

Variation in breeding success and survival of little penguins *Eudyptula minor* in response to environmental variation

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ABSTRACT: Climate change is likely to result in continued warming of the oceans and an increase in the frequency and intensity of storms. To gain some insight into how such changes might affect little penguins, we studied how variation in sea surface temperature, chlorophyll *a* concentrations and the occurrence of severe storms affected little penguin *Eudyptula minor* breeding and survival at Oamaru, New Zealand. We examined the impact of prolonged, extreme storms using the 99th percentile of significant wave heights. Long durations of such wave heights at Oamaru were associated with a reduction in the number of penguins arriving ashore each evening and a reduction in adult survival. Ocean productivity positively influenced the penguins: increases in chlorophyll *a* were reflected by increases in survival of breeders, and by earlier onset of egg laying that generated increases in breeding success. Global climate change is highly likely to have negative impacts on the population of little penguins at Oamaru through impacts from storms. It is unclear, however, how climate change will influence chlorophyll *a* concentrations, and so we cannot predict what impact this will have on little penguins. Potential increases in chlorophyll *a* via increased nutrient input from the land may have positive effects on the penguins.

KEY WORDS: New Zealand · Storms · Chlorophyll · Sea surface temperatures · Seabirds

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INTRODUCTION

Seabirds are profoundly influenced by environmental variation, which can affect foraging behaviour (Catry et al. 2013) and subsequently breeding and survival (e.g. Ramos et al. 2002, Sandvik et al. 2005, Bertram et al. 2009, Cubaynes et al. 2011). Foraging success of seabirds, for example, is directly linked to a combination of prey abundance and prey availability (e.g. Barrett & Krasnov 1996, Henkel 2006), which in turn are strongly influenced by environmental factors such as mixed layer depth and turbidity (e.g. Bertram et al. 2009, Bergeron & Masse 2011). It stands to reason, then, that understanding relationships between demographic parameters of

seabirds and environmental variation can indicate the likely ecological consequences of global climate change.

Globally, ocean temperatures warmed during the 20th century (Levitus et al. 2012) and are likely to continue warming (IPCC 2014). In waters surrounding New Zealand, ocean temperatures increased between 1981 and 2007 along the coast but cooled to the south of the country (Matear et al. 2013). Increasing ocean temperatures can impact marine predators directly via effects on prey abundance. These effects can go either way: for example, New Zealand snapper *Pagrus auratus* show a strong positive correlation between juvenile recruitment and sea surface temperature (SST) (Francis 1993), while other fish species

show increased egg mortality and reduced spawning in warmer than average SSTs (Potts et al. 2014). Increasing SST can also affect predators indirectly via reducing primary productivity (Behrenfeld et al. 2006, Boyce et al. 2010) by reducing surface mixing of the water column and increasing the depth of the mixed layer, which limits nutrient supply to phytoplankton (Boyce et al. 2010). While chlorophyll *a* (chl *a*) concentrations at the sea surface (a reliable measure of productivity) have decreased through the 20th century by around 1% per year globally, it is uncertain how it will change in coastal waters in the future (Boyce et al. 2010). Through increased runoff and input of nutrients into the ocean, coastal waters at some locations have increased in productivity since the 1980s and may continue to do so (Gregg et al. 2005). Seabirds alter their foraging habits in response to variation in productivity. For example, foraging trip distances of Magellanic penguins *Spheniscus magellanicus* increased with decreasing productivity, and the probability of nest failure increased with distanced travelled (Boersma & Rebstock 2009, Boersma et al. 2009).

Research has predicted that climate change will negatively impact breeding success and survival of some penguin species, i.e. emperor *Aptenodytes forsteri* (Jenouvrier et al. 2012) and rockhopper penguins (*Eudyptes chrysocome* and *E. moseleyi*) (Dehnhard et al. 2013b) yet positively affect others, i.e. macaroni penguins *E. chrysolophus* (Horswill et al. 2014). Some studies have identified different effects for different life stages within the same species; for example, Le Bohec et al. (2008) found warm events negatively impacted breeding and survival of adult king penguins *A. patagonicus*, and later, Saraux et al. (2011b) showed juveniles survived better during warmer conditions. Contrasting results have also been found for little penguins *Eudyptula minor*. In New Zealand, research has suggested that warming will delay the onset of egg laying (Perriman et al. 2000), and in Australia, effects appear to vary with location. Breeding success following periods of relatively high SST decreased in Western Australia (Cannell et al. 2012) but increased in Victoria (Cullen et al. 2009). Sidhu et al. (2012) identified that the sea-temperature gradient in Bass Strait, south-eastern Australia, in addition to SST, was important in determining first-year survival of little penguins. Both the gradient and SST are predicted to increase with climate change, yet they showed contrasting effects on first-year survival (gradient negative and SST positive) (Sidhu et al. 2012).

