

# Correlating tropical climate with survival of an Arctic-breeding, trans-equatorial migrant seabird

Danielle T. Fife, Shanti E. Davis, Gregory J. Robertson, H. Grant Gilchrist, Iain J. Stenhouse, Dave Shutler, and Mark L. Mallory

**Abstract:** Extreme climate can negatively affect survival through increased physiological demands or by reducing prey availability. This can have significant population-level consequences for organisms with low reproductive rates, such as seabirds. As an Arctic-breeding trans-equatorial migrant, Sabine's gull (*Xema sabini*) is exposed to a profound variety of climate regimes during the year. Therefore, its annual survival may be affected by broad-scale teleconnection patterns that influence regional climate variability. We used Program MARK to estimate apparent survival and resighting probabilities from 2007 to 2013 for adult Sabine's gulls breeding at a High Arctic colony. We then combined capture–mark–recapture data for the High Arctic colony with those previously published from a Low Arctic colony (1998–2002) to examine influences of climate variability on survival. Mean  $\pm$  standard error apparent survival estimated for the High Arctic colony was  $0.90 \pm 0.03$ , similar to that previously reported for the Low Arctic colony. We found a negative relationship between survival and the Tropical/Northern Hemisphere pattern, an atmospheric mode that is associated with the Pacific jet stream. Our study suggests that although Sabine's gull survival was generally high and relatively constant over time, adult mortality may increase during years of extreme climate events in regions far beyond their Arctic breeding grounds.

**Key words:** apparent survival, Arctic seabird, climate variability, Sabine's gull, *Xema sabini*.

**Résumé :** Le climat extrême peut nuire à la survie par des demandes physiologiques accrues ou en réduisant la disponibilité des proies. Ceci peut avoir des conséquences importantes au niveau de la population des organismes à taux de reproduction faibles, tels que les oiseaux marins. En tant qu'oiseau migrateur transéquatorial se reproduisant en Arctique, la mouette de Sabine (*Xema sabini*) est exposée à une importante variété de régimes climatiques tout au long de l'année. C'est pourquoi son taux de survie annuel pourrait être affecté par des tendances de téléconnexion à grande échelle qui influencent la variabilité climatique régionale. Nous avons utilisé le programme MARK pour estimer les probabilités de survie apparente et d'observations répétées de 2007 à 2013 pour les mouettes de Sabine adultes se reproduisant dans une colonie du Haut-Arctique. Nous avons ensuite combiné les données de capture–marquage–recapture pour la colonie du Haut-Arctique avec celles publiées antérieurement provenant d'une colonie du Bas-Arctique (1998–2002) afin d'examiner les effets de la variabilité du climat sur la survie. La moyenne ( $\pm$  erreur type) estimée de la survie apparente pour la colonie du

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Haut-Arctique était de  $0.90 \pm 0.03$ , similaire à celle indiquée antérieurement pour la colonie du Bas-Arctique. Nous avons trouvé une corrélation négative entre la survie et le modèle de l'hémisphère Nord/tropical, un mode atmosphérique associé au courant-jet du Pacifique. Notre étude suggère que bien que la survie de la mouette de Sabine était généralement élevée et relativement constante au fil du temps, la mortalité adulte pourrait augmenter pendant les années de phénomènes climatiques extrêmes dans les régions bien au-delà de leurs aires de reproduction dans l'Arctique. [Traduit par la Rédaction]

*Mots-clés* : survie apparente, oiseau marin arctique, variabilité du climat, mouette de Sabine, *Xema sabini*.

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## Introduction

Warming climate, increasing climate variability, and extreme weather events may all have negative effects on migrant birds (Stenseth et al. 2002; Frederiksen et al. 2008), particularly on those travelling long distances (Both et al. 2010). For seabirds, effects are typically manifested either by changes in marine food availability, changes in physiological stressors, or by a mismatch in the timing of migration relative to peak food supplies (e.g., Schreiber 2001; Sandvik et al. 2005), and they can have carryover effects across years (Descamps et al. 2010). Although there is much variation among species and effects, generally, poor marine habitat conditions in the winter or on migration have negative influences on adult or juvenile survival (e.g., Thompson and Ollason 2001; Sandvik et al. 2005), whereas poor conditions on the breeding grounds tend to result in reduced reproductive effort (number of breeders, egg size, or clutch size) or breeding success (e.g., Gaston et al. 2005; Moe et al. 2009). Over longer periods, climate trends can influence seabird populations, and thus, understanding seabird migration and population dynamics in relation to climate patterns is essential for understanding current trends and predicting future effects on species (e.g., Trathan et al. 2007; Irons et al. 2008).

