

# Climate and competition in abundance trends in native and invasive Tasmanian gulls

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**ABSTRACT:** Climate and competition influence seabird population size yet are rarely considered simultaneously. Here, we consider the influence of climate on nominal abundance trends, and test for evidence of interspecific competition based on 31 yr of count data from 3 co-occurring gull species in southeastern Tasmania. The silver gull *Chroicocephalus novaehollandiae* and Pacific gull *Larus pacificus* are native, while the kelp gull *L. dominicanus* established in Tasmania from New Zealand in the 1950s. We applied population growth models where either growth rate or carrying capacity was a function of both large-scale climate variables and local conditions. For the kelp gull, a null model without any climate variables was selected, consistent with recent population establishment and increase. For the 2 native species, climate covariates were included, and for both, wind speed was important; for Pacific gulls, the El Niño-Southern Oscillation and regional sea surface temperature were also included in the selected model. These results are consistent with bottom-up forcing in the southeastern Tasmanian marine ecosystem; increased wind forcing leads to increased productivity and higher abundance of an important euphausiid prey species (*Nyctiphanes australis*). In years with lower wind speeds, warmer waters and higher water column stability, *N. australis* production is reduced. Models allowing competition effects by the kelp gull on the 2 native species performed poorly relative to models with climate covariates. Thus, competition alone is not a sufficient explanatory factor for observed changes in the 2 native species, and management strategies to maintain populations of the endemic Pacific gull should seek to reduce other stressors, including factors related to climate change.

**KEY WORDS:** Climate variability · Environment · Time series · Population model · Seabird · Gulls · Invasive species

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## INTRODUCTION

Climate change impacts on biological populations are widespread (e.g. Parmesan & Yohe 2003, Doney et al. 2012), although the degree to which population dynamics are driven by climate remains unresolved for most species, particularly for marine species (Richardson & Poloczanska 2008). In addition, despite potential relationships, the mechanistic linkages be-

tween climate and demographic responses are difficult to discern (Parmesan et al. 2011). The reasons for this difficulty are that the linkages between climate and population dynamics are often subtle or indirect (Hallett et al. 2004, Doney et al. 2012, Hobday & Evans 2013), and the time scales of the dynamics of biological systems (e.g. reproduction) are typically far shorter than those of climate systems, thus making the attribution of ecological changes to either cli-

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mate variability or change problematic (Parmesan et al. 2011). In cases where climate has been shown to be influential, the causal drivers of change may affect only a particular life stage or behaviour, may not be consistent throughout a species range or may be buffered by changes in the animal's behaviour (e.g. changes in foraging strategy) arising from behavioural plasticity. Additionally, the situation may be further complicated by interactions between and among species, as well as by a broad range of non-climatic anthropogenic influences (Barbraud et al. 2011).

Like many groups of birds, seabirds have been used as environmental indicator species for many years, particularly in sub-temperate and polar regions (e.g. Reid et al. 2005, Frederiksen et al. 2007, Durant et al. 2009, Woehler 2012), and evidence for climate influences on the distribution (e.g. Peron et al. 2010), abundance (e.g. Wolf et al. 2010), phenology (e.g. Thompson et al. 2012) and physiology (e.g. Chambers et al. 2011, 2013, 2014) of individual species is mounting. Climate can impact seabirds on a range of temporal scales, from interannual to decadal to climate change scales. Seabirds are also sensitive indicators of periodic oceanographic events such as the El Niño-Southern Oscillation (ENSO) and the Southern Annular Mode (SAM) (e.g. Schreiber & Schreiber 1984, Valle et al. 1987, Ballance et al. 2006, Devney et al. 2009, Surman & Nicholson 2009). For example, reproductive success in Chilean grey gulls *Larus modestus* decreased during El Niño events because of elevated water temperatures and decreased abundances of 2 prey species (Guerra et al. 1988). Broad-scale impacts to seabird communities, including gulls, are evident following both positive and negative ENSO events (e.g. Velarde et al. 2004, Surman & Nicholson 2009, Chambers et al. 2011). Red-billed gulls *Chroicocephalus novaehollandiae scopulinus* in New Zealand have been shown to respond to annual changes in the abundance of their prey species because of environmental forcing, such as regional upwelling associated with winds (Mills et al. 2008). However, most work on climate impacts for seabirds has considered individual species in isolation, without accounting for species interactions, such as competition. Gulls as a group exemplify many of the difficulties noted with detecting climate impacts yet are iconic coastal species in many regions of the world, with generally increasing population size because of anthropogenic activities (e.g. Coulson & Coulson 1998), and are of general interest as a climate indicator species (Chambers et al. 2011). Here, we explore the potential role of large-scale and local climate variables and interspecific competition in the popula-

tion trends of 3 species of gulls in southeastern Tasmania from survey data collected over a 31 yr period by BirdLife Tasmania (formerly Birds Tasmania, Wakefield et al. 1996, Wakefield & Woehler 2002).

There are 2 native species of gulls in Tasmania, the silver gull *C. novaehollandiae* (formerly *L. novaehollandiae*) and the Pacific gull *L. pacificus*, and 1 recently established species, the kelp gull *L. dominicanus*. Silver gull numbers in Australia are generally considered to have increased since European settlement. However, few empirical long-term data exist to support this claim, with limited studies documenting changes (Gibson 1979, Smith & Carlile 1992). Reports from New South Wales and Victoria, where breeding numbers have increased and impacts have been documented (Smith 1992, Smith & Carlile 1992 and references therein, Temby 2000), implicate a strong role of refuse tips/waste disposal sites as supplementary food sources driving regional gull population increases (Smith et al. 1991, Coulson & Coulson 1998). The use of refuse sites is well documented for many species of gulls worldwide and for the silver gull in Tasmania (Auman et al. 2010). Despite some local population decreases in the 1990s (Coulson & Coulson 1998), the silver gull is not considered threatened in any region of its range. Apart from data presented here, no long-term population data for Pacific gulls are available from any breeding population, and the species is relatively rare on a global scale, probably consisting of fewer than 11 000 individuals (Delaney & Scott 2006, Wetlands International 2014). Earlier reports of Pacific gull decreases in southeastern Australia (Garnett 1993) have since been discounted, and at a national level, the population is considered stable (Garnett & Crowley 2000, Garnett et al. 2011, Wetlands International 2014). Kelp gulls are believed to have established in Australia from New Zealand, with early records from the Australian mainland in the 1920s (Ford 1964) and 1940s (McGill 1943, 1955). The first record for Tasmania was in 1955 (Wall 1956), with the first Tasmanian breeding record in 1963 (Wolfe 1969). Kelp gulls have been identified as nest site and food competitors with silver gulls, as winter feeding ground competitors with Pacific gulls and as predators of both Pacific and silver gull chicks (Coulson & Coulson 1993, Higgins & Davies 1996). The global population of the circumpolar kelp gull is estimated in the millions, with a large population in excess of 3 million birds in New Zealand (Delaney & Scott 2006, Wetlands International 2014).

