%) were in the highest precision category (N1 for nests or C1 for chicks), we developed a flexible model that could integrate additional information in the form of chick counts or lower precision nest counts to provide the most complete spatial and temporal assessment of penguin population trends. To integrate these disparate data, we used a hierarchical Bayesian model that incorporated both nest and chick censuses, included a year- and species-specific estimate of breeding productivity, accounted for variable precision among census counts, and corrected for potential bias due to delays in census timing relative to peak egg laying or chick crèching periods.

Very few sites had time series complete enough to assess temporal correlations between local populations and environmental or climatic variables. Instead, our analysis focused on correlations that might explain the spatial distribution of long-term population trends over the period 1979/1980 to 2009/2010. Our analysis focused on two environmental indices pertinent to the debate surrounding drivers of population change (e.g., Clarke et al. 2007, Ducklow et al. 2007): summer chlorophyll *a* concentration and long-term rates of spring (November) sea ice change.

Model details

Census counts (indexed by i) were modeled on the logarithmic scale as being normally distributed about the "true" nest or chick population y with a variance τ^2 that reflected census-specific observation error:

$$\log(\text{Count}_i) \sim N(y_i, \tau_i^2). \quad (1)$$

Note that y, and its derivative z introduced below, reflect abundance on the log scale. Correspondingly, τ reflects the fractional error, consistent with the manner in which measurement error has historically been recorded. The addition of an equation for measurement error allowed us to account for the high degree of variability in data quality across the data set. Taking the upper limits of the five precision categories previously described (5%, 10%, 15%, 50%, and 500% [our quantitative interpretation of the fifth category]) as reflecting two standard deviations, the standard deviation τ is taken to be 0.025, 0.05, 0.075, 0.25, and 2.5 for categories 1–5, respectively.

Nest counts at the peak of egg laying were considered equivalent to the number of breeding pairs. A year- and species-specific breeding productivity (chicks/nest) was used to estimate the number of breeding pairs from counts of chicks, and correction factors for "late" nest or chick counts (n_0 and c_0 in Eq. 2, respectively) were also estimated. The true nest or chick population y is, therefore, related to the number of breeding pairs z in census i at site j in year t, by

$$y_{i,j,t} = z_{j,t} + n_0 I[\text{LNC}_i] + c_0 I[\text{LCC}_i] + \log(\text{prod}_t) I[\text{CC}_i] \quad (2)$$

where y represents the true count from Eq. 1, $I[\ldots]$ represents the indicator variable, LNC and LCC represent late nest counts and late chick counts, respectively (see Appendix), CC represents a chick count, and prod_t represents productivity, the estimated number of chicks/nest in year t as will be described in more detail.

The number of breeding pairs z at site j in year t was modeled as a linear function of time:

$$z_{j,t} = \text{intercept}_j + \text{trend}_j \times (t - 2000) \quad (3)$$

where year t is defined relative to 2000 to provide for a natural interpretation of the population intercept. For each species, the trends at each breeding site j were

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modeled as being drawn from a normal distribution:

$$\text{trend}_j \sim \mathcal{N}(\mu_0 + \alpha \times \text{sea ice}_j + \beta \times \text{chl-}a_j, \sigma^2) \quad (4)$$

where the expectation of the trend at each site is modeled as a linear function of the rate of change in November sea ice ("sea ice"), and average summer chlorophyll *a* ("chl-*a*") (see Appendix). Through μ_0, which represents a species-specific intercept for the expected rate of population change, sites with more data could inform the estimation of population trends at sites with less data, and anomalously high or low trends resulting from sparse sampling were adjusted toward the species mean. Models were fit using WinBUGS (Lunn et al. 2000) and inferences were derived from 10 000 samples drawn following a burn-in period of 10 000 samples. Model convergence was assessed by the Gelman-Rubin convergence statistic (Brooks and Gelman 1998) as applied to a set of randomly initialized chains and was unambiguous in all cases.

All parameters were given broad, noninformative prior distributions (N(0,1000) for μ_0, α, β, n_0, c_0; Gamma (0.01,0.01) for $1/\sigma^2$) with the exception of breeding productivity, whose prior Uniform(0,2) reflected the two-egg clutch size of the *Pygoscelis* penguins (Shirihai 2008).