Sabine's gull (*Xema sabini*) is a small, approximately 190 g larid seabird that has a patchy, circumpolar breeding distribution, nesting primarily on small Arctic islands and in coastal wetland areas (Day et al. 2001). It is the only Arctic-breeding gull with a trans-equatorial migration, making a return trip of more than 28 000 km annually to overwinter at highly productive upwelling zones off the coasts of Peru and southern Africa (Stenhouse et al. 2012; Davis et al. 2016). Limited census data for Sabine's gulls suggest that their numbers are stable or increasing in parts of their breeding range but declining in others (Raven and Dickson 2006; Johnston and Pepper 2009; Mallory et al. 2012). To date, survival of adult Sabine's gulls has only been reported for a Low Arctic colony at East Bay Migratory Bird Sanctuary (Southampton Island, Nunavut), and it was relatively constant and high at  $0.89 \pm 0.02$  from 1998 to 2002 (Stenhouse and Robertson 2005). However, the short duration of that study precluded the ability to detect temporal variability in survival, or assess influences of environmental variables.

To further our understanding of Sabine's gull population dynamics, apparent survival and resighting probabilities were estimated for a High Arctic colony and compared to the Low Arctic colony at East Bay (Stenhouse and Robertson 2005). Furthermore, data for both colonies were combined to test for an influence of climate variability on apparent survival of adult Sabine's gulls breeding in the Canadian Arctic. Because we were interested in adult survival, likely affected by winter or migration habitat conditions, we used three broad-scale climate indices as proxies for climate variability in winter habitats: the North Atlantic Oscillation (NAO), the Southern Oscillation Index (SOI), and the Tropical/Northern Hemisphere (TNH) pattern. We expected that the phases of these indices that are correlated

with warmer water, and a consequent reduced marine productivity (e.g., [Hays et al. 2005](#); [Behrenfeld et al. 2006](#); [Irons et al. 2008](#); [Beaugrand et al. 2015](#)) would also be correlated with lower survival in Sabine's gulls. Data from this study constitute baseline demographic information on Sabine's gulls, which we hope leads to identification of factors affecting survival of long-distance migrants breeding in the Arctic.

## Methods

### Study sites

The High Arctic site used in this study was Nasaruvaalik Island (75°49'N, 96°18'W; [Fig. 1](#)), one of several islands found within Queens Channel, Nunavut, Canada. This area is considered as important breeding and foraging habitat for many marine birds ([Mallory and Gilchrist 2003](#)), largely due to the occurrence of polynyas, which are areas of persistent open water surrounded by sea ice. The 3 × 1 km gravel island has old beach ridges and scattered patches of purple saxifrage (*Saxifraga oppositifolia*), moss, and lichen ([Mallory et al. 2012](#)). Sabine's gulls (16–31 pairs, over eight years of monitoring) nest within Arctic tern (*Sterna paradisaea*) colonies (~600 pairs in total) at either end of the island ([Mallory and Gilchrist 2003](#); [Mallory et al. 2012](#); S.E. Davis, unpublished data).

To obtain a longer time series for the purpose of evaluating effects of climate on survival, Nasaruvaalik Island data were combined with previously published data from a Low Arctic colony at East Bay Migratory Bird Sanctuary (64°01'N, 81°47'W; [Fig. 1](#)), Southampton Island, Nunavut ([Stenhouse and Robertson 2005](#)). Southampton Island is much larger than Nasaruvaalik Island and can essentially be considered a mainland site, of which the East Bay sanctuary covers approximately 1200 km<sup>2</sup>. For a more detailed description of the East Bay study site, see [Stenhouse et al. \(2001\)](#) and [Stenhouse and Robertson \(2005\)](#).