These 3 gull species are relatively long lived (all >20 yr) and often associated with human activity and habitation. In southeastern Tasmania, however, the 2

native species rely largely on marine resources rather than anthropogenic food sources (Coulson & Coulson 1998), and so changes to the marine food chain induced by climate forcing may be important in regulating their population productivity. Several studies have examined the biological oceanography of the waters of southeastern Tasmania and ENSO-related changes in marine food chains. Harris et al. (1992) examined the relationship between climate and the jack mackerel *Trachurus declivis*, finding that Zonal Westerly Wind (ZWW) strength was a key driver of nitrate concentration. High ZWW stress advected cold, nutrient-rich sub-Antarctic water, leading to enhanced marine production. Times of high ZWW were driven by meridional changes in the position of sub-tropical high-pressure cells over southeastern Australia. In years with reduced ZWW stress, waters were calmer with less mixing. These changes manifested farther up the food chain, with drastically reduced production of krill *Nyctiphanes australis*, a key food source of both jack mackerel and the gull species considered here. Other climatic factors such as heat stress on gull chicks during summer may also be a factor in driving changes to recruitment into the population (Chambers et al. 2011), but there are no long-term data currently available on the breeding success for the 3 species.

The aims of this study were to (1) document the population trends for silver, Pacific and kelp gulls in southeastern Tasmania using the longest time series data for these species in Australia; (2) investigate the role of physical environmental drivers (e.g. sea surface temperature [SST], ENSO, SAM) on these populations since 1980; and (3) examine the population data for evidence of interspecific competition by specifying candidate models where kelp gull abundance acts as an explanatory variable of abundance changes in the other 2 species. Of particular interest is determining the relative role of historical climate forcing in the populations of the native gulls; future prospects under climate change; and if management of the non-native gull species would lead to improved population status of the 2 native species, particularly for the less-abundant endemic Pacific gull.

## METHODS

### Gull survey methodology

Annual mid-winter counts were initiated in 1980 for kelp and Pacific gulls in southeastern Tasmania and in 1983 for silver gulls (Wakefield et al. 1996). The counts were conducted as a single regional

snapshot over a 3 to 5 h window on one mid-winter Sunday morning by a large team (40 to 50) of volunteers stationed in a fixed area of foreshore and other known roost sites such as sports fields and waste disposal sites. The number of counters for each site varied, depending on the spatial extent and expected numbers of gulls. Each annual count was highly coordinated to minimise the potential for double counting of gulls. Based on the coordinated count effort and brief window for counts, the magnitude of double counting of gulls moving around the region during the counts is minimal and would have no bearing on population estimates or trends (E. J. W. unpubl. data). The survey area has remained the same since 1980, with additional areas subsequently included in response to the changes in gull roost and feeding site preferences. Silver gulls were not aged during the counts, but the ages of kelp and Pacific gulls were recorded as juvenile (first-year), sub-adult (second-year kelp gulls and second- and third-year Pacific gulls) and adult (third-year and older kelp gulls and fourth-year and older Pacific gulls). For this study, only the total numbers of each species in each winter count were used in analyses. Nominal abundance, as used here, is insufficient to estimate actual abundance. Consequently, the models described in subsequent sections are also unable to discern between changes in abundance and a change in availability (distribution) to the visual survey. While distribution and abundance cannot be disentangled, changes in distribution are also ecologically significant, as they may indicate that the gulls needed to adopt different foraging strategies or disperse to different locations in years of apparently low numbers.

### Climate data and trend extraction

Monthly climate data were extracted for the region of southeastern Tasmania bounded by 45 to 42° S latitude and 146.5 to 148.5° E longitude (Fig. 1; Table 1) from January 1, 1980, to June 1, 2011. For remote sensing data, spatial averages of the data products detailed in Table 1 were calculated across the region for each month of the time period. Monthly average sea level pressure (SLP) data and the air temperature at Hobart ([www.bom.gov.au](http://www.bom.gov.au)) were also included. The climate variables ranged from local-scale SLP and air temperature for Hobart (AIR), to regional-scale wind speed (WINDSP) and SST, to large-scale atmospheric data (ENSO and SAM indices). Tasmania is influenced by both the ENSO and SAM (e.g. Risbey et al. 2009), and both were included in this study. The

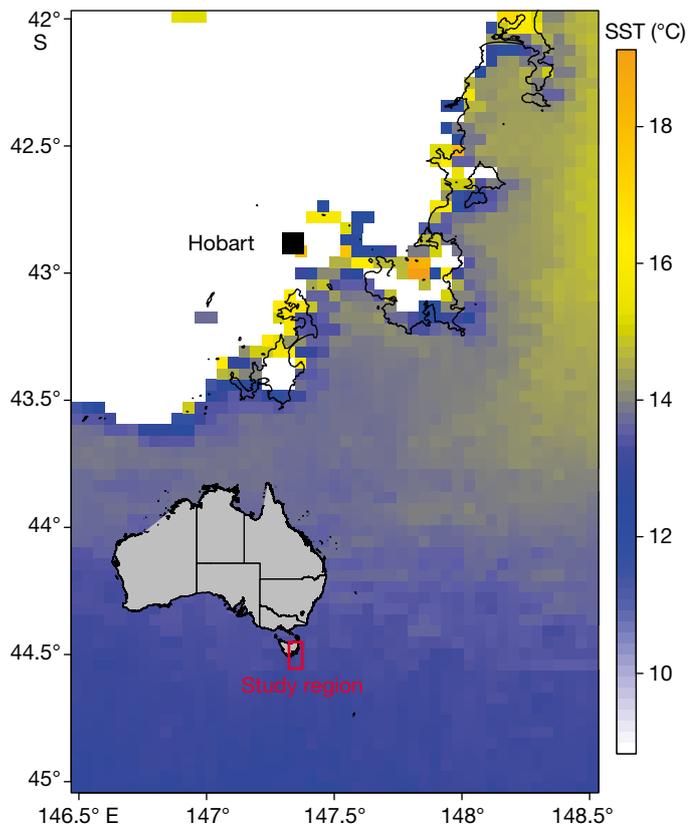


Fig. 1. Study region with average summer sea surface temperature from 2011 as an example (colour bar is °C). Inset shows study region on map of Australia. All climate variables listed in Table 1 were extracted and averaged over the region shown here, except for the El Niño-Southern Oscillation and Southern Annular Mode, which are global indices, and air temperature and rainfall data, which were from observations from Hobart (black square)

SAM is a large-scale alteration of atmospheric mass between middle and high latitudes characterized by pressure anomalies of one sign (e.g. positive) centred in the Antarctic (~65° S) and anomalies of the opposite sign (i.e. negative) centred over about 40° S (Marshall et al. 2003).