For southern New Zealand, climate change is also predicted to result in intensification of winter storms

(Mullan et al. 2011). Increased wind speeds and wave heights associated with storms bring marine sediments into suspension, and the longer increased wave activity lasts, the longer those materials remain in suspension (Verspecht & Pattiaratchi 2010). Increased river outflow following heavy rain also acts to reduce water clarity and lowers the foraging efficiency of seabirds which rely on vision to detect prey underwater (Braby et al. 2011). Further, mixing of the water column caused by storms can disperse fish aggregations associated with stratified layers (e.g. thermoclines) (Peterman & Bradford 1987, Bergeron & Masse 2011), making prey less available (Ropert-Coudert et al. 2009). The energetic demands of foraging increase and food intake is likely to decrease during storms (Grubb 1977, Dehnhard et al. 2013a). Other storm-related impacts on seabirds include reduced survival rates of adults and juveniles (Harris & Wanless 1996, Frederiksen et al. 2008), abandonment of nests and chicks (Wright et al. 2013), chick deaths due to increased rainfall (Boersma & Rebstock 2014) or reduction in the amount of food delivered to chicks (Finney et al. 1999, Stienen et al. 2000).

Little penguins are near-shore foragers with restricted foraging ranges due to their small size (Hoskins et al. 2008). This constraint means that they cannot forage further afield and breed successfully. At Oamaru, New Zealand, the reproductive performance and survival of little penguins has been studied in detail in an increasing population (Agnew et al. 2014). The impact of environmental variation on their breeding and survival is unknown, however. Our objective was to determine whether variation within the coastal marine environment, represented by persistence of storm activity, SST and chl *a* concentration, affected the timing of breeding and annual survival of little penguins at Oamaru.

MATERIALS AND METHODS

Penguin data

The study was conducted at the Oamaru Blue Penguin Colony (OBPC, 45° 06' 37" S, 170° 58' 47" E), Oamaru, South Island, New Zealand. The colony was originally a harbour-side quarry operating from 1865 until the mid-1980s. Penguins began occupying the site in the 1970s (Higham & Lück 2002). The site was established as a tourism facility in 1992, which aimed to manage visitors viewing the penguins coming ashore in the evening and provide the penguins with a safe breeding habitat (Johannesen et al. 2003).

Staff at the colony recorded the number of penguins arriving ashore for 1 h after the arrival of the first penguin every evening from January 1993 onwards. Penguins in the study colony are identified with uniquely numbered metal flipper bands (Agnew et al. 2014), applied to individuals as chicks prior to fledging or when first encountered breeding in the colony. The first penguins were banded in Oamaru in 1985, but regular banding did not occur until weekly nest checks began in 1993, when all breeders and their offspring were banded. Data from weekly nest checks are maintained in a database by OBPC staff. We examined data over 19 breeding seasons from 1993 to the end of the 2011 season in 2012, over which time the population at the OBPC increased from 61 to 288 breeders (Agnew et al. 2014).

At Oamaru the lay date of first eggs in each breeding season has varied by up to 5 mo from May to September (Agnew et al. 2014). For analysis of survival of breeders with respect to storms, we divided the breeding season into 4 mo periods according to the breeding activity: May–August, early breeding; September–December, incubating and chick-rearing; and January–April, late chick-rearing and moulting. For annual survival estimates we defined a breeding season as beginning 1 May and finishing 30 April of the following calendar year (Agnew et al. 2014). Breeding seasons are referred to by the year in which breeding began.

Environmental variables

Data on significant wave height (4 times the square root of the sea surface variance) were obtained from hind-casts generated using numerical modelling by MetOcean Solutions Limited (metocean.co.nz; Beam-sley et al. 2009). The dataset was available as a 3-hourly time series from 1 January 1979 to 31 December 2012. Spatial resolution was 5 km, with data obtained from the nearest offshore node (45° 07' 55" S, 171° 01' 00" E), situated 3.8 km south-east of the study area. We examined mean monthly and annual significant wave heights, then concentrated on the 99th percentile value of all 3-hourly records (as an indicator of extreme values; Mullan et al. 2011) between 1 May 1993 and 30 April 2012. We used the number of consecutive 3-hourly records that exceeded the 99th percentile, defined as 'P99 exceedance', as an indicator of the severity and duration of the most extreme storm in each 4 mo period. We examined the immediate effects of storms on penguins via a comparison of the daily number of penguins arriving ashore before and after

an increase in wave height. Since penguin numbers increased each year, we calculated the lower quartile of arrival numbers that occurred during the 30 d prior to the increase in wave height and counted the subsequent number of days penguin arrivals were below the lower quartile. We used the lower quartile value instead of the median to ensure that metric was not triggered by normal fluctuations in arrival numbers. Two storm covariates were also incorporated: P99 exceedance and 'storm scenario' (a covariate representing years grouped according to the persistence of extreme significant wave heights: Scenario 1, years with a severe storm with ≥ 20 consecutive records above the 99th percentile, P99; Scenario 2, years with < 20 consecutive records).