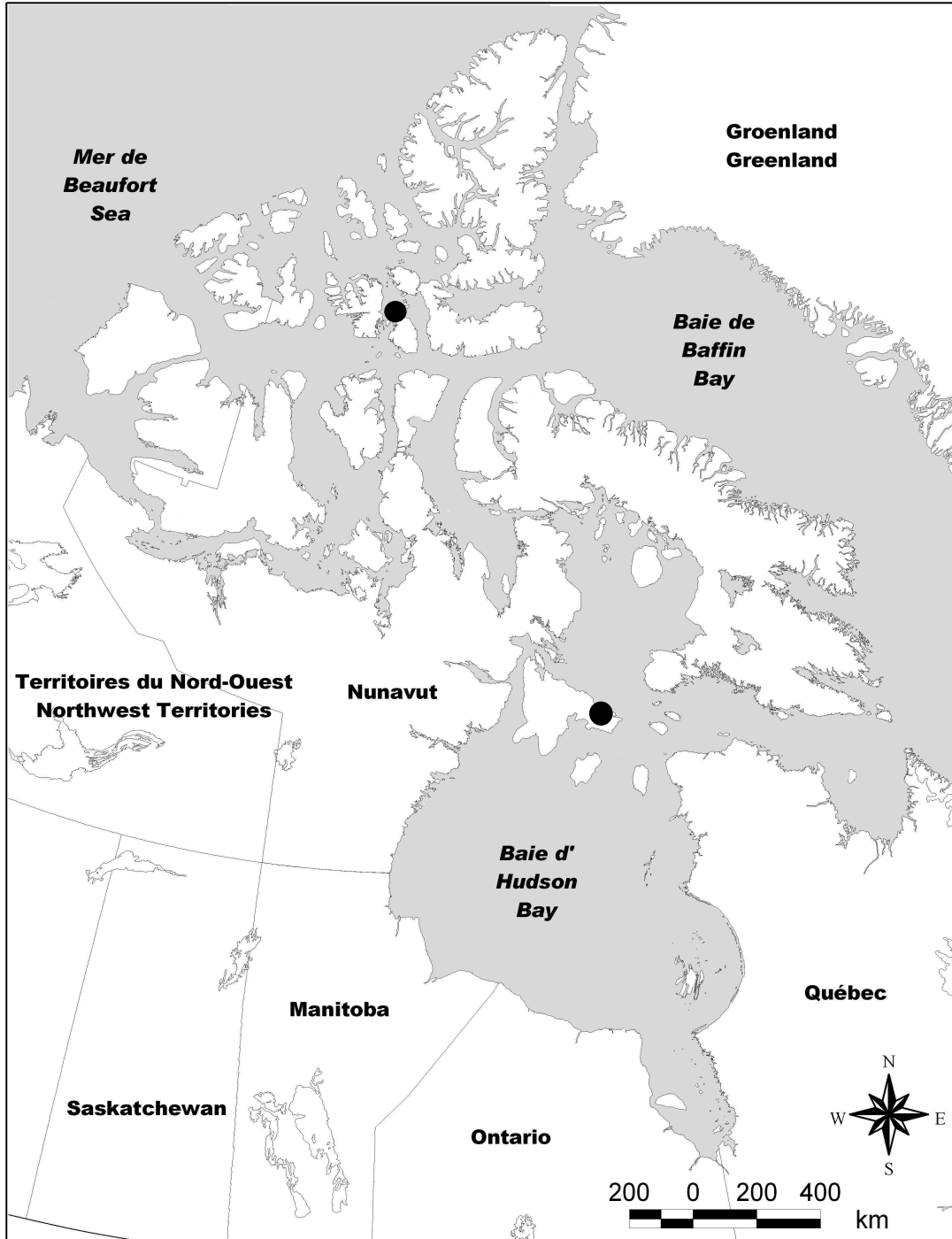
### Capturing and resighting adults

Banding of Sabine's gull adults on Nasaruvaalik Island began in 2007, with additional adults banded in each successive year until 2012. Adults were captured during incubation (starting about late June to early July for ~20–23 days) using a spring-loaded bow-net ([Bub 1991](#)) or a handheld CO<sub>2</sub>-powered net gun ([Edwards and Gilchrist 2011](#)). They were banded with a numbered US Fish and Wildlife Service steel band, as well as a unique combination of Darvic color bands (typically three) on their tarsi for easy identification from a distance. In 2008, three birds had a small geolocator attached to their steel leg band. In 2010–2011, some birds ( $n = 33$ ) also had a small geolocator device attached on Darvic bands in some years representing  $\leq 2\%$  body mass ([Davis et al. 2016](#)); these birds had very high return rates (100% for 2008 birds, 92% resighted overall), and we did not observe any obvious, deleterious effects of the tracking equipment.