Compared to data available for other species of seabirds in southeastern Australia, the gull abundance data represent relatively long biological time series (Chambers et al. 2014). However, the time span of these data is still short in terms of detecting climate-scale trends. Moreover, it is necessary to attempt to decouple any trends in the climate data from background interannual variability. Thus, to identify the regional-scale patterns, we first examined the trends in climate variables. The climate variables used in this analysis are all highly seasonal, with predictable variation occurring throughout the year. Here, we are not interested in seasonal variation but rather anomalies from the usual seasonal trend (for instance, whether a given month/year was warmer or cooler than the long-term average). To remove the seasonal signal, we first detrended climate data by decomposing them into seasonal and trend components using the time series decomposition methods given by Cleveland et al. (1990). The local trend components, averaged over the breeding season of the birds (effectively calculating an anomaly from the long-term seasonal average), were included in further population modelling. Before including these in the population models, we assessed the degree of collinearity. Correlations between the variables were uniformly low (fraction of unexplained variation was 0.79 to 0.99).

Table 1. Variables considered as explanatory covariates for modelling. BAS = British Antarctic Survey; BOM = Bureau of Meteorology; CSIRO = Commonwealth Scientific and Industrial Research Organisation; NCEP = National Centers for Environmental Prediction; SST = sea surface temperature

Climate data product (and source)	Code	Rationale for inclusion
Monthly SST (CSIRO)	SST	Higher SST indicates influx of Eastern Australian Current waters into the study region; lower SST indicates sub-Antarctic water mass dominance
Monthly wind speed (NCEP)	WINDSP	Wind forcing of marine system shown to mediate mixing and enhance productivity
Monthly mean sea level pressure (CSIRO)	SLP	Sea level pressure may indicate atmospheric effects, such as wind
Monthly mean maximum temperature recorded in Hobart (BOM)	AIR	Extremes in air temperature may affect chick survival
El Niño-Southern Oscillation index (Nino 3.4)	ENSO	Large-scale climate index to examine long-term, broad-scale influences; postulated relationship with oceanic productivity in eastern Australia
Southern Annular Mode (BAS)	SAM	Large-scale climate index to examine long-term, broad-scale influences; low-frequency atmospheric mode for the Southern Hemisphere

### Models of population dynamics including climate

To examine the effect of climate on nominal abundances, we developed population models where climate covariates could drive either the rate of population increase or carrying capacity.

Several analyses of population abundance through time have employed log-linear models (e.g. Dennis & Otten 2000). These are readily implemented in a standard multiple regression but also assume that the population counts contain very little error. These could be termed process error only models. More recently, state-space modelling approaches (e.g. De Valpine 2003, Buckland et al. 2004) have been employed which model both process and observation error simultaneously. However, these are typically computationally demanding and mathematically complex. Additionally, for analysis of climate impacts, they may be overly flexible in a stochastic sense. This flexibility is useful for creating purely statistical models but does not necessarily address any of the underlying mechanisms that may be driving this variation. Our approach, similar to that presented in Hilborn & Mangel (1997), was to employ a deterministic process model and hence account for observation but not process error. In our model, process error is to be explained by alternative models with climate covariates. Our task is to model variability in population numbers but also account for density dependence; we expect per capita growth rate to change as populations approach carrying capacity. Therefore, we do not want to mix up systematic growth changes (as would happen in the absence of environmental influences) with year-to-year variability due to productivity changes in the environment. Accordingly, we used a logistic population model of the form:

$$N_{t+1} = N_t \left[ 1 + r_t \left( 1 - \frac{N_t}{K_t} \right) \right] \quad (1)$$

where  $N_t$  is expected abundance at time  $t$ , and the parameters for growth rate  $r_t$  and carrying capacity  $K_t$  are (potentially) time varying and can depend on climate covariates via linear predictors, e.g.  $\log(r_t) = \mathbf{X}_t \boldsymbol{\beta}$  (where  $\mathbf{X}_t$  is a so-called design matrix of covariates and  $\boldsymbol{\beta}$  is a vector of coefficients to be estimated, as per a linear model). The same structure applied to  $K_t$ .

There are *a priori* arguments that could be made for placing the dependence on either growth rate or carrying capacity; in all species considered, annual chick production per pair is always fewer than 3 and so, potentially,  $r$  remains more or less static. However, variation in productivity of the environment may allow  $K$  to fluctuate interannually. In contrast,

climate may influence chick survival, and the apparent level of  $K$  in adult birds may remain more or less constant. In the following analysis, we consider both possibilities with alternative versions of Eq. (1). However, we do not consider models with covariates influencing  $r$  and  $K$  simultaneously. We made this choice because of the relatively small amount of data and the requirement that models be kept as simple as possible.

The data from the gull population surveys are counts, which would generally suggest a Poisson error model. However, because of the unquantified nature of observation errors, we employed the more robust Tweedie (Shono 2008) distribution for observation errors. In a Poisson model, the assumption is that the mean variance relationship is  $E(\mu) = \text{Var}(\mu)$ , (where  $\mu$  is the mean) whereas for the Tweedie distribution, for mean  $\mu$  the variance is  $\phi\mu^p$ , where the parameters  $\phi$  and  $p$  are specified such that  $\phi > 0$  and  $1 < p < 2$ . Here, we assume  $p = 1.5$ , and  $\phi$  was estimated from the data. Our choice of  $p$  was informed by inspection of deviance residuals  $d_i$  against fitted values for a range of  $p$ ; for a well-fitting model, we expect approximately uniform scatter in the relationship between  $\sqrt{|d_i|}$  and  $E(y_i)$  where  $y_i$  is a given observation/population count (see Wood 2006, p 74). The Tweedie distribution has no closed form apart from a few specific cases. However, software exists for computing the density, and we employed the *ldTweedie* function from the R package *mgcv* (Wood 2006). Given this error model, the log-likelihood can be expressed as:

$$\log L(N_t, \hat{\theta}) = \sum_{t=1}^T \log dTweedie(N_t, \theta, p, \phi) \quad (2)$$

where  $\hat{\theta} = [N_t, \beta_j, (K_t, r_t)N_0]$  and  $K_t$  or  $r_t$  may be substituted accordingly as required by the particular model. The  $\beta_j$  values are coefficients on particular climate variables, and  $N_0$  is the estimate of the initial abundance. Estimation of  $\hat{\theta}$  was by numerical minimisation of the negative log-likelihood function (Eq. 2), using the R function *nlnmb*.

We considered a range of variables influencing either  $r$  or  $K$  but not both simultaneously to reduce model complexity, as stated previously. An obvious choice is the null (deterministic) model, where both  $r$  and  $K$  are fixed parameters without dependence on covariates. We also considered models including a variety of terms entering in a purely linear and non-interacting way using a log link function, e.g.  $\log(K_t) \sim \beta_0 + \beta_1 \text{SST} + \beta_2 \text{ENSO} + \beta_3 \text{SAM} + \beta_4 \text{AIR}$ .

Polynomial models on SST were to model situations whereby SST within a particular range was favourable (e.g. allows for negative responses at

either high or low temperatures, with positive conditions in the middle). The full list of candidate models considered in the model selection process is detailed in Table 2. We also considered the situation that the populations of silver and Pacific gulls are being influenced by competition with the invasive kelp gull. Therefore, we considered models for silver and Pacific gulls where the modelled abundance of kelp gulls [denoted  $N_t(KG)$ ] was included as a covariate, and  $K_t$  was a linear function of the number of kelp gulls as predicted by the chosen model for kelp gull abundance, i.e.  $\log(K_t) \sim \beta_0 + \beta_1 N_t(KG)$ .