It is important to emphasize that the model was deliberately restricted to the minimally complex log-linear model described in Eq. 1–4 because our primary goal was to analyze all available data and, using a single model, assess trends over as many locations as possible (including those with as few as two census counts). Although more complex models including, among other things, both process variability and measurement error (sensu Clark and Bjørnstad 2004) are possible for a very small subset of locations with relatively complete time series (e.g., Admiralty Bay, Jougla Point), these models do not permit a synthetic, spatial analysis of trend and hence are not developed in this context.

Productivity sub-model

Our model includes the breeding productivity, prod_t (chicks/nest), as a parameter to be estimated from the census data. Productivity was modeled as a function of year *t* and species, but not of location (i.e., all colonies of a given species were assumed to share the same productivity in a given year). We aggregated all the sites for this adjustment because there were not enough data to estimate site-specific productivity for each year, and doing so reduced the number of productivity parameters to be estimated from 3255 to 93. For each species, the model estimates prod_t as that value which, when applied to the chick counts for year *t*, minimizes model error across all sites. Estimates of productivity derived from the model are shown in the Appendix: Fig. A1 (see also Appendix: Tables A2–4).

Estimating regional rates of change

Regional rates of population change were estimated by a weighted average of draws from the posterior distributions for site-level trend, with weights proportional to total population size at each site. Because the relative weight of each site changes as populations grow or shrink over time, we considered regional rates of change as estimated for the midpoint (1995) of our study period.

Incomplete census counts

There were five sites for which repeated censuses had been conducted for a clearly defined subgroup of the entire site-wide population (fixed "colonies" within the "rookery"): Turret Point (Adélie Penguins), Paulet Island (Adélie Penguins), Cape Lookout (Chinstrap Penguins), Baily Head (Chinstrap Penguins; see Plate 1), and Hannah Point (Chinstrap Penguins). Because census data were either insufficient or unavailable to assess trend at the scale of the entire site, we could not determine whether trends at the colony scale reflected trends at the site scale. Consequently, these sites were not used in the estimation of regional rates of change.

Results

Out of 29 breeding sites for which sufficient data were available to assess trend, the Chinstrap Penguin population was found to be declining significantly at 16 sites and increasingly significantly at seven sites (Appendix: Table A5). Out of 24 breeding sites, Adélie Penguins were declining significantly at 18 sites and increasing significantly at only three sites (Appendix: Table A6). Using rates of change simulated from the model's posterior distribution for trend and weighting by population size (as predicted by the model for the midpoint [1995] of the study period), average rates of decline are found to be 1.1% ± 0.8% and 3.4% ± 1.3% per annum, respectively (Fig. 2; Appendix: Figs. A3–9). Colony size precluded complete censuses of the largest Adélie and Chinstrap Penguin colonies, and estimates of

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Fig. 2. (a) Distribution of Antarctic Peninsula-wide population trends (fractional rate of change per annum) for the Chinstrap Penguin (*Pygoscelis antarctica*), Adélie Penguin (*P. adeliae*), and Gentoo Penguin (*P. papua*), assuming a population-weighted average of the trends shown in panels (b)–(d). (b–d) Population trends for (b) Chinstrap, (c) Adélie, and (d) Gentoo Penguin as estimated for the period of 1979/1980 to 2009/2010 (see also Appendix: Tables A5–7 and Figs. A3–14). The *x*-axis is the location of each site along the northeast–southwest gradient reflected by the dashed line in Fig. 1. The *y*-axis represents the fractional rate of change per annum. Error bars represent ±2 SD for the estimation of population trend. A horizontal dashed line at zero has been added to distinguish between sites with positive and negative trend. Sites with outlying trends (visually assessed) or noted in the text have been numbered: (1) Almirante Brown Station, (2) Biscoe Point, (3) Booth Island, (4) Brown Bluff, (5) Cape Lookout, (6)