Subsequent resightings of adults were obtained each year until 2013. Resightings were recorded daily by two or three observers from about mid-June to mid-August during the rest of the breeding season in the year a gull was captured, and in subsequent years, either from viewing blinds (~150 m away from the colony), or by searching for nests on foot. Typically, 4–5 h were spent each day (weather permitting) scanning Sabine's gulls around the island to determine their unique color band combination and confirm resightings.

Similar methods were employed at East Bay from 1998 to 2002. After 2002, however, banding and resighting effort at East Bay has been intermittent (<10 days per season), and following a series of preliminary analyses, data after 2002 were deemed to be too sparse to be used in this study. Therefore, the analysis takes into account the gap (2003–2006) from the end of the [Stenhouse and Robertson \(2005\)](#) study to the beginning of the Nasaruvaalik Island study.

**Fig. 1.** Locations of the study sites, Nasaruvaalik Island and East Bay Migratory Bird Sanctuary, in Nunavut, Canada.



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### Survival analyses

Apparent survival ( $\phi$ ), that is, true survival confounded by permanent emigration and encounter ( $p$ ) probabilities were estimated using traditional capture–mark–recapture methods in Program MARK (hereafter “MARK”; White and Burnham 1999). Encounter histories displaying initial captures and resightings for each bird were generated using the RMark (Laake 2014) package in R 3.2.1 (R Core Team 2014). To account for the time gap between studies in the combined analysis, all years outside the study period for each colony were treated as “zero” within the encounter history for each individual (i.e., every individual received a “zero” each year from 2003 to 2013 for East Bay, and from 1998 to 2006 for Nasaruaalik Island; reduced m-array summaries for encounters are provided in Supplementary Material, Tables S1 and S2<sup>1</sup>). All unobserved island–year combinations were assigned to a single dummy  $\phi$  parameter, with the associated  $p$  fixed to zero. The dummy  $\phi$  and respective fixed  $p$  were not counted as estimable parameters during model selection.

The Cormack–Jolly–Seber model, an open-population model where apparent survival and recapture probabilities vary over time (Lebreton et al. 1992), was used as the global model for Nasaruaalik Island, as well as the previous East Bay study. A preliminary analysis of the Nasaruaalik Island data was conducted to determine the best-fitting model structure of encounter probability to be used in the combined analysis. The model structure of resighting probability for East Bay was retained from the best model selected by Stenhouse and Robertson (2005), which was constant recapture rates across years, except for the final year which was known a priori to have a reduced resighting effort. Once the best resighting parameterization was determined, it was denoted as  $p_{\text{study}}$  for this analysis.

For analysis of both sites combined, the starting model included annual variation in survival (i.e.,  $\phi_{\text{time}}$ ), a model for which the amount of time-dependent process variation ( $\sigma^2$ ) in survival probabilities for each colony using variance component analysis can be determined (Burnham et al. 1987). Note that because there was no overlap in time between the two studies, effects of colony and time are confounded.

An information-theoretic approach to model selection was employed, using Akaike’s information criterion adjusted for small sample size ( $AIC_c$ ), to choose the best overall model. Finally, to determine the amount of variation explained by a particular covariate ( $R^2$ ), we used model deviances to calculate a fixed-effect-model-based coefficient of determination (eq. (6) in Grosbois et al. 2008).

### Effects of climate variability on survival

Effects of climate variability on survival were assessed by incorporating broad-scale climate indices as covariates in the models. A comprehensive list of indices can be found through the National Oceanographic and Atmospheric Administration (NOAA; available at <http://www.esrl.noaa.gov/psd/data/climateindices/list/>). Selection of climate indices was based primarily on recent geolocator [global location sensing (GLS)] tracking data showing Sabine’s gull migratory routes and wintering areas. The majority (93%,  $n = 25$ ) of the tagged gulls at Nasaruaalik Island migrated west towards Alaska and then followed the Pacific coast south to wintering areas off of Peru (Davis et al. 2016). The remaining 7% travelled through the Atlantic to winter off of South Africa (Davis et al. 2016). Tracking data have not yet been obtained for Sabine’s gulls at East Bay (although some birds travelling to Nasaruaalik Island pass very close to East Bay during spring migration; Davis et al. 2016). However, considering the more southern and eastern location of the East Bay colony, it is possible that they could migrate to Atlantic waters as do a few of the Nasaruaalik birds

<sup>1</sup>Supplementary material is available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/as-2017-0018>.

**Table 1.** Descriptions of climate indices used in this study: the principal-component-based North Atlantic Oscillation (NAO), Southern Oscillation Index (SOI), and Tropical/Northern Hemisphere pattern (TNH).