This allows estimation of a coefficient that is interpretable as an interaction strength between the native species and the newly established invader. All candidate models were fitted using the statistical package R (R Development Core Team 2011).

The Akaike's information criterion (AIC) and the version correcting for small samples,  $AIC_c$  (Burnham & Andersen 2002), were used to select between models with reasonable residual diagnostics (as detailed above). Population trajectories calculated to  $AIC_c$  weights were examined in relation to the selected model.

To assess the uncertainty in the modelled population trajectory, a parametric bootstrap approach was employed. This procedure involves assuming that the uncertainty on the model parameters is asymptotically Gaussian distributed. Therefore, we can draw a sample from the joint posterior distribution on the model parameters as  $\theta^* \sim N_d(\hat{\theta}, \hat{\Sigma})$ . Here,  $d$  is the number of parameters which specify the dimension of the multivariate Gaussian;  $\hat{\theta}$  is the vector of estimated parameters; and  $\hat{\Sigma}$  is the variance-covariance matrix on the parameters, calculated as the determinant of the inverse Hessian matrix using the numerical differentiation method explained in Morgan (2008). The bootstrap itself requires the drawing of a large number of random samples (here 10 000) of new parameter values from  $\theta^*$ . From these, new population trajectories are computed, and an approximate confidence interval (CI) was found by calculating the 95th quantiles on each year's bootstrap replicates.

The individual values of  $r_t$  or  $K_t$  are not particularly meaningful in isolation. Considering  $K_t$  (and fixed  $r$ ), a very large  $K_t$  means that for that year, the population

Table 2. Model selection results for silver gull, Pacific gull and kelp gull. Here, Log(L) is the negative log-likelihood; see 'Methods: Models of population dynamics including climate' for definitions of other terms. The notation  $\text{poly}(SST, 2) = \beta_1 SST + \beta_2 SST^2$

Model	Log(L)	AIC	AIC <sub>c</sub>	ΔAIC	ΔAIC <sub>c</sub>
<b>Silver gull</b>					
Constant	234.04	474.07	474.93	6.65	6.02
SST + ENSO + SAM + AIR + WINDSP	227.86	471.71	477.98	4.29	9.07
NKG	232.73	473.45	474.94	6.03	6.03
WINDSP	229.71	467.42	468.90	0.00	0.00
WINDSP + SST	228.81	467.61	469.92	0.19	1.02
WINDSP + poly(SST, 2)	228.43	468.86	472.22	1.44	3.31
WINDSP + SAM + poly(SST, 2)	228.46	470.92	475.58	3.50	6.68
WINDSP + ENSO + poly(SST, 2)	227.99	469.97	474.64	2.55	5.74
<b>Pacific gull</b>					
Constant	173.17	352.34	353.20	2.15	1.30
SST + ENSO + SAM + AIR + WINDSP	168.29	352.58	358.84	2.38	6.93
NKG	173.22	354.45	355.93	4.25	4.03
WINDSP	171.21	350.42	351.90	0.23	0.00
WINDSP + SST	170.72	351.44	353.75	1.25	1.85
WINDSP + poly(SST, 2)	170.54	353.09	356.45	2.89	4.54
WINDSP + SAM + poly(SST, 2)	168.10	350.19	354.86	0.00	2.96
WINDSP + ENSO + poly(SST, 2)	170.49	354.98	359.64	4.78	7.74
<b>Kelp gull</b>					
Constant	233.94	473.88	474.73	0.00	0.00
SST + ENSO + SAM + AIR + WINDSP	232.73	481.46	487.72	7.58	12.99
WINDSP	233.09	474.17	475.65	0.29	0.92
WINDSP + SST	233.09	476.17	478.48	2.29	3.74
WINDSP + poly(SST, 2)	232.69	477.38	480.74	3.50	6.00
WINDSP + SAM + poly(SST, 2)	232.66	479.32	483.99	5.44	9.25
WINDSP + ENSO + poly(SST, 2)	232.81	479.63	484.29	5.75	9.56

grows at the estimated maximum rate  $r$ , but could be completely different the following year. However, it is worthwhile to consider the mean over the time

$$\text{series } \bar{K} = \frac{1}{T} \sum_{t=1}^T K_t, \text{ where } T \text{ is the number of years in}$$

the count time series. This allows recasting of  $K_t$  relative to what would be expected given current  $\hat{N}_t$  (the estimated numbers at time  $t$ ) and the long-term average  $K_t$ . Annual growth given current population

size is expected to be  $g_t = r \left(1 - \frac{N_t}{K}\right)$ , whereas the

observed growth is  $\hat{g}_t = r \left(1 - \frac{\hat{N}_t}{K}\right)$ . The ratio of these

per-capita growth rates  $\hat{g}_t/g_t$  indicates how high or low the population growth was in a particular year relative to expected average growth. As a summary of variability of population growth, we calculate the standard deviation in this ratio, i.e.  $\sqrt{\text{Var}(\hat{g}_t/g_t)}$ .

## RESULTS

### Climate trends

A strong seasonal signal in SST and air temperature (Fig. 2) within the study area was apparent, with