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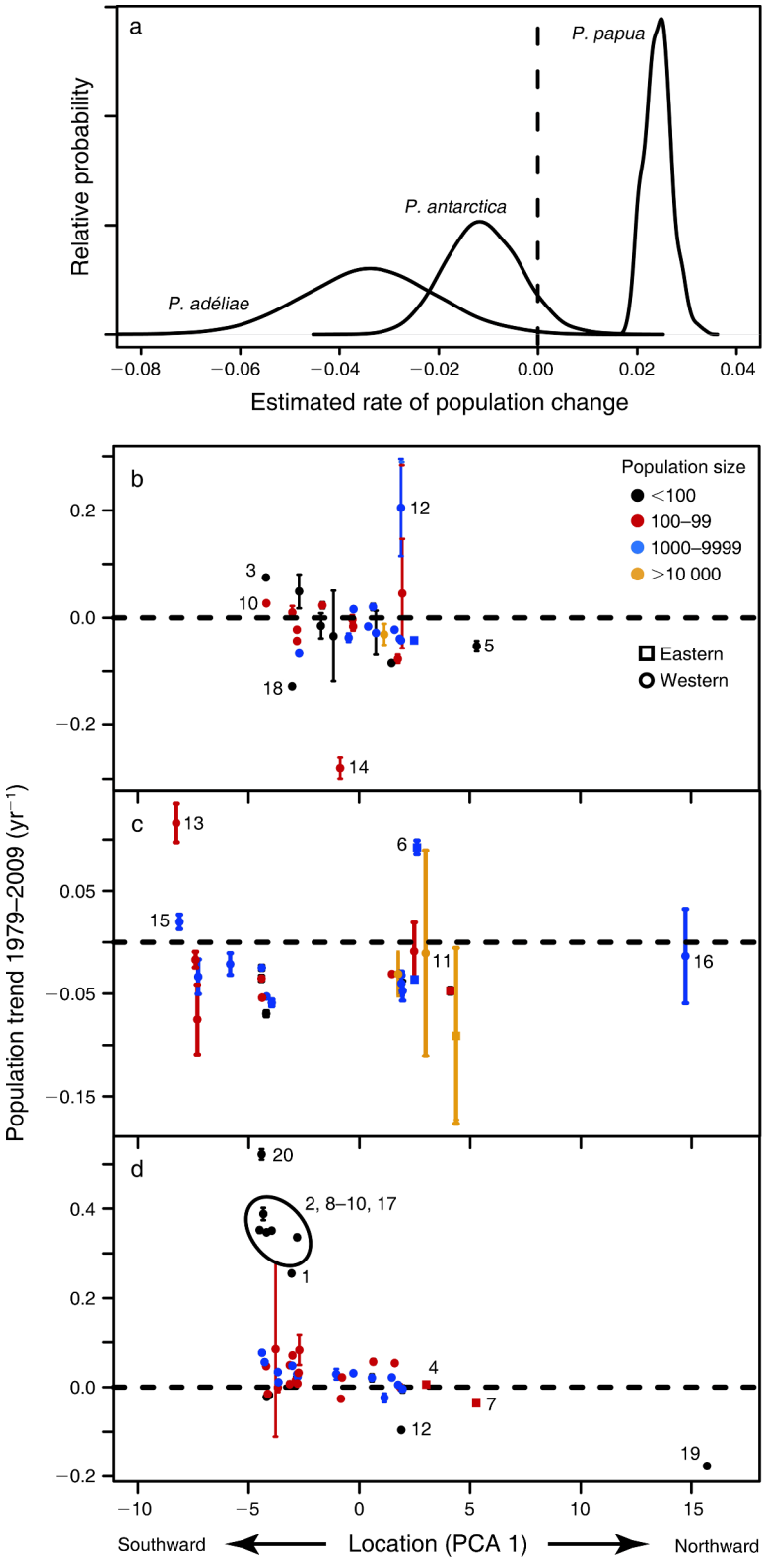

Devil Island, (7) Heroina Island, (8) Moot Point, (9) Orne Islands, (10) Palmer Station vicinity, (11) Penguin Point, (12) Point Thomas, (13) Pourquoi Pas Island, (14) President Head (Snow Island), (15) Red Rock Ridge, (16) Shingle Cove, (17) Vernadsky Station, (18) Waterboat Point, (19) Watson Peninsula, (20) Yalour Islands.