SSTs were extracted from a global dataset produced by the National Oceanic and Atmospheric Administration (NOAA) National Climate Data Center and made available on the Physical Oceanography Distributed Active Archive Center website (<http://podaac.jpl.nasa.gov/dataaccess>, NASA Jet Propulsion Laboratory, Pasadena, CA). The SST data were part of a product referred to as the Group for High Resolution Sea Surface Temperature global Level 4 sea surface temperature analysis. The analysis used optimal interpolation of SSTs measured *in situ* and satellite-derived SSTs from the (Version 5) time series provided by the NOAA Advanced Very High Resolution Radiometer Pathfinder. The data were available from 1985 to the present and were produced daily on a 0.25 degree (ca. 28 km) grid (Reynolds et al. 2007). This analysis was documented originally by Reynolds & Smith (1994) and re-analysed by Reynolds et al. (2002). We calculated area-averaged 4 mo means for the grid encompassing 44.3–45.5° S and 170.8–171.6° E, where little penguins from the Oamaru colony are known to forage during the breeding season (P. Agnew unpubl. data).

Sea surface chl *a* concentration data were gathered by the Sea-viewing Wide Field-of-view Sensor mission and downloaded from the NASA website. The monthly (9 km grid) chl *a* data are available from September 1997 to September 2010; we calculated the 4 mo mean for these data also.

Statistical analysis

We used the Cormack-Jolly-Seber (CJS) live-recapture model in program MARK (White & Burnham 1999) to quantify 4-monthly and annual survival estimates for breeding penguins and annual survival estimates for first-year penguins in response to envi-

ronmental variation. Sample sizes of nests monitored, fledglings and adults captured, banded and then released each breeding season are shown in Table S1 in the Supplement at www.int-res.com/articles/suppl/m541p219_supp.pdf. To estimate survival of breeding penguins, recapture data were extracted from the weekly monitoring programme data and divided into the three 4 mo periods within the breeding season. Multiple records within a 4 mo period were treated as a single recapture in the encounter history matrix. This process generated an encounter history matrix with 54 columns: beginning May–August 1994 (1993 was excluded due to regular monitoring occurring after the beginning of the breeding season) and finishing January–April 2012, at the end of the 2011 season. We began with a general model that incorporated time dependent (t) variation in apparent survival (ϕ) and recapture probabilities (p): [$\phi(t) p(t)$], which was then constrained by covariates using the design matrix. The 4-monthly models tested survival and recapture structures that varied with time, varied annually (Y), varied seasonally (4-monthly) (S), were additive (Y + S), were constant (.) or incorporated the storm covariates.

For estimating annual survival probabilities, we separated the data into 2 datasets: one including all penguins from when they were first recorded breeding (including individuals banded as chicks previously or banded as adults of unknown age and origin) to specifically examine survival of breeding penguins, and one including all fledglings from the colony to examine first-year survival. For the breeding penguins the encounter history matrix included the period from May to the following April each breeding season. We examined annual breeder survival using a CJS model for the years we had data for all 3 environmental variables, from 1998 to 2010. Multiple recaptures within a breeding season were therefore treated as a single recapture; the encounter matrix for this model had 14 columns allowing for the recapture of individuals in 2011. To quantify annual survival estimates of first-year penguins, individuals were first marked as fledglings each season 1993–2009, and later recaptured in the OBPC colony. This second model also had a 14 column encounter matrix (1998–2011). Chicks may leave the colony as late as March; therefore, we included storm intensity in the year after fledging as a variable. The standard CJS model assumes that survival and recapture probabilities do not vary among individuals (Lebreton et al. 1992). To satisfy this assumption for first-year estimates, the general model included 2 age classes. The recapture of little

penguins is lowest in their first year (Sidhu et al. 2007); therefore, the 2 age classes were first-year individuals (¹) and all age classes thereafter (²). As this model was developed to focus on first-year survival, the general model incorporated time-dependent variation in the first age class only: [$\phi^1(t), \phi^2(\cdot); p^1(t), p^2(\cdot)$]. We assessed the fit of the general models using parametric bootstrap GOF tests (performed in program MARK) which simulated encounter histories that exactly met the assumptions of the model and generated a bootstrapped distribution of expected deviances ($n = 100$ replicates). The over-dispersion parameter (\hat{c}) was estimated as the observed deviance of the general model divided by the mean expected deviance, which provided a measure of the amount of over-dispersion in the data. The general model was deemed acceptable if values of \hat{c} fell between 1 and 3 (Sandercock et al. 2005).