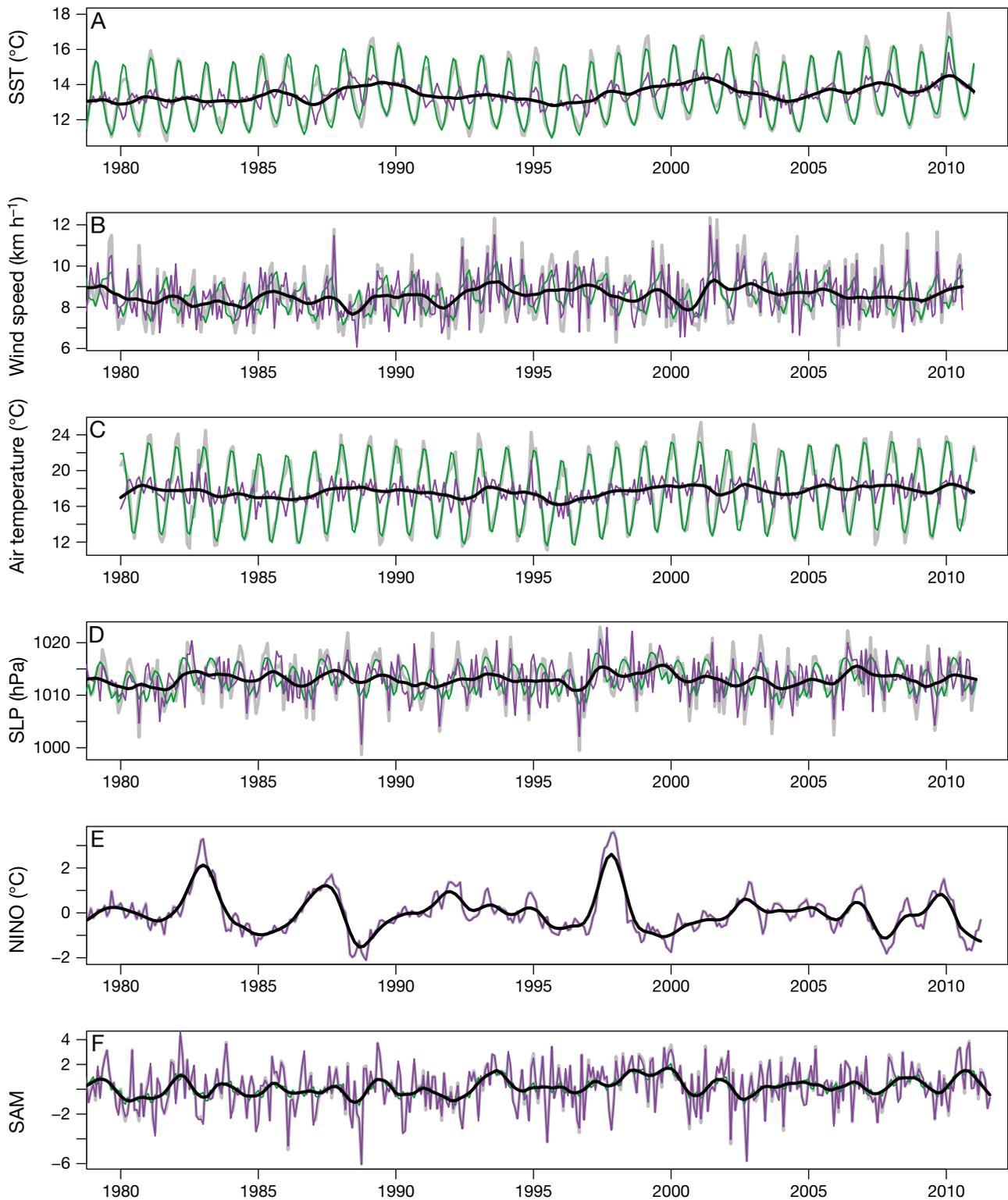


Fig. 2. Detrended climate time series (see Table 1 for descriptions of individual variables). (A) Sea surface temperature (SST); (B) wind speed; (C) air temperature; (D) sea level pressure (SLP); (E) El Niño-Southern Oscillation index (Nino 3.4) (NINO); (F) Southern Annular Mode (SAM). Grey line shows raw data; black line is the local trend component; green line is a seasonal component; and purple line is the remaining residual

relatively little residual component. There was also relatively little variation in the local trend component, which remained relatively constant over the period 1980 to 2012. Wind speed showed a weak seasonal signal, and the residual component remained strong. Accordingly, the trend component showed substantial variation among years. The local mean trend line for the ocean temperature (SST) was more variable than the air temperature and showed periods of relative warming, including from the late 1990s to 2003. The ENSO and SAM time series over the period 1980 to 2012 displayed substantial variation; the time series from 1996 to 2008 was a period of positive SAM. Positive phases are typically associated with increased Southern Ocean productivity (Racault et al. 2012).

### Population trends and model results

Relative to the nominal first observation, the counts in the raw data (Fig. 3) indicate very different population trajectories among the 3 gull species. The nominal kelp gull abundance increased more or less constantly over the period, and the most recent counts are 4.8 times higher than the population at first observation. There was also more variability in the later period of the time series, and the 2003 counts were particularly high relative to initial counts. Nominal counts for the other species show that there have been periods of decrease relative to year 1 survey estimates, down to 10% of the initial count for silver gulls and 15% for Pacific gulls. The 2 native species also seem to exhibit a moderate degree of synchrony (correlation = 0.58) with regional population reductions until around 2000 before increasing in recent years (Fig. 3).

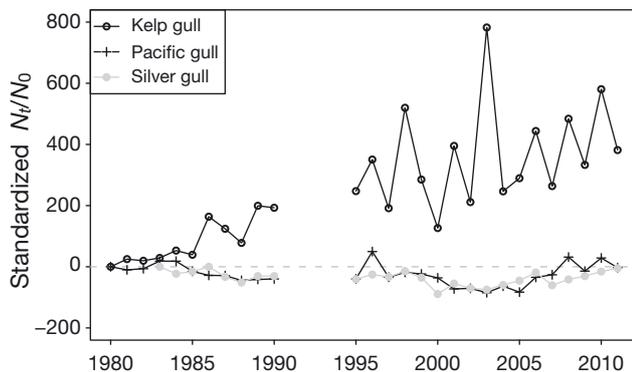


Fig. 3. Percentage increase in total counts relative to the first nominal first-year abundance of each gull species ( $N_t/N_0$ ). No survey data were collected from 1991 to 1994 inclusive, and the SG time series began in 1983

Generally, we found that models where the population growth rate  $r$  was a function of climate variables fit very poorly. Diagnostics for these models supported this assessment, and we removed these from further consideration. Hereafter we restrict our attention to models where the carrying capacity  $K$  was allowed to vary according to covariates. The model selection process indicated that the dynamics of the kelp gull populations are substantially different from those of the silver and Pacific gulls. For kelp gulls, climate variables were not selected, and the null model of simple population growth was selected according to  $AIC_c$  (Table 2), although a model with WINDSP as a covariate was ranked second ( $\Delta AIC_c = 0.92$ ). From the data alone, it is not clear whether the regional population has stabilised, but the selected null model suggests that in the most recent years surveyed, the population was at 96% of carrying capacity (however, we expand on the interpretation of  $K$ ). For the other 2 species, models including climate variables were ranked highly (Table 2). In all cases, models containing wind speed gave the lowest  $AIC_c$  values. For Pacific gulls, a more complex model with WINDSP, ENSO and a polynomial term on SST had the lowest  $AIC_c$ , but  $AIC_c$  values suggested that the models  $\sim$ WINDSP and  $\sim$ WINDSP + SST were more parsimonious. Given the uncertainty across these models, we report on all of them. The coefficients on SST indicate that higher temperatures are associated with relatively lower population growth (Table 3, Fig. 4). Model coefficients on SAM and wind speed indicated that increased values in these variables associate with phases of population growth. The selected candidate model for silver gulls included only WINDSP, and the estimated relationship again indicated a positive value between increased wind speed and population increase (Fig. 4).

Generally, periods of greater stability in wind speeds appear to coincide with population reductions for silver and Pacific gulls (Fig. 4). A similar result was predicted for other variables including SAM and ENSO in less parsimonious models (Table 3). Despite negative model coefficients for SST in the selected models (Table 3), there was indication of a slight trend between expected population growth and SST (Fig. 4). However, this was extremely weak relative to the response of population growth relative to WINDSP. Notably, WINDSP was selected in both models, and the WINDSP-only model was ranked second, with a relatively small  $\Delta AIC_c$  value for kelp gulls (Table 2). The competition model, whereby modelled kelp gull abundance was used as a covariate on  $K_t$ , ranked poorly for both silver and Pacific gulls (Table 2).