Index	Description	Major effects	Literature cited	Data source
NAO	Atmospheric pressure difference between the Azores and Iceland	Positive phase related to warmer waters, and more severe storms crossing North Atlantic to Europe	Hurrell 1995	<a href="https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-pc-based">https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-pc-based</a>
TNH	Derived from a rotated principal component analysis of normalized 500 hPa height anomalies	Positive phase related to colder temperatures in western North America and above-average precipitation over central and eastern subtropical Pacific	Mo and Livezey 1986; Barnston et al. 1991; Liang et al. 2017	<a href="http://www.cpc.ncep.noaa.gov/data/teledoc/tmh.shtml">http://www.cpc.ncep.noaa.gov/data/teledoc/tmh.shtml</a>
SOI	Atmospheric pressure differences between Tahiti and Darwin, Australia	Negative and positive values related to warm (El Niño) and cold (La Niña) eastern tropical Pacific waters, respectively	Trenberth 1984	<a href="http://www.cpc.ncep.noaa.gov/data/indices/soi">http://www.cpc.ncep.noaa.gov/data/indices/soi</a>

and similar to Sabine's gulls breeding in Greenland (Stenhouse et al. 2012). Therefore, we thought it prudent to consider both Pacific and Atlantic indices.

Because multi-collinearity among covariates can interfere with parameter estimation and model selection results (Grosbois et al. 2008), Pearson's correlations were evaluated to further reduce the number of indices considered by excluding indices which were strongly correlated (arbitrarily  $r > 0.35$ ) to multiple other indices in the set. Ultimately, given the large nonbreeding distribution of Sabine's gulls spanning two ocean basins, three indices were tested (details in Table 1): the principal component-based NAO (Fig. 2A), TNH pattern (Fig. 2B), and SOI (Fig. 2C). For each index, winter values were used (December–March for all except TNH, for which only December–February data were available). Results are presented  $\pm$  standard error unless otherwise indicated.

#### Goodness-of-fit

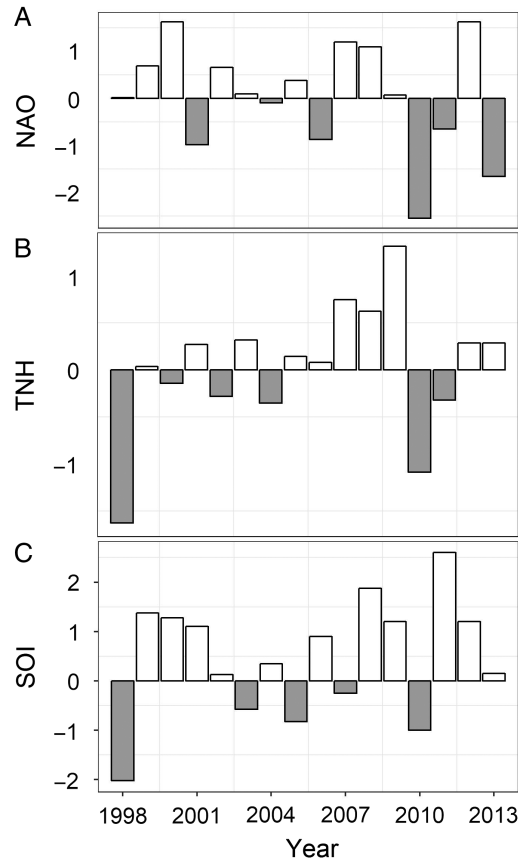
Program UCARE was used to test for violations of Cormack–Jolly–Seber model assumptions (Choquet et al. 2009), which looks for evidence of heterogeneity among individuals (e.g., due to transiency or trap effects; Pradel et al. 1997, 2005) in recapture and survival probabilities, respectively. The variance inflation factor ( $\hat{c}$ ) is a measure of the overall fit of a model and can be used to account for overdispersion. This was estimated for the global model with either the median  $\hat{c}$  method or the parametric bootstrap, using 1000 simulations and taking the ratio of observed to expected deviance (Anderson et al. 1994; White et al. 2001). If  $\hat{c} > 1$ , model selection was based on Quasi-Akaike's information criterion (QAIC<sub>c</sub>), which assigns further penalties for the number of parameters in a model (Anderson et al. 1994).