For each model, we calculated Akaike's information criterion corrected for small sample size (AICc), AICc difference (Δ AICc), model weight (w_i) and deviance. The Δ AICc is the difference between the AICc of the candidate model and the highest ranked model with the lowest AICc. Models were regarded as having substantial support if Δ AIC ≤ 2 (Burnham & Anderson 2004). The model weight is the likelihood of a model given the data and is represented as the proportional weight of evidence for each model relative to the entire set (Johnson & Omland 2004). The proportion of model deviance accounted for by each covariate (R^2_{DEV}) was calculated as: $[(DEV(\cdot) - DEV(cov))/(DEV(\cdot) - DEV(t))]$, where DEV is the deviance for the constant, covariate (cov) and general (t) models (Grosbois et al. 2008). To determine the amount of further deviance explained by the addition of a second covariate to a model, we used the single covariate model as the constant model. The second covariate was deemed to be influential if it explained $>20\%$ of additional variance (Grosbois et al. 2008). We used odds ratios to quantify covariate effects, provided on the logit scale (Zuur et al. 2007).

The lay date of first eggs, and median lay dates of first clutches, were used as proxies for breeding success due to the significant relationship between lay dates and breeding success, where early median lay dates coincide with high breeding success via double brooding (Agnew et al. 2014). We examined relationships between lay dates of first eggs and chl *a* and SST, with linear regressions for each 4 mo mean from the current and from the previous breeding season, 1998–2010. Analyses of median lay dates also examined effects of storms.

RESULTS

Environmental variables

Significant wave heights modelled for the ocean immediately offshore from Oamaru, for the 19 yr from 1 May 1993 to 30 April 2012, ranged from 0.13 to 3.78 m with a mean of 1.05 m and 99th percentile of 2.32 m. The direction of the largest waves was between 90° and 160° with a median of 132° (south-easterly). Across all years the period from May–August had the highest number of consecutive days above 2.32 m (the 99th percentile through 19 yr) (Table S2 in the Supplement at www.int-res.com/articles/suppl/m541p219_supp.pdf).

Immediate effects of storms

Persistent extreme (significant) wave heights had a clear effect on the number of penguins arriving ashore each day. The higher the P99 exceedance (the number of consecutive 3-hourly records that exceeded the 99th percentile), the greater the number of days that arrival numbers remained low (Fig. 1). Each extra 3 h duration of extreme significant wave heights was met with an increase of nearly 1 d (0.88 d) of reduced penguin arrivals (Fig. 1). Biologically, the

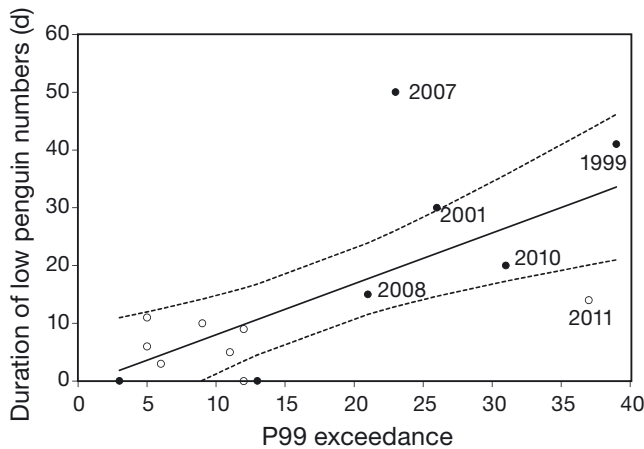


Fig. 1. Relationship between the number of consecutive 3-hourly records above the 99th percentile significant wave height (P99 exceedance) in each 4 mo period and the corresponding number of consecutive days the number of little penguins arriving ashore was below the lower quartile value during evening at Oamaru each breeding season, 1994–2011. Seasons in which breeding had begun prior to (○), and when breeding began after (●), the onset of P99 exceedance (zero consecutive years excluded) are shown. Data labels identify the worst affected years. Linear regression (solid line) and 95% confidence intervals (dashed lines): $R^2 = 0.47$, $p = 0.005$, $y = 0.88x - 0.80$

2011 breeding season was a potential outlier in the relationship; the number of consecutive days of reduced penguin arrivals may have remained low due to the birds having started breeding already (and therefore having more incentive to return to the colony). Statistically, however, 2007 may also be an outlier, and removing either year increased the significance of the relationship (2007: $R^2 = 0.63$, $p = 0.0007$; 2011: $R^2 = 0.61$, $p = 0.001$).

In the seasonal survival analyses, the general model $[\phi(t) p(t)]$ was a good fit to the data (test, $\hat{c} = 1.02$) and revealed strong temporal variation having the lowest AICc (Model 1, Table S3 in the Supplement). Further examination of the R^2_{DEV} showed that the second lowest model (Model 2, Table S3: ϕ (storm scenario + Y) $p(t)$) explained 80% of the variation in the data; however, this was likely driven by the inclusion of annual variation in the model. Model 2 predicted survival to be lower during severe storm periods than for the other periods during the same year (Fig. 2) and also correctly predicted this trend for 4 of the years with the most persistent storms (1999, 2001, 2007 and 2011; Fig. 2).