Table 3. Most highly ranked covariate-driven models. These are from models where covariates influence carrying capacity ( $K$ ), which produced better fits to the data (see Table 2).  $\hat{g}_t/g_t$  — see 'Methods: Models of population dynamics including climate'

Species/model	Fixed parameter				Variability measure		Covariate coefficient		
	$N_0$	SE	$r$	SE	$\bar{K}$	SD ( $\hat{g}_t/g_t$ )	Variable	Estimate	SE
<b>Silver gull</b>									
~WINDSP	10057	5.56	0.25	0.44	8776	6.18	(Intercept)	2.31	2.74
							WINDSP	0.83	0.38
~WINDSP + SST	2347	1.14	1.03	0.39	6839	7.96	(Intercept)	13.92	2.41
							WINDSP	0.08	0.09
							SST	-0.38	0.17
<b>Pacific gull</b>									
~WINDSP	250	0.42	0.28	0.45	287	10.96	(Intercept)	-2.21	2.31
							WINDSP	0.96	0.32
~WINDSP + SST	252	0.33	0.44	0.47	226	7.96	(Intercept)	7.58	5.58
							WINDSP	0.57	0.32
							SST	-0.45	0.23
~WINDSP + SAM + poly(SST,2)	219	0.36	0.45	0.26	8277	33.75	(Intercept)	-0.60	1.96
							WINDSP	0.75	0.26
							SAM	0.32	0.16
							SST	-3.17	1.04
							SST <sup>2</sup>	-0.55	0.69
<b>Kelp gull</b>									
~WINDSP	871	0.35	0.14	0.88	5609	3.41	(Intercept)	4.00	4.24
							WINDSP	0.57	0.60

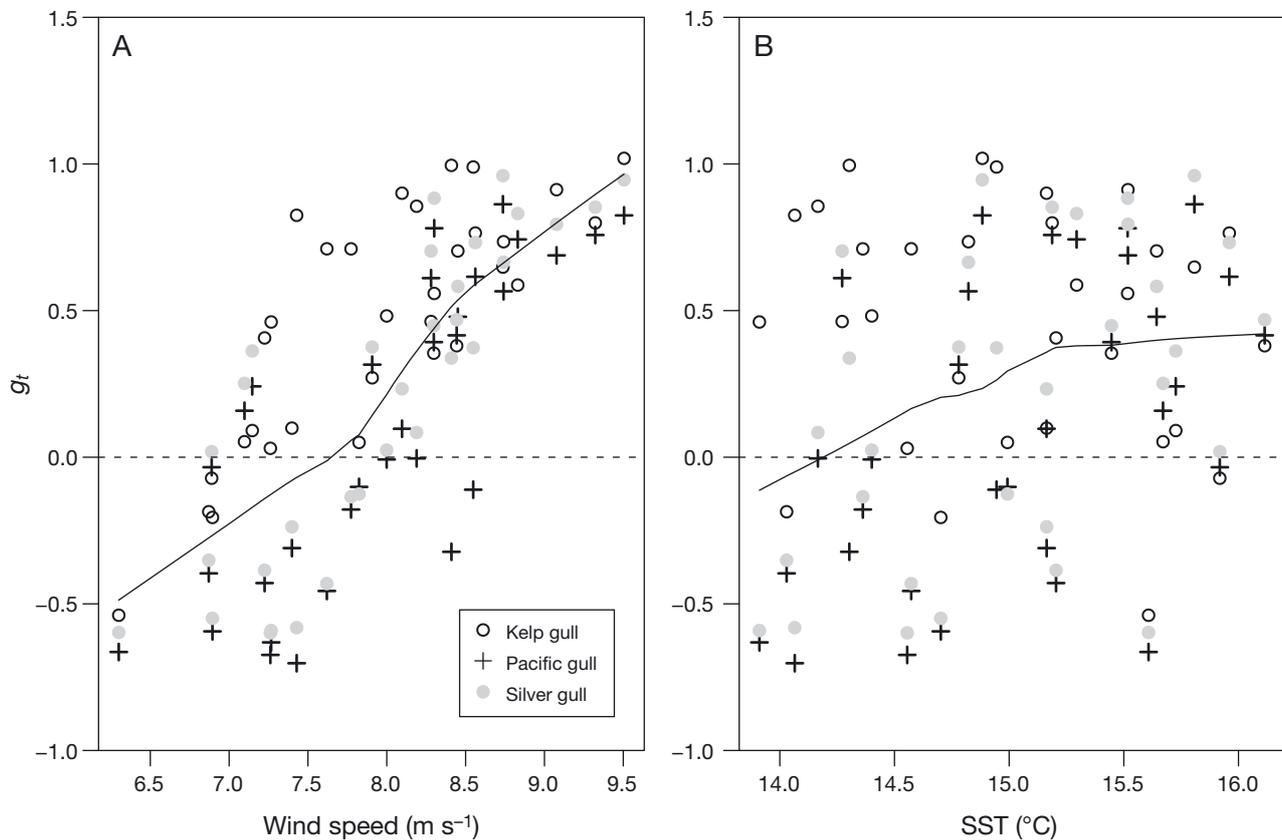


Fig. 4. Relationship between (A) wind speed and expected growth rate,  $g_t$  (see text), from the selected models (Table 2) and (B) sea surface temperature (SST) and  $g_t$ . Both figures show local lowest smoothing (black line) to highlight trends

The selected models fit the data series well in all series, and generally the model-averaged trajectories were in close agreement with the selected model (Fig. 5). The estimates of  $N_0$  were unsurprisingly poor for silver gulls, which led to extremely wide CIs in the first part of the time series (Fig. 5E). The estimates of  $r$  (fixed) for silver gulls were higher than the covariate-free models. These and their high associated uncertainty suggest very limited ability to estimate  $r$  in these models. It is likely that incorporation of covariates means that much of the interannual variability is accounted for in the components describing  $K_t$ . Both the silver and Pacific gull model trajectories indicated dips in abundance around the year 1990 and a decade later (Fig. 5).

The prediction of mean carrying capacity in the selected models varied among species. Null (covariate-free) models (Table 4) suggested that the nominal carrying capacities of silver and kelp gulls were of similar magnitude and that growth rate parameters were also comparable. The Pacific gull null model

Table 4. Model parameter estimates for the covariate-free null logistic population models

Species	$N_0$	$r$	$K$
Silver gull	9942	0.159	5591
Pacific gull	293	0.136	176
Kelp gull	840	0.157	4408