## Results

#### Goodness-of-fit

There was evidence of heterogeneity among individuals in recapture or survival probabilities for Nasaruaalik Island (UCARE combined test:  $\chi^2_{13} = 23.5$ ,  $p = 0.04$ ). Upon examination of individual test components, this was driven by heterogeneity in the timing of bird sightings in subsequent years as a function of when they were first captured (TEST2.CT:  $Z = -2.5$ ,  $p = 0.01$ ; trap happiness; Choquet et al. 2009). This effect was entirely driven by a

**Fig. 2.** Index values from 1998 to 2013 for (A) the principal-component-based North Atlantic Oscillation Index (NAO), (B) Tropical/Northern Hemisphere pattern (TNH), and (C) Southern Oscillation Index (SOI). Mean winter (December–February for Tropical/Northern Hemisphere pattern, December–March for rest) index values used. Note each value includes December of the previous year.



single cell in the final year of the study, so possible trap effects were not pervasive and were addressed with general adjustments for lack of model fit. Median  $\hat{c}$  was estimated at 1.67 for the Nasaruvaalik Island data, and it was used to adjust and model selection criteria and parameter estimates. In [Stenhouse and Robertson \(2005\)](#), results from RELEASE (TEST 2 + TEST 3:  $\chi^2_5 < 0.1$ ,  $p > 0.99$ ) and an estimated  $\hat{c}$  of 0.49 using the bootstrap method both indicated underdispersion (i.e., less variation than expected based on the global model) of the East Bay data. Because the median  $\hat{c}$  method did not perform well for the combined-site analysis, the bootstrap method was used, and model selection criteria and parameter estimates were adjusted by a variance inflation factor ( $\hat{c} = 1.34$ ) calculated from the global model  $\phi_{\text{time}}, p_{\text{study}}$ .

#### Apparent survival on Nasaruvaalik Island

Eighty-four adult Sabine's gulls were banded on Nasaruvaalik Island from 2007 to 2012, with 188 resightings until 2013. The null model ( $\phi, p$ ) was best-supported for Nasaruvaalik Island, with associated annual survival probabilities of  $0.90 \pm 0.03$  (95% CI: 0.83–0.95) and resighting probabilities of  $0.85 \pm 0.04$  (95% CI: 0.76–0.91; [Table 2](#)). This model was approximately five times better supported (based on QAIC<sub>c</sub> weights) than the model with time-dependent survival, indicating that either there was little variability in gull annual survival

**Table 2.** Model selection results from the Nasaruaalik Island and combined (East Bay + Nasaruaalik Island) survival analyses, where  $\phi$  is the apparent survival and  $p$  is the resighting probability.

Model	$\Delta\text{QAIC}_c$	$\text{QAIC}_c$ weight	Model likelihood	$K$	QDev
<b>Nasaruaalik Island (<math>\hat{c} = 1.67</math>)</b>					
$\phi, p$	0.00	0.82	1.00	2	57.63
$\phi_{\text{time}}, p$	3.28	0.16	0.19	7	50.44
$\phi, p_{\text{time}}$	7.93	0.02	0.02	7	55.09
$\phi_{\text{time}}, p_{\text{time}}$	8.84	0.01	0.01	11	47.27
<b>East Bay + Nasaruaalik Island (<math>\hat{c} = 1.34</math>)</b>					
$\phi_{\text{TNH}}, p_{\text{study}}$	0.00	0.89	1.00	5	70.60
$\phi, p_{\text{study}}$	5.72	0.05	0.06	4	78.38
$\phi_{\text{NAO}}, p_{\text{study}}$	7.50	0.02	0.02	5	78.11
$\phi_{\text{colony}}, p_{\text{study}}$	7.70	0.02	0.02	5	78.30
$\phi_{\text{SOI}}, p_{\text{study}}$	7.78	0.02	0.02	5	78.38
$\phi_{\text{time}}, p_{\text{study}}$	12.51	0.00	0.00	12	68.39

**Note:**  $p_{\text{study}}$  in the combined analysis denotes differing structure for resighting probabilities for each colony. For East Bay, resighting is constant from 1998 to 2001, and different in 2002 and for Nasaruaalik Island, resighting is constant from 2007 to 2013.

from 2007 to 2013, or that variability was not detected due to the relatively small sample size and few years of data.