Impacts on annual survival

The general model $[\phi(t) p(t)]$ was a good fit to the data on breeder survival (GOF test, $\hat{c} = 1.44$). The model with the lowest AICc included the 4 mo mean chl *a* for January–April prior to the current breeding season and P99 exceedance (Table 1). The second model, with only P99 exceedance, was similarly well

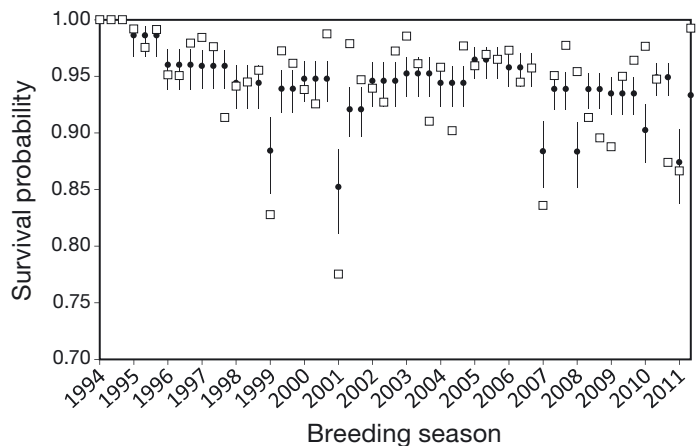


Fig. 2. Four-monthly breeder survival estimates from the time dependent model $[\phi(t) p(t)]$ (□) and predicted estimates (●; $\pm 95\%$ CI) from the best covariate model with the lowest AICc $[\phi$ (storm scenario + Y) $p(t)$], for little penguins at Oamaru each breeding season, 1994–2011

Table 1. Top 10 models in each set examining variation in annual breeder and first year survival rates (ϕ) of little penguins at Oamaru, in relation to 4 mo mean sea surface temperatures (SST), 4 mo mean chlorophyll *a* (Chl) and the number of consecutive 3-hourly records above the 99th percentile significant wave height value (P99) in the season of breeding for adults and the season after first-year penguins. AICc: Akaike's information criterion, the selection criterion corrected for small sample size; Δ AICc: value of the difference between each model and the best model; w_i : Akaike weights; R^2_DEV : proportion of model deviance accounted for by each covariate; PMA: Previous May–August; MA: current May–August; PSD: previous September–December; SD: current September–December; PJA: previous January–April; JA: current January–April; t : time; 1 : first-year penguins; (.) constant variable; p : recapture

Model no.	Variable	AICc	Δ AICc	w_i	k	Deviance	R^2_DEV
Breeder survival							
1	$\phi(\text{Chl-PJA} + \text{P99}) p(.)$	3142.84	0	0.70	4	190.44	0.51
2	$\phi(\text{P99}) p(.)$	3144.94	2.10	0.25	3	194.54	0.43
3	$\phi(t) p(.)$	3148.32	5.48	0.05	14	175.81	
4	$\phi(\text{Chl-PJA}) p(.)$	3154.19	11.35	0.00	3	203.80	0.27
5	$\phi(\text{SST-JA}) p(.)$	3158.18	15.34	0.00	3	207.79	0.20
6	$\phi(t) p(t)$	3159.00	16.16	0.00	26	162.19	
7	$\phi(\text{Chl-SD}) p(.)$	3159.52	16.67	0.00	3	209.12	0.18
8	$\phi(\text{SST-MA}) p(.)$	3160.93	18.09	0.00	3	210.53	0.16
9	$\phi(\text{SST-SD}) p(.)$	3161.62	18.78	0.00	3	211.23	0.14
10	$\phi(\text{SST-PMA}) p(.)$	3166.05	23.21	0.00	3	215.65	0.07
First-year survival							
11	$\phi^1(\text{Chl-MA} + \text{P99}) p^1(t)$	5120.50	0	0.72	17	390.41	0.86
12	$\phi^1(\text{P99}) p^1(t)$	5122.67	2.17	0.24	16	394.60	0.79
13	$\phi^1(\text{Chl-JA}) p^1(t)$	5127.79	7.29	0.02	16	399.72	0.70
14	$\phi^1(t) p^1(t)$	5130.48	9.98	0.00	26	382.20	
15	$\phi^1(\text{Chl-MA}) p^1(t)$	5131.73	11.23	0.00	16	403.65	0.63
16	$\phi^1(\text{SST-PSD}) p^1(t)$	5132.18	11.68	0.00	16	404.11	0.62
17	$\phi^1(\text{SST-MA}) p^1(t)$	5132.26	11.76	0.00	16	404.19	0.62
18	$\phi^1(.) p^1(t)$	5132.37	11.86	0.00	15	406.31	
19	$\phi^1(\text{Chl-SD}) p^1(t)$	5132.63	12.13	0.00	16	404.56	0.61
20	$\phi^1(\text{Chl-PJA}) p^1(t)$	5133.37	12.87	0.00	16	405.30	0.60