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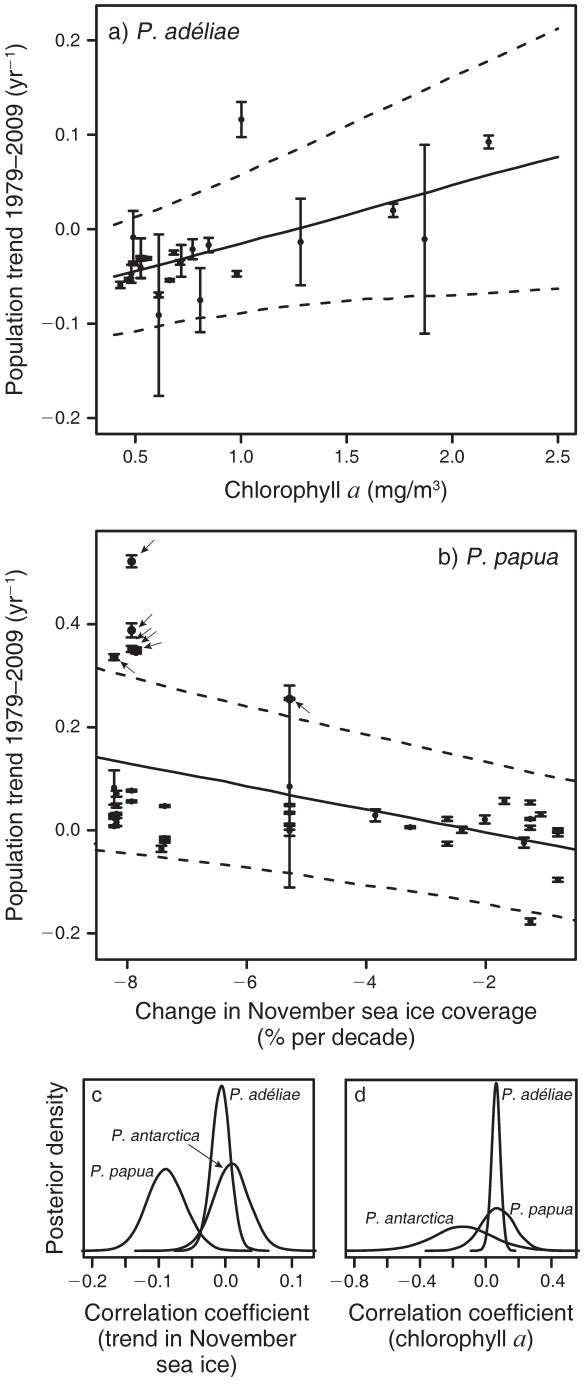

FIG. 3. (a) Adélie Penguin (*Pygoscelis adeliae*) population change vs. summer chlorophyll *a* concentrations with the regression line from Eq. 4 in black (95% CI in black dashed lines). (b) Gentoo Penguin (*P. papua*) population change vs. rate of change in November sea ice concentration (1979–2007) with the regression line from Eq. 4 in black (95% CI in black dashed lines). Black arrows point to colonies established since 1979/1980. (c, d) Posterior distributions reflecting model estimates for α (regression coefficient for November sea ice) and β (chlorophyll *a*). No *y*-axis scale numbers are included because the actual absolute values are not meaningful.

regional change do not reflect trends at these sites. However, we found no relationship between colony size and population trend (Appendix: Fig. A2) to suggest a corresponding bias in our aggregated assessment of regional trend (Fig. 2). In contrast to the other two *Pygoscelis* species, Gentoo Penguin populations are significantly increasing at 32 of 45 sites and significantly decreasing at only nine sites, yielding a weighted average rate of increase of 2.4% ± 0.3% per annum (Fig. 2; Appendix: Table A7, Figs. A10–14).

Adélie Penguin population trends were significantly and positively correlated with mean summer chlorophyll *a* (posterior mean ± SD for α in Eq. 4 = 0.061 ± 0.026), which has been used as a proxy for phytoplankton and their consumers, *Euphausia superba*, Antarctic krill (Dierssen et al. 2000, Atkinson et al. 2004; Fig. 3a, d). Adélie Penguin trends were not significantly correlated with loss of November sea ice (Fig. 3c). Although they are generally declining, Chinstrap Penguin trends were uncorrelated with mean summer chlorophyll *a* and November sea ice trends.