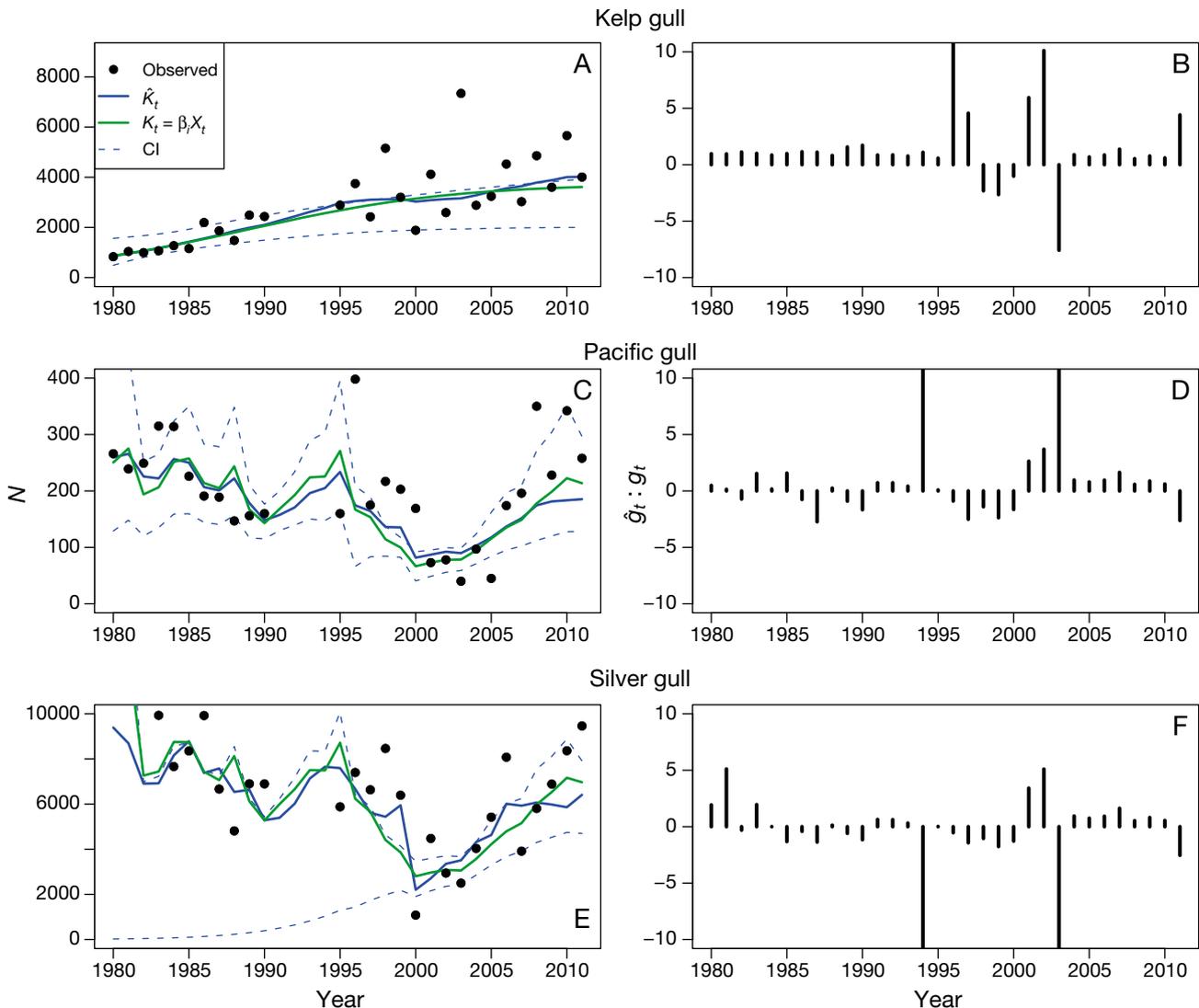


Fig. 5. (A,C,E) Model fits to raw count data (dots) from the best-fitting time-varying  $K$  models (green line) and model-averaged (population) trajectories (blue line). Dashed lines show 95% CIs on the selected time-varying  $K$  model (see Table 2). (B,D,F) Estimated time series of the ratio  $\hat{g}_t/g_t$  (see 'Methods: Models of population dynamics including climate')

result suggested lower growth rates and a lower carrying capacity (Table 4). The poor fit of these models for silver and Pacific gulls suggests that these results are not informative. In contrast, covariate-driven models with much better fits (Fig. 5) suggested a higher growth rate for silver and Pacific gulls but with substantial errors (Table 3). For kelp gulls, in the most parsimonious covariate-driven model (~WINDSP), the growth rate was similar to the null model, and  $\bar{K}$  was comparable to the null model. This was reflected in the close agreement between the null model and the model-averaged trajectory (Fig. 5A).

The averaged carrying capacity,  $\bar{K}$ , was comparable to covariate-free/null models across species (Table 3) but with very large swings in the ratio of observed to expected growth despite long runs with lower variability (Fig. 5), indicating that the model predictions were in accordance with the long-term average. Periods with large swings indicative of the influence of extreme observations could be due to underlying shifts in abundance, distribution/availability or higher degrees of observation error.

## DISCUSSION

Determining the influences of environmental conditions on trends in abundance remains a central goal for marine ecology, particularly in the face of climate change. This study considered the trends in nominal abundance in 3 co-occurring coastal seabirds in a region experiencing rapid climate change (Lough & Hobday 2011). We developed models of population dynamics driven by climate variables to consider whether climate forcing may be influencing the observed changes in apparent abundance. The selected models were consistent with both the population dynamics of an establishing and expanding species and documented climate effects in the region. The latter suggests that prevailing climatic conditions may be involved in regulating population numbers for the native species. Changes in ocean productivity are often driven by changes in the winds, which drive ocean mixing and hence influence the supply of nutrients to surface waters and the resultant productivity. Wind was a significant model term in the models for the 2 native species of gulls examined here.

Competition can also have an influence on population sizes but is often overlooked in studies of apex marine species. Candidate models that allowed for competition between the native species and the colonising kelp gull were ranked poorly in this study.

From these data, increases in kelp gull abundance do not correspond with the observed periods of apparent population reductions in the native species. Note that the models used here assume a carrying capacity and, in the absence of covariates, necessarily predict an asymptotic carrying capacity. Given that covariate-free models were selected, this situation may be the case. However, further monitoring of the populations will be important to evaluate if the kelp gull population continues to increase beyond the current size. If the kelp gull population has not yet reached its approximate carrying capacity for southeastern Tasmania and continues to increase, competition effects on the other 2 gull species may become evident in the future.

These surveys were conducted on non-colony attending individuals, whereas most seabird time series for southeastern Australia are for periods when birds are breeding at colonies (Chambers et al. 2011). This allows estimation of breeding effort and reproductive success that can allow more complex population models to be used (e.g. Barbraud et al. 2011). Ideally, counts of gull species would be conducted at nesting sites during a breeding season to more reliably identify the annual breeding population size. However, southeastern Tasmanian waters contain approximately 20 islands supporting gull nesting colonies and many more occasionally used sites. This means it would be very difficult to conduct annual counts at all colonies to generate an overall regional abundance index for a breeding season. Additionally, silver gull breeding is asynchronous, and birds are capable of laying replacement clutches if eggs or chicks are lost (Woehler 2013 and references therein). The disadvantage of the survey approach used here is that counts are conducted during winter, when birds are off their breeding islands and are dispersed throughout a variety of natural and anthropogenic habitats such as refuse disposal sites and sports fields, although these are included in the survey.