supported (Table 1: Model 2, Δ AICc = 2.10). These models explained 51 and 43 % of the variation in the data (Table 1). Results from Model 1 predicted survival to increase with increasing chl *a* concentrations ($\beta = 0.69$, 95 % CI: 0.02, 1.37) and decreasing P99 exceedance ($\beta = -0.02$, 95 % CI: -0.02, -0.01). Other combinations of variables did not lower AICc values. There was no support also for the constant (null) model: Δ AICc = 25.00. Examined separately, the model with P99 exceedance as the predictor resulted in a lower AICc than the model with chl *a* (by 9 points, Table 1), indicating that P99 exceedance was more important in determining survival rates. Furthermore, the addition of chl *a* as a second covariate to the P99 exceedance model explained an additional 13% of variation, indicating this covariate was not significantly influential. The multiplicative change in the survival odds ratio was a decrease by 2% ($e^{-0.02}$) for each unit increase in P99 exceedance (Fig. 3).

The general model [$\phi^1(t) p^1(t)$] was a good fit to the annual first year survival data (GOF test, $\hat{c} = 1.17$). The best model included the 4 mo mean chl *a* for May–August of the season of fledging and P99 exceedance of the season following fledging, followed closely by the second best model (Δ AICc = 2.17) with P99 exceedance only (Table 1). There was no support for the constant (null) model: Δ AICc = 23.39. Survival was predicted to increase with decreasing chl *a* ($\beta = -0.47$, 95 % CI: -0.92, -0.02) and decreasing consecutive records of extreme significant wave height ($\beta = -0.02$, 95 % CI: -0.02, -0.01). Independently, P99 exceedance explained 79% of variation in the data, higher than chl *a* (Table 1); however, there was some evidence that the covariate chl *a* was influential because the addition of this covariate to the P99 model explained an additional 34 % of variance. The multiplicative change in the survival odds ratio followed the same trend as for breeders: a decrease by 2% ($e^{-0.02}$) for each unit increase in P99 exceedance (Fig. 4).

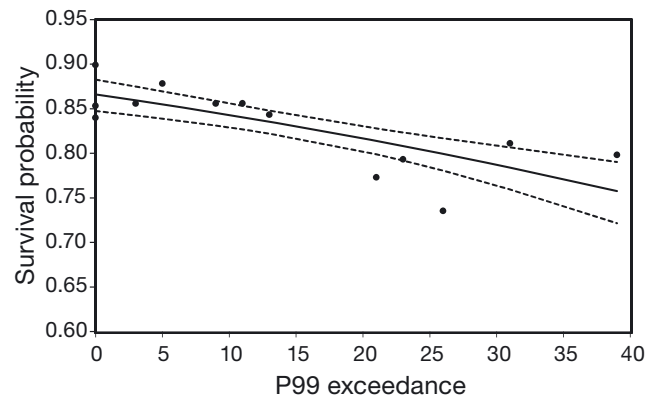


Fig. 3. Modelled estimates from the general model [$\phi^1(t) p^1(t)$] (•) and covariate model [$\phi(\text{P99}) p(.)$] (solid line; \pm 95 % CI: dashed lines) for survival probabilities of breeding little penguins at Oamaru, 1998–2010. P99 exceedance: number of consecutive 3-hourly records above the 99th percentile significant wave height value

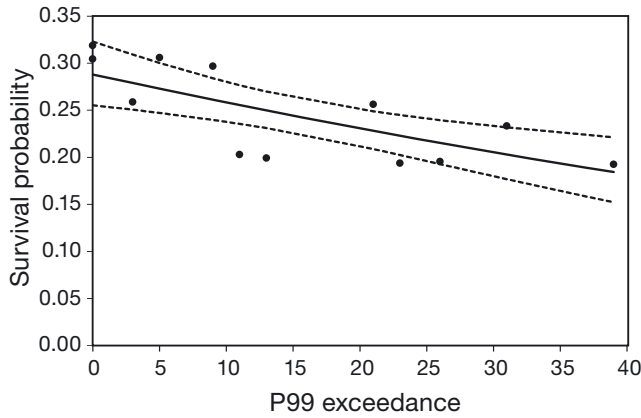


Fig. 4. Modelled estimates from the general model [$\phi^1(t)$ $p^1(t)$] (•) and covariate model [$\phi^1(\text{P99})$ $p^1(t)$] (solid line; $\pm 95\%$ CI: dashed lines) for survival probabilities of first-year little penguins at Oamaru, 1998–2009. P99 exceedance: number of consecutive 3-hourly records above the 99th percentile significant wave height value

Impacts on breeding

The proxy for storms (P99 exceedance) was excluded from the analyses of lay date of first eggs because the date of P99 exceedance occurred after the onset of egg laying in 6 of the 13 breeding seasons from 1998–2010. The 2 best supported models for lay date of first eggs included the 4 mo mean chl *a* and SST for January–April prior to the breeding season (Table 2). These variables explained little variation in lay dates, however, as the third model in the set, the null model, also had $\Delta\text{AICc} < 2$.