In contrast to region-wide declines in offshore-foraging Chinstraps and Adélie Penguins, inshore-foraging Gentoo Penguins are increasing throughout the western Antarctic Peninsula. Gentoo Penguins are declining or highly variable on the eastern AP (Fig. 2d: Sites 4 and 7), in contradiction to reports implying that they may be increasing or expanding their range in this region (McClintock et al. 2010). Gentoo Penguin populations grew fastest at seven sites near the southern boundary of their breeding range where Gentoos have established new colonies within the last 20 years (Fig. 2d, arrows in Fig. 3b; Appendix: Figs. A10–14). Gentoo Penguin colonies are restricted to areas with <50% November sea ice coverage (Fig. 4) and Gentoo Penguin population increases are significantly correlated with loss of November sea ice (posterior mean ± SD for β in Eq. 4 = −0.089 ± 0.029; Fig. 3b, c), largely due to rapid population growth at new colonies near the Gentoo Penguin's southern range boundary on the western AP. These new, rapidly growing, Gentoo colonies are part of a southward movement of the Gentoo Penguin's southern breeding range, facilitated by an expansion of breeding areas with <50% November sea ice coverage.

DISCUSSION

Since the early 1990s, penguin population dynamics on the Antarctic Peninsula have been interpreted largely within the context of the "sea ice hypothesis" (Fraser et al. 1992). Developed in light of ecological observations and divergent trends observed in the pagophilic (ice-loving) Adélies and the pagophobic (ice-avoiding) Chinstraps at long-term study sites on the AP, the sea ice hypothesis asserted that penguin population dynamics are controlled "bottom-up" through sea ice and its effect on over-winter survival. With years of heavy sea ice occurring with decreasing frequency on the western AP, Adélies were predicted to decline while Chinstraps

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(and, in subsequent versions of the hypothesis, Gentoos) were predicted to increase. The sea ice hypothesis was developed in response to an earlier, although not incompatible, alternative hypothesis positing that penguin population dynamics were instead controlled through "top-down" factors such as competition for prey, particularly with whales that were once harvested intensely (Laws 1977) but have more recently rebounded (Fraser et al. 1992, Ainley et al. 2007). Because all three of the pygoscelids prey extensively on Antarctic krill during the breeding season, this "krill surplus" hypothesis suggested that all three pygoscelids should have benefitted from reduced intra-trophic competition. A recent analysis of population and mark–recapture banding data from the South Shetland Islands (Trivelpiece et al. 2011) focuses on declining juvenile recruitment among Adélie and Chinstrap Penguin populations that, it is argued, reflects decreasing krill availability on the western AP.

Arguments for or against these various hypotheses have relied heavily on time series analyses of individual breeding populations. In the absence of a regional perspective on population trends, it is difficult to know to what extent differences between studies are driven by spatial variation in environmental conditions and species' responses to them. To date there has been no regional-scale analysis of population trends in which to contextualize these more detailed studies, and no way to extrapolate trends at individual sites to rates of population change at the regional scale. By sampling a large number of sites distributed broadly over the Antarctic Peninsula, our results resolve the apparent paradox between studies showing Chinstrap population increases (Fraser et al. 1992, Smith et al. 1999, Ducklow et al. 2007, McClintock et al. 2008) and those showing Chinstrap population declines (Forcada et al. 2006, Hinke et al. 2007, Trivelpiece et al. 2011). Despite the decreasing extent and duration of sea ice in the Bellingshausen-Amundsen Seas sector (Smith and Stammerjohn 2001, Parkinson 2002, Zwally et al. 2002), our analyses make clear that ice-avoiding Chinstrap Penguins are declining regionally along with Adélie Penguins, a species whose decline has been widely reported as indicating widespread changes in the Antarctic marine ecosystem (Fraser et al. 1992, Trathan et al. 1996, Trivelpiece and Fraser 1996, Smith et al. 1999, Croxall et al. 2002, Forcada et al. 2006, Clarke et al. 2007, Ducklow et al. 2007, Forcada and Trathan 2009). Data suggesting Chinstrap population increases have come primarily from populations in the vicinity of Palmer Station (64°46′ S, 64°05′ W; site 10 in Fig. 2b) near the species' southern range limit; in the context of a spatially integrated assessment, they do not reflect the majority of other AP breeding sites.

Chlorophyll *a* has declined in the waters off the northwestern coast of the AP over the last two decades (Montes-Hugo et al. 2009), consistent with other studies showing long-term declines in krill stocks (Loeb et al. 1997, Atkinson et al. 2004). Krill are the dominant prey for Adélie Penguins on the AP (Lishman 1985, Lynnes et al. 2002, Hinke et al. 2007) and their spatially extensive population declines are consistent with time series analyses suggesting the importance of krill dynamics for foraging effort, reproductive success, and juvenile recruitment (Fraser and Hofmann 2003, Lynnes et al. 2004, Hinke et al. 2007). Despite the opposing tolerances of Chinstrap and Adélie Penguins for sea ice coverage during the breeding season (Fraser et al. 1992), population trends for these two species were not correlated with changing November sea ice conditions, suggesting that sea ice conditions during the breeding season do not represent a significant constraint for existing colonies.