#### Combined analysis and effect of climate variability

In the combined analysis, a colony effect on survival was not detected ( $\Delta\text{QAIC}_c > 2$ ; Table 2). Variance component analysis of apparent survival estimates from the global model ( $\phi_{\text{time}}, p_{\text{study}}$ ) indicated that process variance ( $\sigma^2 = 0.001$ , 95% CI:  $-0.001$  to  $0.015$ ) accounted for only a small proportion of the total annual variance (process + sampling variance) in the data. Taking into account sampling error, mean annual survival for both colonies was  $0.92 \pm 0.02$ .

In spite of limited evidence of temporal variation, the model with TNH had considerable support and was the best model overall, with approximately 17.5 times more support than the null model (Table 2). This model describes a negative relationship between TNH and survival ( $\beta = -1.08 \pm 0.39$ , 95% CI:  $-1.84$  to  $-0.32$ ) and explained 33.5% of the variation in survival (Fig. 3). Models including NOA and SOI were not supported (Table 2).

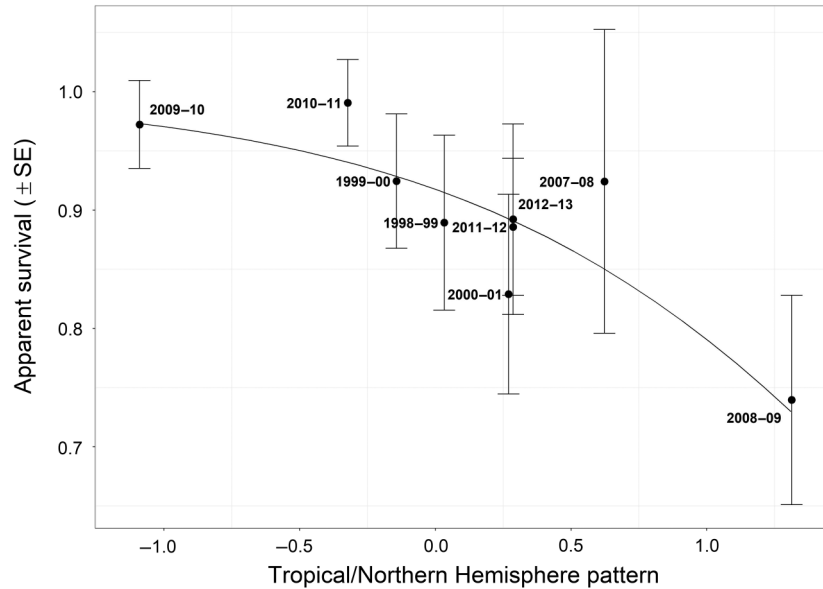
## Discussion

### Apparent survival on Nasaruaalik Island

This study presents the first estimate of apparent survival ( $\sim 0.90$ ) for a High Arctic colony of breeding Sabine's gulls. Our estimate was in the upper range of those reported for other Arctic-breeding gull species (Stenhouse et al. 2004; Allard et al. 2010) and was similar to that reported for the Low Arctic colony of Sabine's gulls at East Bay (Stenhouse and Robertson 2005). Similar to other colonial nesting seabirds, Sabine's gulls have strong fidelity to their breeding grounds, even if they experienced breeding failure in previous years (Stenhouse and Robertson 2005). Furthermore, the High Arctic colony is relatively small (16–31 pairs), with nearly all banded birds resighted each year. Therefore, the high annual survival rate is not unexpected. We were not able to directly test for a colony effect on survival due to confounding effects of time. Our results indicate that survival was constant over time for the Nasaruaalik Island colony, but it is difficult to detect temporal variability



**Fig. 3.** Unconstrained annual apparent survival estimates of adult Sabine's gulls at East Bay (1999–2001) and Nasaruaalik Island (2007–2013) ( $\pm 1$  SE) and fitted line of their relationship with the winter (December–February) Tropical/Northern Hemisphere pattern. SE, standard error.



in short-term survival studies. Indeed, models with fewer parameters (e.g., constant models) tend to be better-supported (Anderson et al. 1994).

Attachment of tracking devices, such as GLS, may influence survival probabilities and other demographic parameters for seabirds (Igal et al. 2005; Quillfeldt et al. 2012); however, we do not believe this was the case in our study. The birds in our study that received GLS in 2008, all returned in the following year, so the low survival estimate during 2008–2009 was unlikely a result of GLS attachment in 2008. The majority of the GLS were deployed in 2010 ( $n = 23$  birds, one of which was previously tagged in 2008) and 2011 ( $n = 21$  birds, 10 of which were previously tagged in 2010), and there were no differences in return rates or nest success between tagged and untagged birds in any year (S.E. Davis, unpublished data).