For the median lay dates, the model with the lowest AICc included the 4 mo mean chl *a* for January–April prior to the breeding season (Table 2). Annual median lay dates were 12 d earlier for each increase in chl *a* by 0.1 mg m^{-3} ; the relationship was significant ($p = 0.008$) and explained 49% of variation in the data (Fig. 5). The next model in the set was only slightly better supported than the null model. In the model, median lay dates were earlier through time ($R^2 = 0.25$).

DISCUSSION

Impacts from storms

At Oamaru, fewer penguins came ashore during periods of rough seas. The longer a storm persisted, the longer the number of penguin arrivals ashore remained low. High winds and wave action during

Table 2. Top 10 linear models examining variation in the lay date of first eggs for the colony and median lay date of first clutches of little penguins at Oamaru, 1998–2010, in relation to 4 mo mean sea surface temperatures (SST), 4 mo mean sea surface chlorophyll *a* concentration (Chl) and the number of consecutive 3-hourly records above the 99th percentile significant wave height value (P99). Abbreviations as in Table 1

Variable	AICc	ΔAICc	w_i	R^2
First eggs				
Chl-PJA	132.48	0	0.25	0.29
SST-PJA	133.07	0.59	0.19	0.25
Null	133.42	0.94	0.16	
SST-MA	134.92	2.44	0.07	0.14
SST-JA	135.05	2.57	0.07	0.13
Chl-SD	135.47	2.99	0.06	0.10
Year	135.52	3.04	0.05	0.10
Chl-MA	135.91	3.43	0.05	0.07
SST-PMA	136.03	3.55	0.04	0.04
SST-SD	136.67	4.19	0.03	0.02
Median eggs				
Chl-PJA	122.31	0	0.74	0.49
Year	127.40	5.09	0.06	0.25
Null	127.64	5.33	0.05	
P99	128.80	6.49	0.03	0.16
SST-JA	129.60	7.29	0.02	0.11
SST-MA	129.67	7.36	0.02	0.10
SST-PJA	129.86	7.55	0.02	0.09
Chl-MA	129.90	7.59	0.02	0.09
SST-PMA	130.09	7.78	0.02	0.08
Chl-SD	130.91	8.60	0.01	0.02

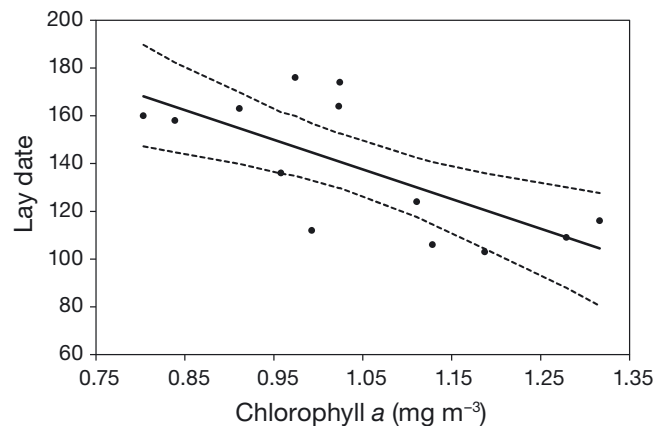


Fig. 5. Observed (•) and predicted (solid line) estimates of the median lay date of first clutches for breeding pairs of little penguins at Oamaru, 1998–2010. Predicted estimates ($\pm 95\%$ CI: dashed lines) generated from the fit of the model with the lowest corrected Akaike’s information criterion (AICc; Table 2), in relation to the 4 mo mean sea surface chlorophyll *a* concentration from January–April prior to the breeding season. Linear regression: $R^2 = 0.49$, $p = 0.008$, $y = -123.8 \times \text{chl } a + 267.5$

intense storms likely caused increased mixing of the water column resulting in the re-suspension of sediments, reducing water clarity (Verspecht & Pattiaratchi 2010) and impeding visual feeding. Berlincourt & Arnould (2015) found the proportion of time spent diving by little penguins decreased with increasing wave height in south-eastern Australia. The propensity of penguins to return to the colony may be higher when storms occur after the onset of egg laying. This was difficult to assess in the current study because only one severe storm occurred after egg laying began, and in this season (2011) the penguins returned to the colony sooner than in other years of comparative storm intensity. The 2011 storm was still severe enough to disrupt egg laying and incubation: failure of penguins to return to the colony caused incubating partners to abandon eggs, and subsequently 15 of 16 nests failed (Agnew et al. 2013). Egg laying ceased in August and recommenced late September. Further research into the impacts of storms after the onset of egg laying will allow assessment of effects on feeding and provisioning rates, and body condition.