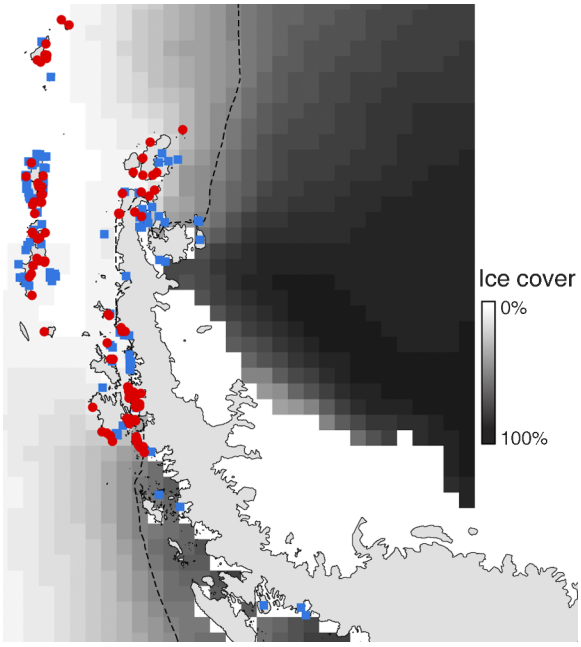

FIG. 4. Presence (red circles) and known absences (blue squares) of Gentoo Penguin breeding overlaid on a map of average November sea ice concentrations (1979–2007; Cavalieri et al. 1996, updated 2008). The dashed line indicates the 50% ice coverage contour.

Our results provide regional-scale support for the view that sea ice dynamics play a more complex role in the ecology of the pygoscelid penguins than is reflected by the classic sea ice hypothesis, and that other factors, such as over-winter juvenile survival (Hinke et al. 2007, Trivelpiece et al. 2011), periodic krill recruitment events (Fraser and Hoffmann 2003, Miller and Trivelpiece 2007, Trivelpiece et al. 2011), and episodic climate anomalies (Forcada et al. 2006) must mediate the impact of sea ice on Chinstrap and Adélie Penguin abundance. Additionally, our results are consistent with the hypothesis that offshore-foraging Adélie Penguins and Chinstrap Penguins (Lynnes et al. 2002) may be more negatively impacted by the AP's rebounding humpback whale population (Branch 2011) than in-

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PLATE 1. Chinstrap Penguins (*P. antarctica*) nesting on the slopes of Baily Head, Deception Island. Photo credit: R. Naveen.

shore-foraging Gentoo Penguins. Although quantitative, spatially resolved estimates of krill consumption rates are lacking for both penguins and whales, efforts to develop these data (e.g., by the Commission for the Conservation of Antarctic Marine Living Resources' Status and Trend Assessment of Predator Populations) may allow such hypotheses to be tested.

We find significant evidence for increasing Gentoo populations, particularly at the southern end of their breeding range on the western AP. Our spatial analysis of Gentoo Penguin breeding locations finds that Gentoo breeding is restricted to areas with $<50\%$ November sea ice coverage. This is particularly important in light of declines in sea ice extent and concentration on the western AP (Liu et al. 2004), as well as earlier retreat of the pack ice in spring (Smith and Stammerjohn 2001, Stammerjohn et al. 2008). Whereas previous analyses have focused on constraints imposed by post-breeding conditions, particularly extended parental care and its effect on overwinter survival (Hinke et al. 2007, Polito and Trivelpiece 2008), our finding that Gentoo populations are growing most quickly in areas with decreasing November sea ice points to pre-breeding conditions as a key constraint to Gentoo colony establishment and recruitment. Unlike more highly colonial Adélie and Chinstrap Penguins, Gentoo Penguins are excellent colonizers of new breeding territory and quickly take advantage of snow-free breeding space where conditions are suitable (Bost and Jouventin 1990). Early studies found that winter sea ice precluded Gentoo Penguins from residing year-round in the waters adjacent to and south of Petermann Island (Gain 1914); however, recent satellite imagery suggests that, at least in some years, considerable open water persists throughout the winter (Appendix: Fig. A15), consistent with winter sightings of Gentoo Penguins at Akademik Vernadsky Station (65°15′ S, 64°16′ W, 10 km south of Petermann Island). Although future sea ice conditions in the vicinity of the Antarctic Peninsula are difficult to predict (Stammerjohn et al. 2008), we expect continued declines in spring sea ice to facilitate expansion of the Gentoo Penguin breeding range south to the Berthelot Islands and beyond.