#### Effects of climate on survival

From the analysis combining both colonies, we found evidence of a negative relationship between anomalous winter climate and apparent survival of adult Sabine's gulls. The best supported model suggested that annual survival probabilities were generally high, although they declined nonlinearly as TNH moved from negative to positive, and dropped in 2008/2009, in relation to a notably high TNH pattern in that year. A similar pattern was observed for adult razorbills (*Alca torda*), which maintained high annual survival probabilities in all years except 1997/1998 when Labrador Current SSTs were particularly high (Lavers et al. 2008). Likewise, annual survival of Cassin's auklets (*Ptychoramphus aleuticus*) was lowest during 1997/1998, coinciding with an El Niño event in the Pacific (Bertram et al. 2005; Morrison et al. 2011). These patterns suggest, for some long-lived seabirds, that the capacity to maintain consistently high survival probabilities is diminished during pronounced shifts in broadscale weather patterns.

Although adult mortality can be a direct consequence of extreme weather events (Frederiksen et al. 2008; Mallory et al. 2009), effects of regional climate on seabird

population dynamics tend to manifest indirectly via changes in food availability (Durant et al. 2004; Sandvik et al. 2005; Gaston 2011; Hovinen et al. 2014). A reliable food source leading up to the breeding season is important for maintaining body condition, and thus it influences adult survival and reproductive effort (Monaghan et al. 1989; Oro et al. 2004; Davis et al. 2005; Harding et al. 2011). Sabine's gulls are surface foragers that feed primarily on various zooplankton species (e.g., amphipods; Duffy 1983; Day et al. 2001). Climatic conditions may have negatively influenced Sabine's gull survival indirectly by limiting access to or reducing their primary food source at some point during the nonbreeding season (see Vincent et al. 2002; Dorresteijn et al. 2012). Unfortunately, with our data we are unable to pinpoint where or when this might occur. For example, we found lower Sabine's gull survival with higher TNH indices, opposite to what we predicted, because high TNH usually is associated with cooler sea surface temperature conditions in the Pacific (Barnston et al. 1991), which should mean higher marine productivity (e.g., Hays et al. 2005). However, recent findings suggest that high, positive TNH is associated with stronger development of warm Pacific Blob conditions in the northeastern Pacific (Liang et al. 2017), in the staging and migratory route of Sabine's gulls in our study. The late arrival at the colony and below-average reproductive effort (clutch size) and hatching success in 2009 (Mallory et al. 2012) would be consistent with this interpretation.

Spatial variability in climate regimes throughout the range of habitats encountered by long-distance migratory species presents obvious challenges for investigating influences of climate on adult survival (Grosbois et al. 2008). Climate systems across such large areas are governed by interdependent atmospheric fluctuations; thus, multiple indices and other factors (e.g., time of year, small-scale weather variables; Sandvik et al. 2005; Lavers et al. 2008) likely contribute to overall effects of climate on Sabine's gull survival. Potential variation in migratory routes among, and even within, colonies should also be acknowledged. For example, Sabine's gulls returning north to Nasaruvaaalik Island from their wintering habitat off the coast of Peru follow three routes: all Pacific coastal, Pacific coastal plus a terrestrial "short cut" across Alaska, or Pacific coastal plus a major terrestrial route across Canada to Hudson Bay and then north (Davis et al. 2016). Exposure to food supplies, predation, and weather conditions should differ markedly on these routes. More tracking work is needed to determine the proportion of gulls going to each location, so we can be more confident in selecting climate indices to test.

Although the model with TNH was best-supported among the given set of models, it is possible that a different index, or a suite of indices and/or local climate variables, better explains variability in Sabine's gull survival estimates. However, testing effects of interactions requires high statistical power that is beyond the present data. We also wanted to avoid finding spurious results by taking an "all possible models" approach (as described by Anderson et al. 2001). Nevertheless, findings from this study add to growing evidence that variability in climate influences the survival of long-lived seabirds (e.g., Grosbois and Thompson 2005; Sandvik et al. 2005; Lavers et al. 2008; Dorresteijn et al. 2012; Sydeman et al. 2012; Genovart et al. 2013; Hovinen et al. 2014), and it highlights the role of global climate in affecting Arctic-breeding species, notably those that are long-distance migrants (Both et al. 2010).

### Conflicts of interest

The authors have no conflicts of interest to report.

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