Storms clearly had an impact on the survival of little penguins. A reduction in annual survival of breeders occurred during years with the highest P99 exceedance. Increased P99 exceedance in the year following fledging, when the penguins are first at sea, caused a reduction in first-year survival. Foraging difficulty, resulting in decreased food intake and subsequent loss of body mass, is probably the mechanism driving the effect of storms on survival rate. Climatic perturbations may negatively affect flipper-banded penguins more so than unbanded penguins (Saraux et al. 2011a) and will be the subject of future research for little penguins at Oamaru. Population growth rates in long-lived vertebrates are highly sensitive to variation in adult survival rates (Sæther & Bakke 2000). Frederiksen et al. (2008) showed that reduced survival attributable to winter storms leads to reduced population growth and increased probability of extinction of European shags *Phalacrocorax aristotelis*. Reduced annual survival rates of both adults and first-year penguins is likely to lead to reduced population growth of little penguins at Oamaru.

Influence of chl *a* and SST variation

Annual survival increased with increasing chl *a* concentrations recorded during January–April prior to the breeding season. A negative relationship was

apparent between chl *a* and the median date of egg laying, indicating earlier onset of laying with increasing chl *a* from January–April prior to breeding. Small, inshore schooling fish predominate in the diet of little penguins at Oamaru, mainly slender sprat *Sprattus antipodum* and Graham's gudgeon *Grahamichthys radiata* (Fraser & Lallas 2004, Flemming et al. 2013). Slender sprat grow to 120 mm in length (Whitehead et al. 1985), spawn from June to November (Colman 1979, Robertson 1980) and are very abundant in Canterbury Bight, including off Oamaru (Colman 1979). Fish production is known to be influenced both by spawning conditions and primary productivity (Basilone et al. 2004). The abundance of sprat is likely to be influenced both by conditions during spawning and in the year following. Slender sprat eaten by little penguins at Oamaru during the 1994 breeding season were largest (50–60 mm) during January to April (Fraser & Lallas 2004). Inter-annual variability in primary productivity during this time seems likely to influence the abundance and size of fish available to little penguins. Correlations between chl *a* and body growth have been found for other marine fish species (Iverson 1990, Basilone et al. 2004). Fish abundance during the January–April prior to breeding therefore may act as an indicator of prey availability for penguins in the coming year.

Studies examining the effects of environmental variation on little penguins have reached contrasting conclusions. Studies at Phillip Island noted that an earlier start to egg laying and higher breeding success was associated with warmer SST (Cullen et al. 2009), yet earlier work found the opposite (Mickelson et al. 1992). A study in Western Australia also found an earlier start to egg laying but reduced breeding success with higher SST (Cannell et al. 2012), and in New Zealand a later start occurred, but climatic perturbations did not influence breeding success (Perriman et al. 2000). Cullen et al. (2009) and Cannell et al. (2012) both attributed their findings to variation in fish abundance; however, the underlying ecological mechanisms are unclear, as warm water was predicted to cause a decrease fish abundance in Western Australia yet an increase in Victoria. Investigations of relationships with chl *a* variation during each of the studies in Australia may have helped explain their results, as in our study lay dates related to chl *a* concentration rather than SST. Berlincourt & Arnould (2015) found a link between both SST and chl *a* and the timing of breeding, suggesting that earlier changes in SST and/or chl *a* lead to earlier egg laying. Links between productivity and pen-

guin reproductive success have been found in other temperate penguin species (Boersma & Rebstock 2009, Boersma et al. 2009).

In response to global climate change, primary productivity is predicted to decline with increasing SST in open oceans (particularly at low latitudes) and with increasing SST at high latitudes (Behrenfeld et al. 2006). Seabirds at both extremes of latitude are sensitive to variation in productivity. For example, tropical roseate terns *Sterna dougallii* had higher breeding success in years of higher chl *a* and phytoplankton growth than in years of weak growth (Monticelli et al. 2007). Seabirds in the Southern Ocean concentrate their foraging on highly productive areas (Péron et al. 2010). Productivity is highly variable in coastal waters due to the complex nature of land–sea interactions, which makes predictions of the effects of global climate change difficult (Cloern 1996, Cloern & Jassby 2008). There may actually be an increase in productivity in coastal waters due to increased nutrient input from the land (Gregg et al. 2005). Seabirds may well be differently affected depending on their location and proximity of their foraging to land.

In conclusion, the ecological mechanisms driving prey abundance are complex, and even though SSTs are predicated to increase with global climate change, chl *a* concentrations may also increase independently (Gregg et al. 2005). As the current study emphasises, it is therefore important to consider the effects of multiple environmental variables on several demographic parameters. Not only are average conditions changing, the frequency and intensity of extreme events is increasing. We suggest that extreme events linked to global climate change are likely to affect both breeding and survival of little penguins at Oamaru. How local variation in productivity will be affected by climate change, and subsequently affect the penguins, is unknown but may be positive. If so, it may mitigate, at least to some extent, impacts from storms or increases in SST.

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