These results, which illustrate the potential for opportunistic surveys to detect regional patterns of population change, paint the first regional-scale picture of penguin population change on the AP and place findings of more detailed, but geographically limited, studies in a regional context. The three pygoscelid penguin species have different life history traits that are reflected in their varying responses to changing environmental conditions and prey availability. Chinstrap Penguin populations have declined on the AP since 1979/1980 despite a decrease in sea ice thought to be to their benefit. The spatial pattern of Adélie Penguin decline highlights its strong association with regional phytoplankton biomass and, by extension, with krill stocks that have apparently declined over large areas of

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the AP, perhaps due to changing environmental conditions (Atkinson et al. 2004) or a resurgence of whales following cessation of intensive harvesting (Ainley et al. 2007, Branch 2011, Trathan et al. 2012). Gentoo Penguin populations are increasing most rapidly at new colonies near their southern range limit, and their expansion southward should continue as declining spring sea ice makes more ice-free territory available for colony establishment. Overall, these data reveal a new dichotomy in population trends between the pygoscelids that forage inshore vs. offshore (resident and migratory, respectively) during the post-breeding period.

Spatial variability complicates regional inference

Our spatially resolved analysis finds multiple examples of significant fine-scale spatial heterogeneity in population trends. In the Anvers Island vicinity, Chinstrap populations have been generally increasing at Useful Island and in the Palmer Station vicinity, but decreasing at Georges Point, the Orne Islands, and Waterboat Point, the most distant of which are separated by less than 80 km. Likewise, there seems to be a breakpoint between Andresen Island and Pourquoi Pas Island, north of which Adélie populations are declining and south of which Adélie populations appear to be increasing. Evidence of significant differences in population dynamics over relatively small spatial scales cautions against casual extrapolation of trend or its apparent underlying mechanism from the study of a single population. Further, our regional- and local-scale spatially resolved analyses are not confounded by the complex issue of flipper banding, thought to be important in some population analyses, especially in the context of environmental change (Saraux et al. 2011; but see Boersma and Rebstock 2009). Our results clearly demonstrate that characterizing landscape-scale ecological changes requires spatially extensive abundance monitoring to complement detailed studies of local populations.

Our approach to data synthesis, applied here to Antarctic seabirds, is broadly applicable to population studies in which large spatial scale or logistical constraints force regional-scale inference to be drawn from aggregated and sometimes patchy time series. Here we have provided a framework by which data of opportunity can be synthesized in a meaningful analysis of regional change within which detailed long-term data sets may be contextualized.

Future directions

Our study was designed specifically to address the spatial variability of pygoscelid penguin population dynamics on the Antarctic Peninsula, which necessitated the use of a relatively simple log-linear model. Although our approach did account for measurement error (Eq. 1), it did not include process variability (Clark and Bjørnstad 2004), which has been shown in simulations of similar state-space models to increase the confidence intervals for slope (Humbert et al. 2009). Additional factors such as density dependence and spatial autocorrelation in model residuals were also not considered, because only the most complete time series in our data set could support the estimation of these additional model parameters. Nevertheless, the development of these more complex state-space models remains a priority for future research, particularly as continued data collection expands the set of time series for which such models are appropriate.

From the perspective of additional data collection, site-wide census data for the largest penguin colonies are a top priority. Such data not only will correct a bias in the size distribution of monitored populations, but also will be necessary to determine if population changes (both interannual and long-term) of individual colonies (e.g., Baily Head; see Appendix: Table A5) reflect changes at the scale of the entire breeding site. Satellite imagery has been shown to provide reasonable population estimates for penguins (Lynch et al. 2012) and will be key to filling in census data for sites that, by virtue of their size or location, are impossible to census regularly.

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Supplemental Material

Appendix

Additional details on data, model development, and analysis results (*Ecological Archives* E093-120-A1).

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