Another issue is how closely nominal abundance counts, as used here, relate to actual changes in population size. Although the 2 must be linked, we do not consider that our approach produces a robust estimate of population size; rather, our analysis aims to model trends in apparent abundance in relation to environment only. Our overall assessment of the success of these models is that while they are able to reproduce the year-to-year variability and show consistency with the prevailing understanding of the southeastern Tasmanian regional marine ecosystem, we have limited ability to estimate population parameters such as  $r$ ,  $N_0$  and  $\bar{K}$ . This is likely because of

both the limitations of the data in terms of accuracy as well as the low sample size. The models we consider here are admittedly complex relative to both sample size and accuracy, which leaves the possibility that our models are overfitting the data at hand. But part of our aim in doing so is to consider the potential pitfalls and implications for survey design of using more complex models. Additionally, purely statistical models, those without any attempt to model underlying population dynamics, often can also become quite complex when they account for statistical issues of overdispersion and autocorrelation (e.g. Zuur et al. 2009). Also, conclusions about population trajectories are often made based on extremely simple models (e.g. a linear trend through time, see Chambers et al. in press).

Conceivably, changes in nominal abundance result from dispersal to areas outside those surveyed and may explain some of the deviance between the best-fit model and observations. Additionally, further investigation of the error distribution on counts is advisable. This might involve systematic trials of multiple counts conducted at the same sites by independent teams of counters. This would allow approaches such as those of Royle (2004) to be applied to enable direct estimate of observation variance terms. Factors influencing variability in counts, such as the intra-annual dispersal and movement of these species, are generally poorly known (but see Murray & Carrick 1964 for an early analysis of movements of silver gulls in south-eastern Australia). All 3 species examined here are relatively long lived, with records for all 3 species exceeding 23 yr (see [www.environment.gov.au/cgi-bin/biodiversity/abbbs/abbbs-search.pl](http://www.environment.gov.au/cgi-bin/biodiversity/abbbs/abbbs-search.pl)), and the populations in southeastern Tasmania are considered relatively closed because of both high breeding colony and winter feeding site fidelities (BirdLife Tasmania, E. J. Woehler & W. C. Wakefield unpubl. data). An intensive colour-banding program and extensive resight effort of kelp and Pacific gulls in southeastern Tasmania during the early to mid-1980s showed high site fidelity to winter feeding sites (refuse tips) for first-year birds of both species, with no resightings of colour-banded birds elsewhere in Tasmania, despite extensive searches at refuse tips and coastal roosts elsewhere in the state (BirdLife Tasmania unpubl. data).

Inclusion of additional data, such as from long-term banding studies, would also aid in independent estimation of age-specific mortality rates for each species and thereby address the problem of confounding between nominal abundances obtained from the winter surveys and population mortality and recruitment (e.g. Véran & Lebreton 2008). In particular, the

design of the survey and the fact that regular annual sampling of the entire regional populations of all 3 species is impossible means that the strict interpretation of  $K$  in these models is vague, as it is unclear precisely to what spatial domain or habitats  $K$  refers. The use of banding studies may also assist in estimating total regional population sizes for all 3 species and at least determining whether the values of  $K$  estimated here are plausible. We also assume throughout that counts are unbiased but imprecise. This assumption is impossible to test given the current data, and requires future empirical work such as the repeat counts discussed previously. In light of the preliminary analyses of resightings of first-year birds and the lack of evidence of long-distance movement of banded kelp and Pacific gulls in Tasmania, it is proposed that these initial estimates of  $K$  are conservative and quite likely to be considerable underestimates of the true values. Further incorporation of analyses of available historic banding data may increase these estimates of  $K$ . Nonetheless, recent community perceptions of long-term increases in silver gull numbers are not supported by the winter data, and a redistribution of silver gulls closer to human settlements and especially close to Hobart may influence these perceptions (Woehler 2013).

Overall, single-metric (i.e. abundance) time series data restricts the types of population modelling which can be performed and also the types of predictions which can be made (Williams et al. 2002). The data series analysed here would be greatly enhanced by incorporation of auxiliary data on the populations. Age-specific abundance indices, and independent data on chick production and survival, would be extremely useful in building more sophisticated population models, assessing the potential influence of future climate change(s) and developing any required appropriate management responses for the species. Further modelling should also consider specific parameterisation of both observation error and process stochasticity in the estimation process. However, the approach considered here has advantages over other climate-driven population models such as log-linear models of abundance (e.g. Dennis & Otten 2000, Wang et al. 2002) where abundance data are assumed to be known without error.

The competition models included the raw abundance data of kelp gulls, as opposed to the modelled population trajectory. This is an advantage arising from having comparable time series from the same surveys. Yet it is possible that noise in the abundance trajectory is obscuring an actual competition effect. We consider this unlikely, as the overall signal in the

data is consistent with the model fit. Additionally, the selected kelp gull model itself did not include further covariates, indicating that the model and winter count data were in broad agreement. Without these climate and competition analyses, a management response to assist the population of the Pacific gull might be to reduce the population size of the potential competitor, the non-native kelp gull, through direct or indirect intervention (Coulson & Coulson 1998). Culling of competitor species has been undertaken in other seabird systems elsewhere, with mixed results (e.g. Bosch et al. 2000, Oro & Martínez-Abraín 2007, Sanz-Aguilar et al. 2009, Paracuellos & Nevado 2010), but these data and the modelling conducted using them in this study show no evidence of a long-term relationship between Pacific and kelp gull numbers in southeastern Tasmania. However, this finding is subject to the limitations of the survey design and may well have been different if the same analysis had been conducted on the first decade of survey data. This highlights the importance of long-term monitoring, particularly of long-lived species such as these investigated here. If the regional kelp gull population in southeastern Tasmania continues to increase, competition with Pacific gulls may become apparent, and our current conclusion will need to be revisited.

These analyses indicated that the dynamics of the regional gull populations are broadly consistent with known climate forcing of the marine ecosystem in southeastern Tasmania; conditions associated with increased oceanic production also corresponded to times when native gull abundance increased. The eastern coast of Tasmania is predicted to warm further in the future, which may depress marine productivity (Hobday & Lough 2011) and, according to our analyses, impact negatively on the already small populations of the native Pacific gull. The influence of the large-scale climate drivers is noteworthy, as previous studies have also shown that the marine ecosystem responds to such changes (e.g. Harris et al. 1992), suggesting that population changes in the native gulls are mediated through the food chain, for example, in bottom-up forcing of annual euphausiid production (e.g. Mills et al. 2008). Thus, as enhancing the productivity of the coastal environment on large scales is difficult to conceive, any management options for 'maintaining a viable Pacific gull population' would presumably be restricted to attempts at reducing non-climate stressors on the species, including human disturbance of nesting colonies, or potentially enhanced feeding opportunities in years of difficult environmental conditions. Our results provide possible indicators of these poor years, which

are characterised by relatively low wind forcing and stable, warm conditions. For silver and kelp gulls, with robust populations, potential management actions are mainly about reducing unwanted interactions with human activities (Coulson & Coulson 1998). If such interventions are to be pursued, this study has provided an initial assessment of the environmental context and drivers that may also operate on these populations. Given the data on which these conclusions are based and the uncertainty we have described in the model estimates, it would be advisable to treat the results from these models as working hypotheses which should be tested by dedicated field experiments or surveys. Additionally, modifications to the design of annual abundance counts should be considered to estimate associated uncertainty.

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